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Laser chasing behaviour of wild fishes exploited as a tool to compare space use between size, sex and species

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Abstract

The spatial extent of animal movement is a key consideration when designing conservation measures, such as marine protected areas. Methods to assess territory size in the marine environment, however, are labour intensive and/or expensive. Here, we explore a novel method to investigate the spatial ecology of territorial fishes by examining their reactions to an artificial light stimulus. During benthic towed video surveys conducted in Lyme Bay, southwest England, several species of wrasse (Labridae) have frequently been observed pursuing a laser projected onto the seabed. While the motivation behind 'laser-chasing' is unclear, we quantified the spatial aspects of this behaviour by comparing chase distance and chase likelihood between and within species, to determine the potential utility of this method for investigating space use and aggression in wild fishes. Cuckoo wrasse (*Labrus mixtus*) were significantly more likely to display agonistic behaviour towards the laser than Goldsinny wrasse (*Ctenolabrus rupestris*). Goldsinny wrasse displayed a positive relationship between total length and chase-distance, but not Cuckoo wrasse. The observed species differences may relate to behavioural factors affecting the motivation behind 'laser-chasing', which is discussed. Chases by the cuckoo wrasse were significantly longer than those by Goldsinny wrasse, and these chase distances were used to estimate theoretical territory sizes for each species. To our knowledge, this is the first study to explore the spatial aspects of the reactions to an artificial stimulus by wild fishes. The potential to develop the method to directly investigate aspects of territoriality and aggression in wild fishes is discussed, including necessary further refinements and testing. Wild wrasses are increasingly exploited in Europe to provide cleaner fish for salmonid aquaculture, and we encourage the development of methods to inform spatial conservation measures for these ubiquitous and iconic species.

KEYWORDS

aquaculture, fishing, marine protected area, new techniques, reef

1 | INTRODUCTION

The wrasse family (Pisces: Labridae) is a large group of marine fishes with over 600 species in 82 genera, found throughout the tropics and temperate waters (Parenti & Randall, 2000). Many wrasse remove ectoparasites from larger fish and other marine organisms,

and these mutualistic 'cleaner-client' relationships are among the most well-studied behavioural systems in fish (e.g. Arnal, Côté, & Morand, 2001; Cheney & Côté, 2005; Poulin & Grutter, 1996). Studies on cleaner-wrasse have focused on tropical obligate cleaners, but many wrasse in temperate waters are facultative cleaners, who rely only in part on cleaning for their nutritional requirements

(Francini-Filho & Sazima, 2008). Historically, wrasses have not been considered of great economic value in Europe (Muus & Dahlström, 1974) but since the late 1980s, a targeted fishery for Labrids has developed to provide cleaner fish that control parasites in salmonid aquaculture (Darwall, Costello, Donnelly, & Lysaght, 1992; Davies, 2016; Skiftesvik, Durif, Bjelland, & Browman, 2015). Salmon and trout farmers face multi-million euro annual costs as a direct result of sea lice (*Caligus elongatus* and *Lepeophtheirus salmonis*), with economic impacts relating to chemical parasite control and culling of infected fish (Costello, 2009). Further, the widespread development of resistance to industry preferred medicines (P. G. Jones, Hammell, Gettinby, & Revie, 2013) has resulted increased demand for cleaner fish in many areas (Skiftesvik et al., 2015).

In northern European waters, five species of wrasse are commonly found; cuckoo (*Labrus mixtus*), ballan (*Labrus bergylta*), goldsinny (*Ctenolabrus rupestris*), rock cook (*Centrolabrus exoletus*) and corkwing wrasse (*Symphodus melops*), of which the latter four are currently targeted by the live wrasse fishery (Davies, 2016). The use of these species as cleaner fish may be seen as an environmentally friendly alternative to chemical lice treatments (Migaud, 2015). However, there are concerns that their life history traits, including territoriality and late age at maturity could make them vulnerable to overexploitation. European wrasses have distinct habitat preferences, resulting heterogeneity of species assemblages within small areas, and temporal variation in spawning timing (Skiftesvik et al., 2015). While goldsinny are pelagic spawners, ballan, corkwing, rock cook and cuckoo wrasse are benthic spawners, which limits the ability of their larvae to disperse in the plankton. Further, fishing of nest-building species during their spawning season could affect egg survival by removing nest-guarding males (Darwall et al., 1992; Pinder, Velterop, Cooke, & Britton, 2017). For the purposes of managing the live wrasse fishery are currently considered as one stock, but variation in life history characteristics between species means that this 'one stock' approach may not be appropriate. To ensure sustainable exploitation of wrasse, we require a deeper understanding of their territorial breeding structures, including spatial aspects such as territory size and home range, and how these structures may be affected by fishing.

Knowledge of territory size and home range of marine organisms is an important factor that can affect the success of spatial protection measures such as marine protected areas (Kramer & Chapman, 1999). Methods to quantify spatial aspects of territoriality in fish, have traditionally involved direct observation studies (Hilldén, 1981; Keeley & Grant, 1995; Norman & Jones, 1984) or mark-recapture tagging (Hilborn, 1990). In recent decades, improvements in technology have provided researchers with electronic tagging methods including radio, satellite and acoustic telemetry (Nielsen et al., 2009), which allow remote collection of precise real-time observations of space-use. These techniques have greatly expanded our ability to study space-use in wide-ranging animals that occupy habitats that make direct observation impossible (Potts & Lewis, 2014). In general, however, direct observation and tagging/telemetry methods to investigate space-use are labour intensive, expensive or both.

Artificial stimuli have been employed in numerous lab and field experiments to investigate the behavioural ecology of territorial fish species. Stimuli have included auditory cues (Brintjes & Radford, 2013), and dummy models of conspecifics to examine aggression responses in territorial species (Barlow & Siri, 1994; Sowersby, Lehtonen, & Wong, 2017). New technologies are continually advancing our understanding of territoriality and aggression in fish, both in the lab - through combining light stimuli and robotic fish (Polverino, Karakaya, Spinello, Soman, & Porfiri, 2019; Romano et al., 2017; Romano, Benelli, Hwang, & Stefanini, 2019), as well as computer-animated virtual stimuli (Witte, Gierszewski, & Chouinard-Thuly, 2017) to study aggression responses - and in the field, where modern benthic video survey systems have invoked responses among fish, which are opportunistically studied in a behavioural context (Frid, McGreer, & Frid, 2019). While valuable, these studies have focused on observing behavioural responses, without attempting to quantify spatial aspects of territory. Here, we exploit the tendency of wild wrasse to chase an artificial light stimulus projected onto the seabed as part of benthic biodiversity surveys. By estimating the distances over which chases occur, and comparing these distances across species, sex and size classes, we provide preliminary evidence that the method could be used as a high-throughput, non-invasive method for quantifying space-use and territoriality in wild fishes.

2 | MATERIALS AND METHODS

Since 2008, a statutory instrument preventing the use of towed fishing gear within a 125 km² area has been in place in Lyme Bay, Southwest England. As part of the continued monitoring of benthic assemblages post-closure, surveys using a towed video camera (Sheehan, Stevens, & Attrill, 2010) have been conducted within and outside the statutory protected area at 75 sites across Lyme Bay (Figure 1). (see Sheehan, Cousens, et al., 2013; Sheehan, Stevens, Gall, Cousens, & Attrill, 2013). 36 of these sites are within the statutory instrument, of which 18 are within previous voluntary closure areas. The remaining sites are outside the statutory protected area and are open to benthic towed fishing gear.

Video surveys are conducted using a towed underwater video system (TUVS) for 20 min transects of target distance 200 m. The towed camera system floats above the seabed to reduce impact - see Sheehan et al. (2010) and Sheehan et al. (2016) for detailed information on how the TUVS is configured and operated. In order to measure the variable field of view and the size of benthic organisms, two green 532 nm lasers (Beam of light technologies, Inc: Scuba-1 Underwater dive laser) were mounted either side of the camera, pointing forward at 30 cm apart. During video surveys, many species of fish, and in particular wrasse, have been observed 'chasing' these green lasers projected onto the seabed (Figure 2). The observed interactions between wrasse and the camera/laser apparatus are the focus of this study.

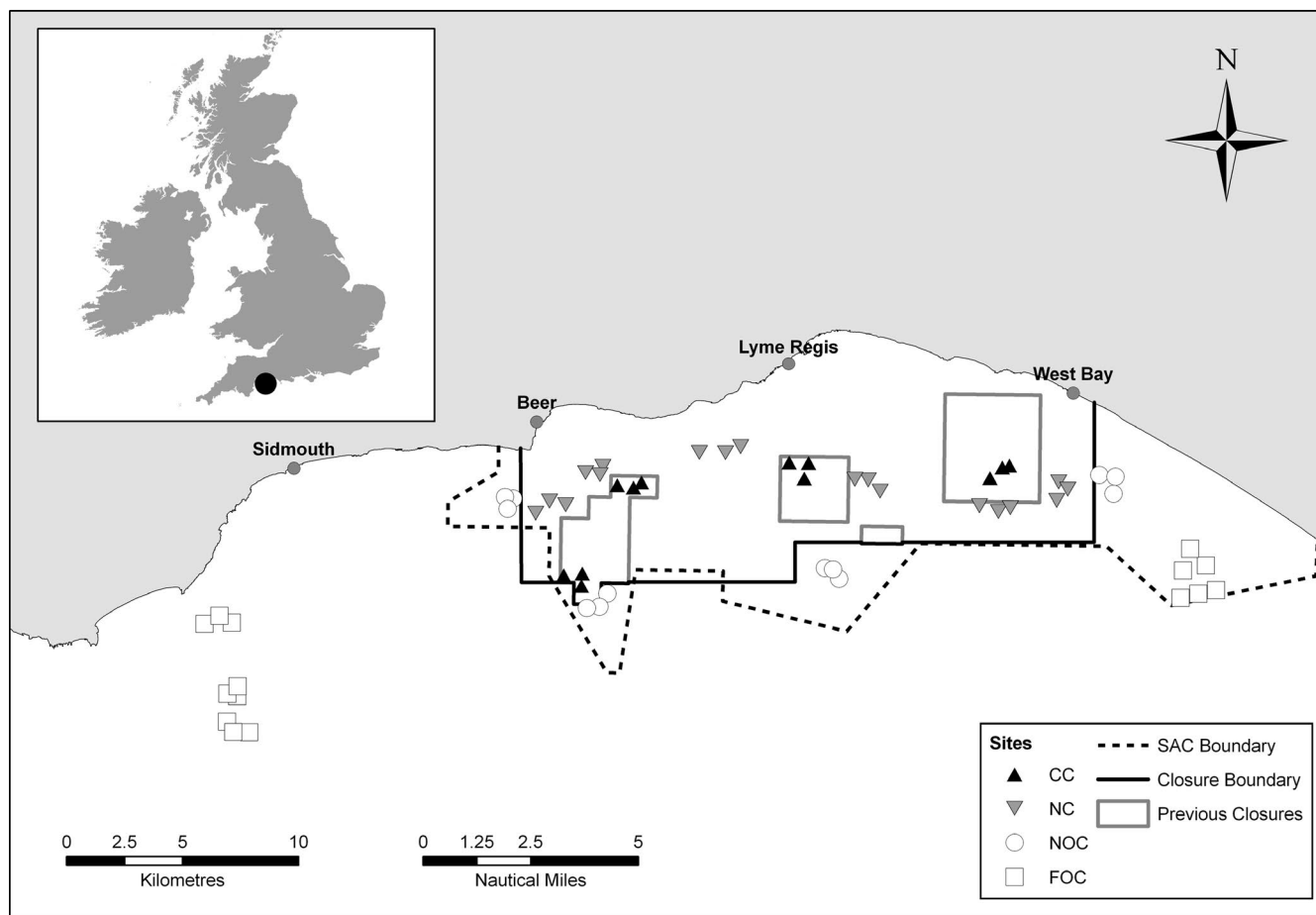


FIGURE 1 Map displaying towed video survey sites. Dark triangles = previously closed to towed fishing gear (pre-2008), grey triangles = new closure (statutory instrument), open circles and open squares = open control sites. Taken from Sheehan, Cousens, et al., 2013: Recovery of a Temperate Reef Assemblage in a Marine Protected Area following the Exclusion of Towed Demersal Fishing. PLoS One, 8(12), p.e83883



FIGURE 2 Two Goldsinny wrasse (*Ctenolabrus rupestris*) interacting with the benthic laser scale of the towed video camera (see Sheehan et al., 2010). The distance between the green points is 30 cm, allowing estimation of total length

2.1 | Video analysis

Surveys from 2011 and 2013 were selected for analysis as they were the years with the best visibility, which allowed detailed observation of wrasse behaviour. In 2011, surveys were carried out between

20–29 July, and in 2013, surveys were conducted between 15–19 July. All surveys were conducted between 10:00 AM. and 3:30 PM. (BST). Each wrasse encountered during towed video surveys was visually identified to species, and where possible, total length relative to a 30 cm laser scale (Figure 2) was estimated using imageJ (Schneider, Rasband, & Eliceiri, 2012). Cuckoo wrasse were categorised by colour morph into 'dominant male' and 'female/subordinate male' categories, as determination of sex by colour alone is not possible in this species due to the presence of 'sneaker males', which display a female colour morph but possess male gonads (Matland, 2015).

2.2 | Behavioural classification and determination of chase distance

Each wrasse sighting was classified into one of four categories of behaviour toward the towed video apparatus and laser scale: flee, neutral, interest and chase, representing escalating levels of aggression (Benelli, Romano, Desneux, Messing, & Canale, 2015) (Table 1). For 'chase' interactions, the length of pursuit of the laser was determined in seconds, and converted into an estimate of 'chase-distance' using logged GPS data from the research vessel (2013) or

TABLE 1 Categorisation method used to classify aggressive and non-aggressive behavioural displays made by wrasse towards the laser during towed video surveys

Behaviour Type (rank)		Definition
Aggressive	Chase (4)	Clear movement toward laser projection – may include attempts to 'bite' the laser
	Interest (3)	Interest in laser without movement towards it; fish 'watch' the laser or camera as it passes
	Neutral (2)	No apparent interaction with either laser or camera; appears to ignore towed apparatus
Non-aggressive	Flee (1)	Flees off screen or into refuge, apparently in response to approaching laser/camera

average speed over the transect (2011). In cases where the camera was stationary due to physical obstructions on the seabed, these interactions were excluded from further analysis of chase distance, as well as instances where chases were cut short by the end of a video recording. In 2011, chases were also excluded if they occurred at a time when the camera was moving substantially faster than the average tow speed, such as after release from a physical obstruction.

2.3 | Statistical analysis of chase likelihood and chase distance

All statistical analyses were performed using R (3.2.5; <http://cran.r-project.org>). Although four species of wrasse were observed over the two years of sampling, statistical tests focused on Goldsinny (*Ctenolabrus rupestris*) and Cuckoo wrasse (*Labrus mixtus*), as occurrences of other species were infrequent. Initial data exploration was conducted according to the procedure described by Zuur, Ieno, and Elphick (2010). Upon examination of kernel density plots, frequency histograms and qq-plots, the variable 'chase-distance' was found to be non-normally distributed with positive skew, so non-parametric univariate tests were chosen. Permutation tests were conducted on the categorical variables species and sex against chase-distance, and Spearman's rank correlation coefficient was generated for the continuous variable total-length against chase distance. To examine likelihood of the laser eliciting a chase response between different groups, a chi-squared goodness of fit tests were conducted on species and sex versus the categories of interaction described in Table 1. Categories were combined into 'aggressive' and 'non-aggressive' in a 2 × 2 contingency table by combining the groups interest, neutral and flee.

3 | RESULTS

In 2011 and 2013, a total of 536 wrasse from four species were sighted during towed video surveys in Lyme Bay (Table 2). 73% of wrasse

TABLE 2 Occurrences of wrasse (Family: Labridae) species on towed video surveys conducted in Lyme Bay, 2011 and 2013

Species	2011	2013	Total
Goldsinny Wrasse (<i>Ctenolabrus rupestris</i>)	163	134	297
Cuckoo Wrasse (<i>Labrus mixtus</i>)	151	52	203
Ballan Wrasse (<i>Labrus bergylta</i>)	5	9	14
Rock Cook (<i>Centrolabrus exoletus</i>)	18	0	18
Total	341	195	536

sightings were from areas previously closed to fishing (pre-2008 voluntary closure), while 23% were from areas within the statutory instrument created in 2008 (new closure). Only one wrasse was sighted in areas open to towed fishing gear. The mean and range of estimated total length of each wrasse species observed are displayed in Table 3.

3.1 | Wrasse-laser interactions

Wrasse-laser interactions for each species observed are described in Table 4. Cuckoo wrasse were significantly more likely to chase the laser than goldsinny wrasse ($\chi^2 = 36.0997$, $p < .001$; Figure 3). Between colour morphs of cuckoo wrasse, there was no difference between dominant males and females/subordinate males in the likelihood of a towed camera sighting resulting in a laser chase ($\chi^2 = 0.1556$, $p = .69$).

Cuckoo wrasse chases were significantly longer than Goldsinny wrasse chases (Figure 4). The mean cuckoo wrasse chase was 1.83 m (range 0.15–9.6 m, 95% bootstrapped CI: 1.51–2.18 m), while the mean goldsinny wrasse chase was 1.04 m, (range 0.14–4.8 m, 95% bootstrapped CI: 0.89 m–1.21 m). There was no relationship between total length and chase distance in cuckoo wrasse (Figure 5a) ($n = 120$, $r_s = 0.07$, $p = .45$), but there was a significant positive correlation between total length and chase distance in goldsinny wrasse (Figure 5b; $n = 104$, $r_s = 0.41$, $p < .01$). There was no difference between dominant male and female/subordinate male cuckoo wrasse morphs in mean chase distance (Figure 6).

4 | DISCUSSION

This paper presents a preliminary investigation of a novel method for investigating spatial aspects of territoriality in fishes in the wild. The results reveal differences in laser interaction within and between species, and these findings are discussed in the context of wrasse behavioural ecology. The limitations of the method as presented here are considered, as well as suggestions for future work.

4.1 | Laser-chasing: predatory or territorial?

Light is a vital environmental cue for fish, and the reactions of fish to artificial light, both as an attractant and deterrent, have found

TABLE 3 Mean and range of total lengths estimated for wrasse species on towed video surveys conducted in Lyme Bay, 2011 and 2013. 'No estimate' refers to the occurrences where a total length estimate was not possible

Species	N	Mean TL	TL Range	No estimate
Goldsinny Wrasse (<i>Ctenolabrus rupestris</i>)	297	10.2	6–14	64
Cuckoo Wrasse (<i>Labrus mixtus</i>)	203	23.8	14–35	41
Ballan Wrasse (<i>Labrus bergylta</i>)	14	34.6	24–42	7
Rock Cook (<i>Centrolabrus exoletus</i>)	18	11.8	8–15	5

TABLE 4 Number and type of wrasse-laser interactions occurring on towed video camera surveys conducted in Lyme Bay, 2011 and 2013

Species	Aggressive	Non-aggressive		
	Chase	Interest	Neutral	Flee
Goldsinny Wrasse (<i>Ctenolabrus rupestris</i>)	126	27	112	28
Cuckoo Wrasse (<i>Labrus mixtus</i>)	142	11	38	11
Ballan Wrasse (<i>Labrus bergylta</i>)	0	0	10	3
Rock Cook (<i>Centrolabrus exoletus</i>)	11	1	4	2

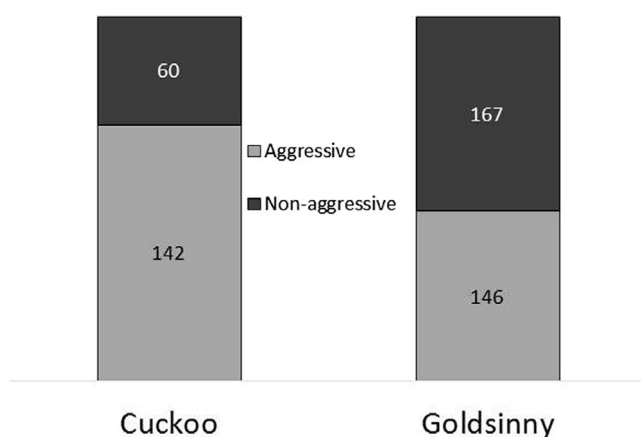


FIGURE 3 Aggressive and non-aggressive interactions by Cuckoo wrasse and Goldsinny wrasse toward laser scale during towed video camera surveys in Lyme Bay, 2011 and 2013. Cuckoo wrasse were significantly more likely to 'chase' the laser ($\chi^2 = 36.0997, p < .001$)

widespread applications in fisheries (Marchesan, Spoto, Verginella, & Ferrero, 2005) and potential applications in conservation (Ford, Elvidge, Patrick, Sills, & Cooke, 2019). Here, the motivation behind the conspicuous attraction of wrasses to an artificial light – laser chasing – is difficult to positively identify. Laser chasing in other fish species has been assumed to represent predatory behaviour (Frid, McGreer, & Frid, 2019), and attempts to 'bite' the laser were made during some chases in this study. However, this cannot be assumed to represent a predatory action, as territorial displays in some wrasse are known to include 'mouth-fighting', where two aggressors lock their mouths together in a display of strength (Hilldén, 1981).

Regardless of the motivation behind laser chasing, in order for chases to be related to space use, a key assumption is that individuals do not cross territorial boundaries during the course of their pursuit of the laser. In the goldsinny, a long term observational study by Hilldén (1981) provides support for this assumption; goldsinny wrasse did not venture outside their fixed territorial boundaries for the duration of the annual study period, a behavioural trait consistent with studies in other territorial fish species (eg. Hixon, 1981). However, there are several reasons that chase distance may not be precisely related to space use. Wrasse probably do not chase the laser for the entire intersection of their territory, and the likelihood and length of chase may depend on many other factors that were not tested here, including camera speed, visibility and habitat rugosity, which can result in the laser being obscured from view and chases being terminated.

Despite these caveats, assuming individuals do not cross territorial boundaries, chase distances may be considered as a 'minimum territory diameter', and therefore allow a basic estimation of 'minimum territory area'. The maximum chase distance for goldsinny estimated in the study was 4.8 m, and there were several chases estimated over 3 m. Assuming a circular territory, a territory diameter of 3 m yields an estimated territory size of 9.4 m² (area = $\pi \times \text{diameter}$). Hilldén (1981) found an average territory size in goldsinny wrasse of 1.4 m², range 0.5–2 m². The chase distances observed here therefore suggest that some Goldsinny territories may be much larger than those observed by Hilldén.

Territory sizes may vary significantly between individuals. In other territorial species, females occupy substantially smaller areas within a dominant male's territory (Norman & Jones, 1984). Further, larger males may occupy much larger spatial areas than smaller males (Hixon, 1981). Difficulties in differentiating between sexes in

goldsinny wrasse made it impossible to directly compare male and female chases, but the relationship between size and chase distance suggests larger males may defend larger territories than females. However; these differences may also reflect how individual of different sizes perceive the laser, or differences in aggression levels rather than differences in territory size. Territory size may depend on many factors, including habitat type; Hildén's (191) observational study was conducted in shallow water kelp habitat between 0.5–10 m, and although depth was observed to affect territory size, it was not studied directly. Goldsinny wrasse observed in Lyme Bay all inhabited deep water rocky reefs between 20–30 m; further study

over a range of habitat types and depths are needed to investigate the effect of these factors on territoriality.

Here, the higher average and maximum chase distances of cuckoo wrasse suggest that they occupy substantially larger spatial areas than Goldsinny wrasse, which is to be expected given that territory size generally increases with body size; in a study of six Caribbean Labrid species, Jones (2005) found that home range was positively correlated with total length. However, given that the motivation behind laser chasing is not necessarily territorial, direct comparisons between species are risky, as the observed differences between species may reflect differences in how these species perceive and react to the laser, as discussed above. Unlike goldsinny wrasse, there are no observational studies in the literature recording the territory size or home range of cuckoo wrasse. Further work is needed to confirm whether cuckoo wrasse display territory fidelity to the same degree as goldsinny before chase distance can reasonably be used to make inferences about territory size.

4.2 | Species differences in aggression

Here, according to the proportions of fish that were sighted on the video that then initiated an aggressive response to the laser, cuckoo wrasse were significantly more likely to behave agonistically toward the laser than goldsinny wrasse, perhaps suggesting differences in how these species perceive and react to the artificial stimulus. Cuckoo wrasse are protogynous hermaphrodites, with mature females becoming males above a total length threshold of around 24 cm (Darwall et al., 1992). It is believed that nest building is by mating pairs of males and females, with males undertaking nest defence once eggs are laid and fertilised (Dipper & Pullin, 1979). In this study, female/subordinate males cuckoo wrasse were as likely to engage in laser-chasing as dominant males, and the mean chase distance observed was the same between these morphs. There was also no apparent relationship between total length and chase

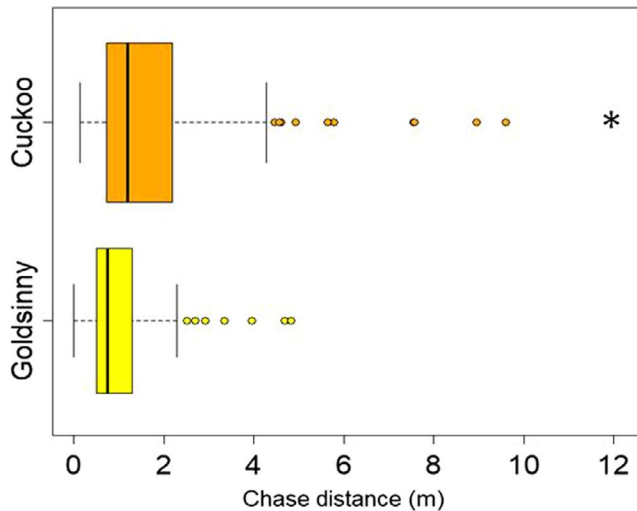


FIGURE 4 Boxplot of chase distances estimated for Cuckoo Wrasse (top, orange) and Goldsinny Wrasse (bottom, yellow), encountered during towed video surveys in Lyme Bay in 2011 and 2013. Mean Cuckoo wrasse chase: 1.83 m ($n = 142$, range: 0.15–9.6 m, 95% bootstrapped CI: 1.51–2.18 m); mean Goldsinny wrasse chase: 1.04 m, ($n = 126$, range: 0.14–4.8 m, 95% bootstrapped CI: 0.89 m–1.21 m) Permutation test: $p < .001$

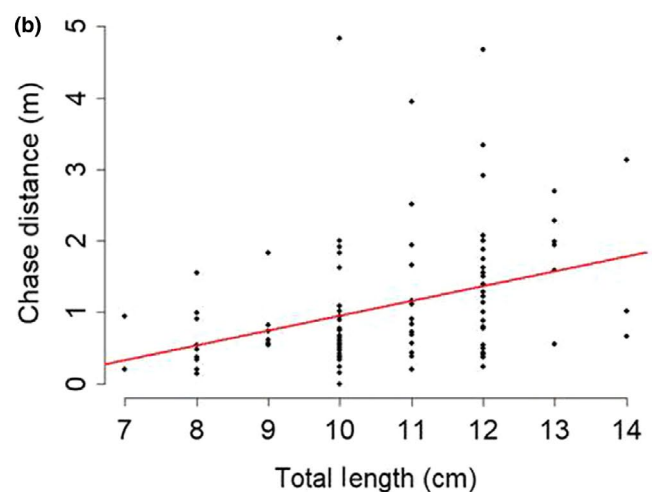
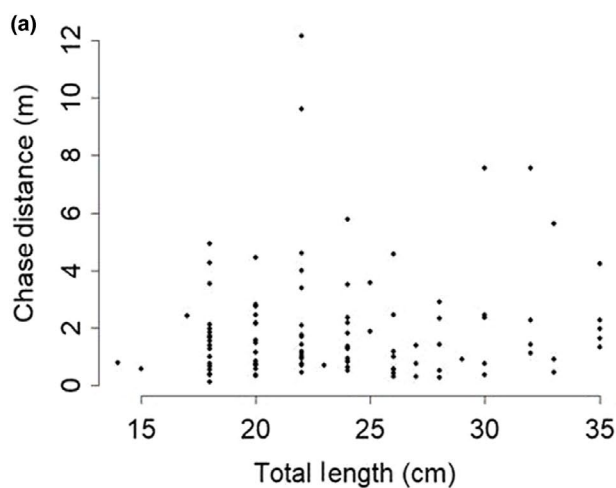
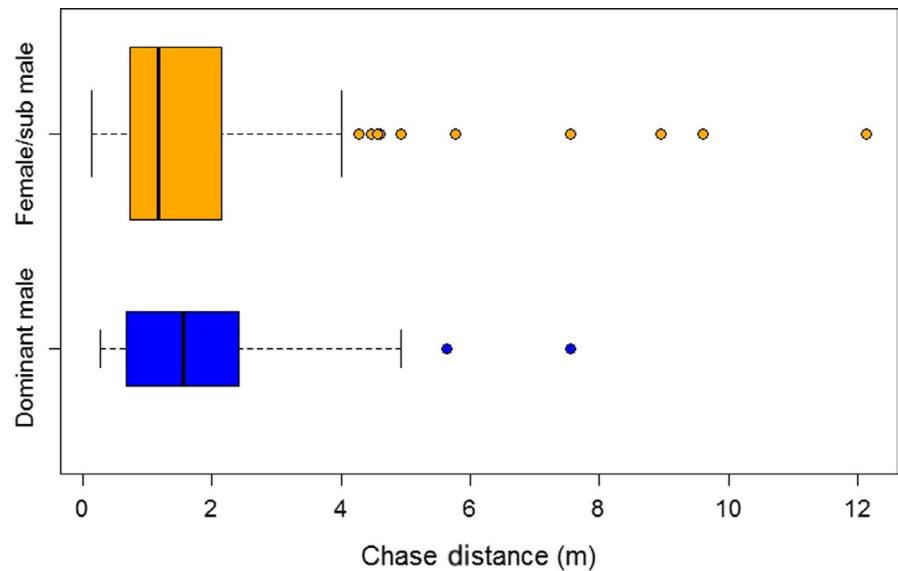


FIGURE 5 (a) Scatterplot of total length versus chase distance for Cuckoo wrasse Spearman's rank correlation coefficient: $n = 120$, $r_s = 0.07$, $p = .45$. (b): Scatterplot of total length versus chase distance for Goldsinny wrasse Spearman's rank correlation coefficient: $n = 104$, $r_s = 0.41$, $p < .01$

FIGURE 6 Boxplot of chase distances estimated for female (top, orange) and male (bottom, blue) Cuckoo wrasse (*Labrus mixtus*) encountered during towed video surveys in Lyme Bay in 2011 and 2013. Mean male chase: 2.15 m, ($n = 21$, range: 0.22–7.55 m, 95% bootstrapped CI: 1.38–3.01 m); mean female chase: 1.78 m, ($n = 110$, range: 0.15–9.6 m, 95% bootstrapped CI: 1.44 m–2.17 m) Permutation test: $p = .43$



distance, with some of the longest chase events from small female/subordinate male individuals. Since nest-defence is generally considered a male-only behaviour in protogynous hermaphrodite wrasse species (Darwall et al., 1992), it thus seems unlikely that the motivation behind laser-chasing observed here is related to territorial nest defence in cuckoo wrasse.

Unlike Cuckoo wrasse, Goldsinny wrasse showed a significant positive correlation between total length and chase distance. Goldsinny wrasse do not show pronounced sexual dimorphism, but males tend to be longer-at-age, reaching a maximum size of 15 cm (Darwall et al., 1992; Treasurer, 1994). A direct comparison of chase distance between sexes was not possible, but the correlation between total length and chase distance suggests males are responsible for the longer chases. This relationship may be more pronounced than observed in this analysis; by definition, longer chases had a greater likelihood of obtaining a total length estimate, because these individuals were on screen for longer. Conversely, there were many short chases by smaller fish for which obtaining a total length estimate was not possible. However, without accurate visual identification of sex, inferences regarding the chase distance between sexes are not possible.

4.3 | Developing the method and future applications

The data used in this study derive from a methodology for surveying benthic fauna, but our results suggest potential to apply the method to investigate territoriality directly, and combine a high-throughput, non-invasive survey of abundance/stock assessment with a survey of territorial structures. Our results are preliminary, and at present, reactions to the laser may represent a predatory response, or a weak, or partial territorial response (Rowland, 1999). Eliciting a reliable chase response, motivated by territorial defence rather than predation would allow more justified and reliable inferences as to the spatial extent of territory. A valuable next step would be to develop and explore the use of different artificial stimuli, a process to which

recent experimental work could provide valuable input, for instance by using various forms of replica or robot model and identifying the most appropriate cues (Romano, Donati, Benelli, & Stefanini, 2019). This would not necessarily preclude the use of the two methods in tandem (video survey and territorial survey), but adjustments to the towed apparatus would be required if a physical dummy or robot was used.

Across Europe, the annual landings of wild wrasse for cleaner fish is increasing rapidly (Skiftesvik et al., 2014); concerns over this developing fishery have arisen in several countries, including Norway, where wrasse populations outside protected areas have been significantly depleted due to commercial exploitation (Halvorsen et al., 2017). In the United Kingdom, live wrasse fisheries began in Scotland and Northern Ireland (Darwall et al., 1992), and since 2015, live wrasse fishing has occurred in south-west England, with wrasse caught in Dorset, Devon and Cornwall and transported to farms in Scotland (Davies, 2016). Previous studies have incorporated video abundance surveys as a precursor to telemetry to investigate fisheries-induced behavioural trait selection on fish in the wild (Alós, Palmer, Rosselló, & Arlinghaus, 2016). A potential direct application of the method explored here could be to combine abundance and behavioural surveys, allowing the effects of fishing on both abundance and territorial behaviour to be assessed simultaneously. Questions deserving attention include whether the observed spatial territoriality may vary before and after exploitation, between the breeding and non-breeding seasons, and between fished and unfished areas.

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CONFLICT OF INTEREST

None declared.

AUTHOR'S CONTRIBUTION

Conceived and designed the field experiments: EVS. Conducted video analysis: PD. Wrote the paper: PD. Edited the Paper: EVS.

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DATA AVAILABILITY STATEMENT

Data from this study will be archived at DASSH, an archive for marine species and habitats data <http://www.dassh.ac.uk/>

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