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1 Automated identification of invasive rabbitfishes in underwater images
2 from the Mediterranean Sea

3

4

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16

17 **Abstract**

18 1. Coastal ecosystems of the Mediterranean Sea are among the richest in non-indigenous
19 species, mostly due to the establishment of species coming from the Red Sea through the
20 Suez Canal. Two herbivorous rabbitfishes, *Siganus rivulatus* and *Siganus luridus*, are
21 already invasive in the South-Eastern part of the Mediterranean Sea where they cause
22 ecological damage by overgrazing algae.

23 2. The early detection and the counting of these non-indigenous species in the rest of the
24 Mediterranean Sea is thus a major challenge for scientists and ecosystem managers.
25 However, analyzing images from divers or remote cameras is a demanding task.

26 3. Here, a dataset of 31,285 images of *Siganus* spp and of six common native fishes to the
27 Mediterranean Sea was built from 40 underwater videos recorded in three reef habitats. A
28 deep learning algorithm was then trained to identify *Siganus spp* on images mixing the eight
29 Mediterranean species. Finally, the algorithm and a post-processing filtering were tested with
30 an independent dataset of 2,024 images.

31 4. The model had a recall of 0.92 for the *Siganus* genus (i.e. two *Siganus* species combined).
32 After a confidence-based post-processing the recall increased to 0.98 with only 4 out of 272
33 images of *Siganus spp* being misclassified. Accuracy reached a score of 0.61 meaning that
34 experts would have to discard false positives. Images of five native species not present in the
35 training dataset yielded similar false positive rates than species present in the training dataset.
36 Overall, the automatic processing of images by our model then the checking of putative
37 *Siganus* images by experts require up to five times lower effort than a full processing by
38 experts.

39 5. Our algorithm can efficiently help to detect these two invasive fishes in underwater images
40 to evaluate progress towards conservation objectives and accelerate citizen-based monitoring
41 of coastal ecosystems.

42 **Keywords** : coastal ecosystems, deep learning, image analysis, Mediterranean sea, non-
43 indigenous species, *Siganus* spp

44 Introduction

45 Biodiversity has been increasingly impacted by global change in all ecosystems
46 (Jaureguiberry et al., 2022). Among those impacts, climate warming and introduction of non-
47 indigenous species are acting synergistically in many regions (La Sorte & Jetz, 2010; Bennett
48 et al., 2021). Mediterranean coastal ecosystems are an emblematic case of such marked
49 changes in biodiversity (Albano et al., 2021). Indeed, the opening of the Suez Canal in 1869
50 and its recent expansion have permitted the entry of many fish species from the Red Sea into
51 the Mediterranean Sea. To date, the total number of these non-indigenous species (NIS
52 hereafter) is above 150 (Azzurro, Smeraldo & D'Amen, 2022). The northward and westward
53 geographic range expansion and the increase in abundance of those tropical NIS has been
54 favored by the rapid warming of Mediterranean Sea surface waters (>1°C since 1980)
55 (Shaltout & Omstedt, 2014).

56 Rabbitfishes *Siganus rivulatus* and *Siganus luridus* have become the most abundant
57 herbivorous fishes along the South-Eastern coast of the Mediterranean Sea since their
58 establishment in 1927 and 1956, respectively (Ben-Tuvia, 1964; Bariche, Letourneur &
59 Harmelin-Vivien, 2004; Sala et al., 2011). They now contribute to more than 50% of the
60 herbivory activity (Magneville et al., 2023). Importantly, in many of these coastal habitats,
61 *Siganus spp* have overgrazed macroalgae to the point that the diversity of other organisms
62 has decreased and ecosystem functioning has been disrupted (Vergés et al., 2014; Peleg et
63 al., 2019). *Siganus spp* have been colonizing northward up to the Aegean Sea and westward
64 up to Sicily for the last two decades (Azzurro & Andaloro, 2005). Some individuals were even
65 observed along the coast of France (Daniel, Piro & FranCour, 2009) and Croatia (Dulčić et al.,
66 2011). Yet, their long-term establishment and new colonization pathways are still under
67 scrutiny.

68 In this context of accelerating NIS expansion, it is thus of utmost importance for scientists and
69 ecosystem managers to early detect the arrival of such potentially invasive species and then
70 to monitor their settlement and abundance dynamics. Monitoring non-indigenous marine
71 fishes has been mostly carried out using standardized surveys by scuba divers (Brock, 1954;

72 Thresher & Gunn, 1986; Holland et al., 2020) and opportunistic records from fisheries landings
73 (e.g. Kleitou et al., 2022). Yet, underwater visual census of fish requires trained divers who
74 may still miss elusive species, such as *Siganus*, especially when they are rare. As an
75 alternative, monitoring NIS based on underwater remote cameras and underwater pictures
76 from divers have been increasingly applied (Peters, Sink & Robinson, 2019). However, the
77 identification of target NIS on such images is a demanding task in terms of time and expertise
78 in fish taxonomy.

79 Owing to the recent development of artificial intelligence and especially Deep Learning
80 algorithms (DLA) there is a growing effort to automate the identification of fish species in
81 underwater images (Ditria, Jinks & Connolly, 2021). DLa have been demonstrated to efficiently
82 identify indigenous reef fishes in several coastal ecosystems (Villon et al., 2018; Lopez-
83 Marcano et al., 2021) but none addressed the key issue of detecting NIS in the Mediterranean
84 Sea. As *Siganus spp* can change color rapidly from olive green to dark brown with a mottled
85 pattern, training an algorithm able to identify them remains challenging. In this study, images
86 of the two *Siganus spp* and six common native fish species were collected across the
87 Mediterranean Sea. Then, a DLa was trained to identify polymorphic *Siganus spp* in
88 underwater images, and its performance was tested in various conditions.

89

90 **Material and Methods**

91 Image datasets

92 DLa require two independent image datasets: the first one used to train the model, *i.e.* to find
93 the optimal parameters discriminating the species of interest, and the second one used to test
94 the trained model reliability in the various conditions of application. To build those datasets,
95 underwater remote videos were recorded during three field campaigns in Northern Crete
96 Island (Greece) and the Gulf of Lion (France) in 2017, 2019, and 2020 (Table 1).

97

98 Table 1. Summary of underwater videos and fish images used to train and test the deep

99 learning classifier.

Use	Territory	Site	Date (year-month)	Habitat	Number of videos	Number of annotated images of fishes	Presence of <i>Siganus</i> spp
Train	France	Frontignan	2019-09	macro-algae / bare rocks / turf	1	134	
Train	Crete	Hersonissos	2019-10	macro-algae / bare rocks / sand	26	5247	X
Train	Crete	Kokkini Hani	2019-10	macro-algae / turf / seagrass	13	4636	X
Test	France	Banyuls	2017-07	macro-algae / bare rocks / turf / seagrass	2	114	
Test	Crete	Hersonissos	2019-06	macro-algae / bare rocks / sand	3	292	X
Test	Crete	Kokkini Hani	2019-06	macro-algae / turf / seagrass	1	831	X
Test	Crete	Bali	2019-06	macro-algae / turf / seagrass	1	139	X
Test	France	Carry le Rouet	2020-05	macro-algae / bare rocks / turf / seagrass	2	783	

100

101 All videos were recorded with GoPro HERO5 Black (GoPro Inc., USA) set with “linear” angle-
 102 of-view, full HD resolution (1920*1080 pixels) and 25 frames per second. The cameras were
 103 set up on the seafloor in shallow (1-5m deep) coastal habitats dominated by seagrass,
 104 macroalgae, bare rocks, or sand (Table 1).

105 To ensure that the test of the algorithm was performed independently from the training, the
 106 two datasets were built using videos recorded in different locations or seasons (Table 1). The
 107 training dataset was built with images from 40 videos for a total of 140h recorded between the

108 2nd and the 10th of October 2019 in Crete (Greece). For the testing dataset, nine videos
109 recorded in France (July 2017 and May 2020) and in Crete (June 2019) were used.

110 Videos of different lengths were extracted from the raw recordings based on the presence of
111 fish and images were extracted at the rate of one or three images per second yielding 11 to
112 1,064 frames from a video. On each of these frames, fish individuals which body was entirely
113 visible (i.e. not hidden by another fish, rocks or algae and not facing camera and not recorded
114 from the face or behind), and which could be identified to the species level were annotated
115 using a bounding box encompassing the body and labeled with species name. Because of
116 these rules, most of the annotated fish individuals were not present on temporally successive
117 frames. Furthermore, as fish individuals were of various sizes and were at various distances
118 from the camera, the annotated images had variable sizes and length/depth ratios. Given the
119 diversity of seafloors among videos (rocks, algae, seagrass), varying hydrological conditions
120 (turbidity, light), as well as the movement of filmed components (algae, other fishes), the
121 images displayed different backgrounds even within a single video (Figure S1). Additionally,
122 considering the mobility of the target fish species, the images exhibited a range of fish body
123 orientations. Special attention was given to ensuring that images of *Siganus* spp represented
124 the diversity of colorations encountered in the wild (Figure 1).



125

126 Figure 1. Examples of the different body shapes and colors of *Siganus luridus* (a, b, c) and *Siganus rivulatus* (d,
 127 e, f, g) in the test dataset

128 For this study, images of the two non-indigenous *Siganus luridus* and *Siganus rivulatus*, were
 129 used along with images of the six most common fish species in our videos (*Chromis chromis*,
 130 *Diplodus sargus*, *Diplodus vulgaris*, *Sarpa salpa*, *Sparisoma cretense*, and *Thalassoma pavo*),
 131 which are also prevalent in the Mediterranean Sea. Each species represents a class learned
 132 by the deep learning classifier.

133 A total of 31,285 images were annotated from videos of the training dataset. For each class,
 134 1,250 to 1,256 unique images were randomly selected among those available and horizontally
 135 flipped to augment the representativity of the dataset (Villon et al., 2018). For the test, 2,159
 136 images (Table S1) of the eight species common with the training dataset (two *Siganus* spp.
 137 and six common fishes) were used, along with 100 images of five species not present in the

138 training dataset (*Diplodus puntazzo*, *Oblada melanura*, *Mullus surmuletus*, *Lithognathus*
139 *mormyrus*, *Trachurus mediterraneus*, N = 20 individuals for each species).

140 Training of the classifier

141 The classifier involved fine-tuning a ResNet50 model that had been previously trained on the
142 ImageNet dataset using PyTorch (torch 1.8.1). At the beginning of the training, all images were
143 resized to 224x224 pixels. The batch size was set at 16. The Adam algorithm was employed
144 as the optimizer, and the negative log-likelihood loss function was used. To prevent overfitting,
145 it was ensured that the loss was decreasing after each epoch. If this was not the case for 20
146 consecutive epochs, the training was stopped. The algorithm was trained using an Nvidia
147 Quadro RTX 3000 GPU card on a Dell Precision 7550 laptop with an Intel® Core™ i7
148 processor and 62GiB RAM.

149 Testing the classifier

150 For each class, the number of true positive (TP) images, representing correctly identified
151 images, was computed. Additionally, the number of false negative (FN) images, indicating
152 images belonging to a given class but missed by the classifier, and the number of false positive
153 (FP) images, representing misidentified images in a given class, were also calculated.

154 The model efficiency was assessed using the recall and precision metrics for each class. The
155 recall is the proportion of correctly labeled individuals among all individuals of this class and
156 is computed as: $\frac{TP}{TP+FN}$. It is maximal (and equals 1) when all individuals of the class are
157 correctly identified, and it decreases when some individuals of the analyzed class are
158 misidentified as fish species from other classes.

159 The precision is the proportion of correctly labeled individuals among the items identified as
160 this class and is computed as: $\frac{TP}{TP+FP}$. It is maximal (and equals 1) when there are no individuals
161 belonging to another class, and decreases when some individuals of other classes are
162 misidentified as the analyzed class.

163 Metrics were also computed for the two *Siganus* spp combined, considering that in most
164 applications, the goal is to detect the presence of this non-indigenous genus. For this purpose,
165 a new class “siganus” was created, that bundles the classes “siganus_luridus” and
166 “siganus_rivulatus”.

167 In the context of automated identification of NIS, the priority is to ensure that NIS individuals
168 are not missed, hence to maximize recall (i.e. few FN). However, the time of experts required
169 for checking the images classified as NIS has also to be as low as possible, hence precision
170 should remain as high as possible (i.e. few FP).

171 For each image processed by the Dla, the most likely class returned has an associated
172 confidence score ranging from 0 to 1, with values close to 1 indicating the most reliable
173 classes. Thus, images with a confidence score lower than 0.8 were transferred to an “unsure”
174 class. The recall was computed after removing these “unsure” images.

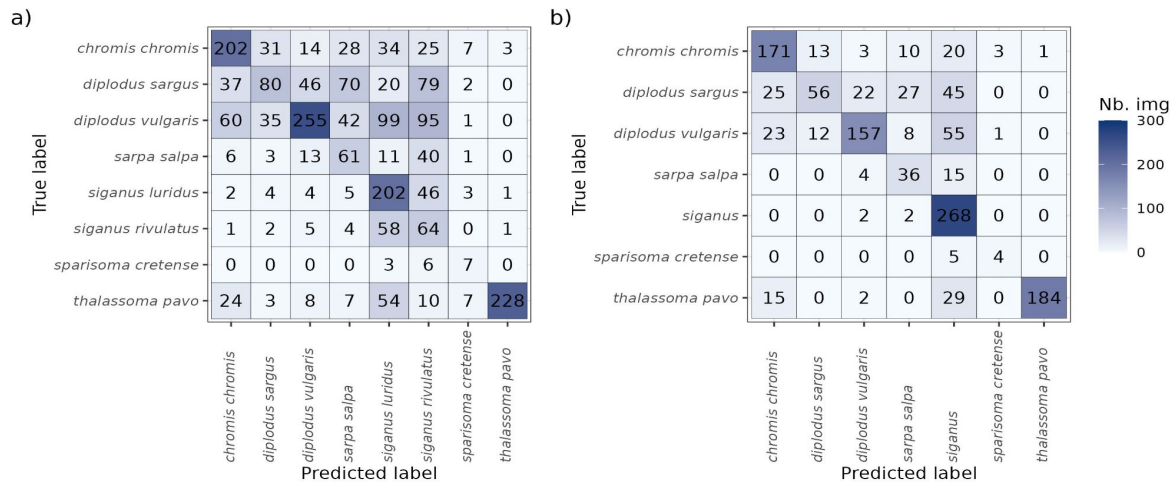
175 Image size may play an important role in fish identification. Indeed, a smaller image can be
176 indicative of an individual which is far away from the camera and difficult to identify. Thus, the
177 influence of image area (height x width in pixels) on TP and FP rates was analyzed.

178

179 **Results**

180 The training lasted 31 minutes and ran 36 epochs when the early stopping procedure ceased
181 the training as the loss did not decrease for the last 20 epochs.

182 The average recall was 0.62 among the eight classes, the confusion matrix being shown in
183 Figure 2. The recall for the classes *S. luridus* and *S. rivulatus* were 0.74 and 0.47, respectively.
184 When merging the two *Siganus* species in a single class, the recall reached 0.92. The
185 precision was 0.42 for the class *siganus_luridus*, 0.18 for the class *siganus_rivulatus*, and 0.44
186 when considering the merged class “siganus”.



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Figure 2. Performance of the Deep-Learning algorithm in identifying fish species in underwater images using a confusion matrix where correct classifications are on the diagonal. Largest numbers of individuals are highlighted. Comparison between the initial confusion matrix (a) and the confusion matrix after merging the two *Siganus* classes and removing the images for which the confidence score was lower than 0.8 (b). Each row of the matrix represents an actual class while each column represents a predicted class.

193

194

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196

After the post-processing removal of unsure predictions, the recall for the class *Siganus* increased to 0.99 and the precision increased to 0.61. On the four videos with at least one *Siganus* individual, the *Siganus* genus was detected in at least one frame (84% up to 100% of *Siganus* spp were detected per video).

197

198

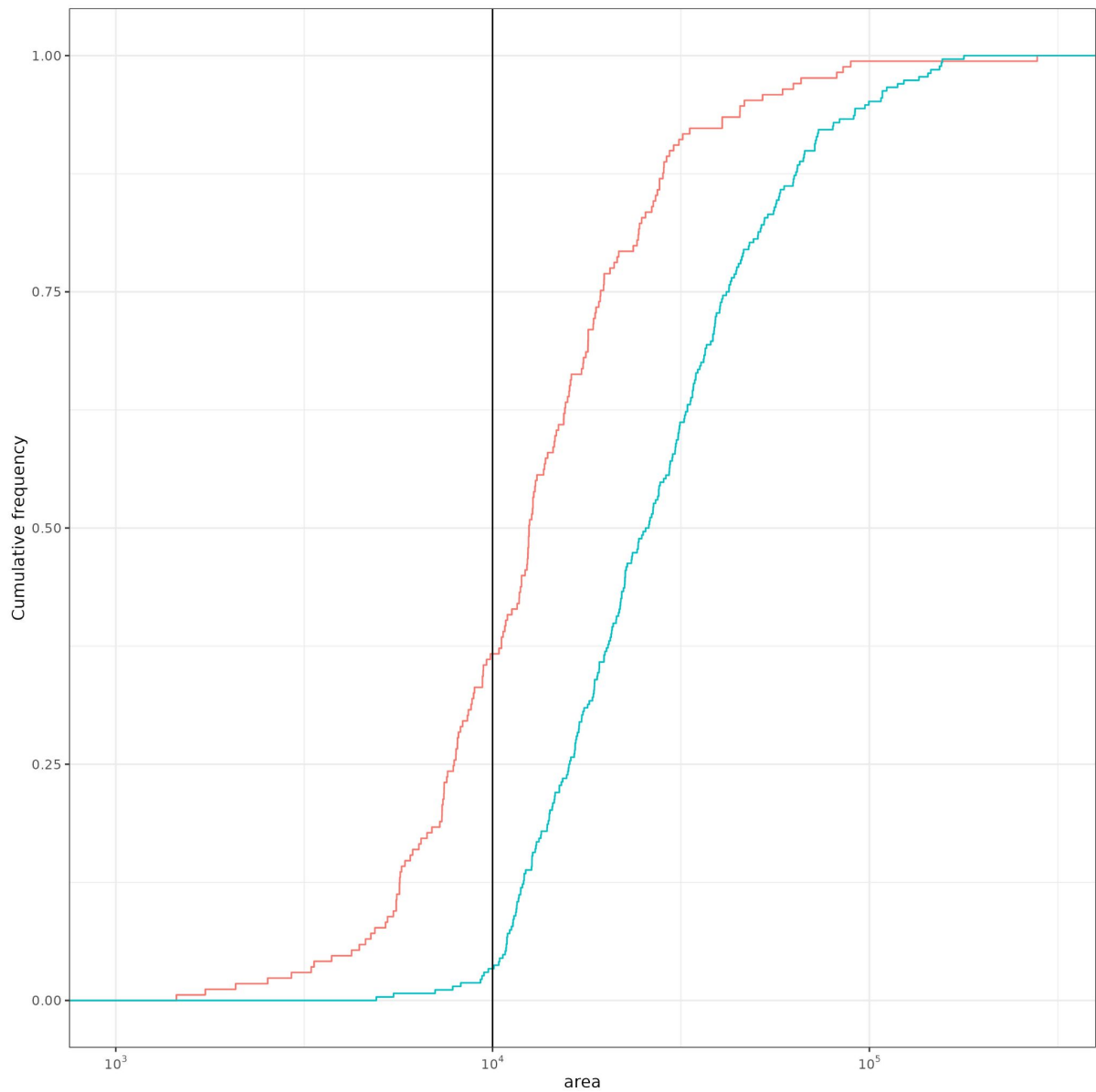
199

200

201

Among the 100 images of species not present in the training database, only 17 (5 *Diplodus puntazzo*, 5 *Lithognathus mormyrus*, 3 *Mullus surmuletus*, 3 *Oblada melanura*, 1 *Trachurus mediterraneus*) were misidentified as *Siganus* spp among which seven remained misidentified as *Siganus* spp after the post processing removing unsure predictions.

201



202
 203 Figure 3. Effect of image area on algorithm output. Cumulative frequency distribution of *Siganus* images correctly
 204 identified by the algorithm as *Siganus* (i.e. True Positive in blue) and of native species images misidentified as
 205 *Siganus* (i.e. False Positive in red) along the gradient of image area (log10 scale). The vertical black line
 206 illustrates the cutoff at 10,000 pixels.

207

208 None of the correctly identified *Siganus* images had an area < 4,900 pixels while all the 13
 209 images with area <4,900 pixels, which were labeled as *Siganus*, were in fact of one of the six
 210 native species (Figure 3). Choosing a cut-off at 10,000 pixels removes 62 FP (36%) and 9 TP
 211 (3%) increasing the precision to 0.71 while marginally decreasing the recall for the class
 212 *Siganus* to 0.98.

213

214 **Discussion**

215 The recall of 0.92 for the class “siganus” demonstrates the reliability of the trained DL since
216 only 32 out of 402 images of *Siganus spp* were misclassified as images of indigenous fish
217 species (Figure 2a). Among those 32 incorrectly labeled images (FN), 28 had a confidence
218 score lower than 0.8 and only 4 (Figure 2b) had a confidence score greater than 0.8 so were
219 retained in the final model outputs after post-processing. Those 4 false negatives were images
220 of *Siganus* individuals shot in turbid water, exposed to direct sunlight, and of an individual
221 masked by a *Sarpa salpa* (Figure 4). If an expert checks the 28 unsure images (7% of the
222 images analyzed) and identifies *Siganus* on all of them, only 1% (4 out of 272) of *Siganus spp*
223 images would be missed (false negatives). Besides, ignoring the 28 unsure images had no
224 impact on the detection of *Siganus* at the scale of the video sequence as each of our videos
225 contains at least 10 images of *Siganus spp*. So, our classifier coupled to long running videos
226 would most likely detect rabbitfish presence even when elusive or rare.

227 The precision of 0.44 for the class "siganus" means that 56% of images labeled as "siganus"
228 were actually indigenous species. The confidence-based post-processing removal of unsure
229 predictions increased the precision for the “siganus” class to 0.61, meaning that among the
230 437 images labeled as *Siganus* 169 were actually images of native species. This model's
231 performance level is within the average performance level of existing models. The recall for
232 *Siganus* obtained by this model is lower to other studies on a single fish species (Ditria et al.,
233 2020; Lopez-Marcano et al., 2021). The overall performance on the 8 species is higher to the
234 classification algorithm by Catalán et al., (2023) for 9 Mediterranean indigenous fishes (recall:
235 0.76, precision: 0.37) and to the one by Jenrette et al., (2022) on 47 species of tropical sharks
236 and rays, which proposes a combination of three models (a detection model, a binary sorting
237 model and a classification model), achieving an overall accuracy of 70%. The two species
238 most commonly misidentified as *Siganus spp* were the two seabream *Diplodus vulgaris*
239 (194FP) and *Diplodus sargus* (99FP) (Figure 2a). Yet, these two species have a shape and
240 color pattern different from *Siganus spp*. Visual inspection of these confidently misclassified
241 images revealed they mostly depict individuals in the background or with their body partially
242 hidden (because of their orientation relative to the camera, or movement of the tail) making
243 them more difficult to identify even by humans (Figure 4). Meanwhile, the *Diplodus* individuals

244 close to the camera and not masked were correctly classified (i.e. among the 921 *Diplodus*
245 *vulgaris* and *D. sargus*, 44% were classified as a *Diplodus*). Hence, the confusion between
246 *Diplodus* and *Siganus* is context dependent.

247



248

249 Figure 4. Illustration of automated identification of fishes by the Deep Learning algorithm.

250 *Siganus luridus* (a) and *Siganus rivulatus* (b), partially masked by the head of a *Sarpa Salpa*, misidentified as
251 *Sarpa salpa*. *Siganus rivulatus* (c, d) misidentified as *Diplodus vulgaris*.

252 Individuals of *Siganus luridus* (e), and *Siganus rivulatus* (f) correctly identified by the model despite their partially
253 masked bodies. Individuals of *Diplodus vulgaris* (g), *Thalassoma pavo* (h), *Chromis chromis* (i), and *Diplodus*
254 *sargus* (j) misidentified as *Siganus spp.*

255

The number in the top right corner of each image is the image area in pixels.

257 As a consequence, not accounting for *Siganus* identified in images of less than 10,000 pixels
258 discarded more than one third of false positive *Siganus* identifications while keeping recall
259 above 98% (i.e. only 9 images of *Siganus* would be misidentified as a native fish species).
260 Such small images correspond to individuals filling less than 1/20th of a FullHD video frame
261 (1920×1080, > 2 millions pixels). Hence, as in all our remote underwater videos, it is likely that
262 when present *Siganus* individuals will be recorded with an apparent size > 10,000 pixels.

263 The processing of the 2,024 images belonging to the test dataset took 10s on a laptop
264 computer and the optional checking of the 28 predictions of *Siganus* with low confidence
265 threshold would take less than 3 minutes for an expert (assuming 5s per image). Checking
266 only the 437 images identified as *Siganus* would take 36 minutes and would allow discarding
267 false positives. Hence, as the analysis of the 2,024 images by an expert would take 168
268 minutes (assuming 5s per image with no break), the DL_a thus provides at least a 5-fold gain
269 of time.

270 One limitation of our DL_a classifier is the identification of *Siganus* only in images containing a
271 single individual at its center. Thus, in practice, raw videos or pictures from underwater
272 cameras must be cropped to focus only on fish individuals, which requires no expertise in
273 taxonomy and is fast using any software able to save a screenshot (e.g. VLC). A future priority
274 will be to couple this identification model with a general fish detection model able to segment
275 all fish individuals from a video frame or a picture (e.g. Knausgård et al., 2022). Then our
276 model will process those extracted images. Even if current detection models are only able to
277 identify a single species (Lopez-Marcano et al., 2021), recent advances in other taxa show
278 encouraging results such as DeepFaune (Rigoudy et al., 2023) for French terrestrial fauna, or
279 for insects (Teixeira et al., 2023). However, these detection models require images with all
280 individuals annotated, which is time-consuming as underwater images could contain >100 fish
281 individuals. Another limitation is that classifiers are only able to identify species in the training
282 dataset, which requires collecting more than 1,200 images per species or applying few-shot
283 learning techniques that usually decrease recall and precision (e.g. Villon et al., 2021). In our

284 case, among images from the five indigenous species not present in the learned classes, only
285 7% were confidently classified as *Siganus spp*, which was lower than the false positive rate
286 for the six indigenous species present in the training dataset. Hence, our model would likely
287 not misidentify as *Siganus* species that are not present in the training dataset.

288

289 **Conservation perspectives**

290 Developing rapid and robust knowledge on the distribution and density of NIS is crucial to
291 evaluate progress against international agreements, including the UN Sustainable
292 Development Goals, Convention on Biological Diversity Targets, EU Biodiversity Strategy, and
293 the Green Deal. Towards this goal, improving our capacity to automate data collection and
294 processing is needed to dramatically increase the amount and quality of information and
295 knowledge available to scientists and decision-makers.

296 Remote or diver-operated underwater videos have been increasingly used by scientists and
297 ecosystem managers to monitor fishes for the last decade across the Mediterranean Sea
298 (Nalmpanti et al., 2023). We believe that our DLAs will be useful for ecosystem managers to
299 accelerate the analysis of videos collected during those monitoring programs of NIS, ensuring
300 detection of *Siganus spp*. Towards this aim we release it in a public repository
301 (https://github.com/valentine-fleure/Siganus_identifier). Our classifier applied to long
302 underwater videos will pave the way to high-frequency monitoring of rabbitfishes throughout
303 the Mediterranean basin. Such massive data are needed to describe the geographic
304 expansion of rabbitfishes through time to ultimately unravel its driver (climate, connectivity),
305 and test the potential benefit of MPAs on lowering their abundance through increased level of
306 predation by large fishes.

307 In addition, as the Mediterranean coastal ecosystems are a popular place for underwater
308 activities (snorkeling, freediving, SCUBA diving) and as many of these recreational users own
309 underwater cameras, there is a high potential to collect a large number of images in many
310 places. As most recreational users have no to little ability to identify all fish species, our publicly
311 available algorithm will favor current citizen science monitoring of NIS. Indeed, our algorithm

312 will favor the participation of new users to those programs as well as help them improving their
313 identification skills so that less individuals of rabbitfish will be missed. Ultimately, these
314 recorded and validated new occurrences would be integrated in the Global Biodiversity
315 Information Facility (GBIF) and the Ocean Biodiversity Information System (OBIS) to actualize
316 rabbitfish geographic range size and estimate of invasion rate.

317 Given the increasing number of NIS entering the Mediterranean Sea as well as the expansion
318 of those already present in the South-Eastern part (Azzurro & Andaloro, 2005; Azzurro,
319 Smeraldo & D'Amen, 2022), video-algorithm based monitoring programs should be able to
320 monitor more species. Toward this aim, it would be relevant to upgrade the model by
321 identifying more indigenous species as well as more NIS. Among the NIS that should be
322 prioritized to be added to the training database, lionfish (*Pterois miles*), silver-cheeked toadfish
323 (*Lagocephalus sceleratus*), yellowspotted puffer (*Torquigener flavimaculosus*), and sweepers
324 (*Pempheris spp*) are of the highest priority given their abundance in the Eastern Mediterranean
325 and their rapid northward and westward expansion (Zenetos et al., 2022). These Lessepsian
326 species are morphologically distinct from one another and from indigenous species and should
327 thus be easily identified by algorithms.

328 One step further, AI algorithms may unlock the potential of video-based monitoring beyond
329 the case of non-indigenous species detection through automated identification of all fish
330 species, including endangered one, as well as estimating their size and behaviors (Ditria, Jinks
331 & Connolly, 2021) to assess a large set of indicators as envisioned by the Essential
332 Biodiversity Variable framework (Kissling et al., 2018). These variables would deliver multiple
333 indicators of coastal ecosystem status, climate change effects, and spatio-temporal trends in
334 fish biodiversity, as required to meet the monitoring requirements of the EU Water Framework
335 Directive (WFD) and the Marine Strategy Framework Directive (MSFD).

336

337

338

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348 the GNAUM (<https://www.gnaum.fr/>) who helped with annotation of fishes.

349

350 **Conflict of interest**

351 The authors have no conflict of interest to declare.

352

353 **Author contributions**

354 Valentine Fleuré, David Mouillot and Sébastien Villéger conceived and designed the study;
355 Camille Magneville and Sébastien Villéger collected the data. Valentine Fleuré wrote the first
356 draft of the manuscript. All authors contributed to subsequent revisions and approved the
357 final version.

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