

BRIEF COMMUNICATIONS**Aggregation dynamics and foraging behaviour of striped red mullet *Mullus surmuletus* in the western Mediterranean Sea**M. J. AJEMIAN*†, M. D. KENWORTHY‡, J. L. SÁNCHEZ-LIZASO§ AND
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Habitat-related heterogeneity of striped red mullet *Mullus surmuletus* heterospecific foraging assemblages was examined off the coast of Spain. Video-based focal-follows conducted on 122 *M. surmuletus* assemblages (446 total individuals) revealed an array of attendant species ($n = 7$) with composition linked to benthic habitat complexity; bare sandy substrata were characterized by homospecific groups of *M. surmuletus*, while habitats with rock and vegetation attracted a variety of scrounging labrids and sparids. Although the nature of the relationship between *M. surmuletus* and attendants requires further exploration, the present study indicates that substratum composition can be a driving factor explaining the dynamics of this heterospecific assemblage.

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The striped red mullet *Mullus surmuletus* L. 1758 is a common inshore schooling goatfish (family: Mullidae) of growing economic value in the north-east Atlantic Ocean and Mediterranean Sea (Uiblein, 2007). This species is well known for its benthic foraging behaviour, which is mediated by its morphological specialization (*i.e.* barbels) for excavating the substratum for invertebrate prey (McCormick, 1995). This excavation behaviour, common to mullids worldwide, may play an important ecological role in 'ecosystem engineering' (Uiblein, 2007) and often attracts a number of scrounging attendant fishes (De Pirro *et al.*, 1999; Sazima *et al.*, 2006; Tipton, 2008). As such, *M. surmuletus* serves as a potentially important focal species in heterospecific foraging aggregations, which may greatly benefit attendants, although the impacts on *M. surmuletus* remain unknown (Lukoschek & McCormick, 2000).

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To date, the role of benthic habitat on *M. surmuletus* foraging behaviour has received little attention in the scientific literature. While it has been demonstrated that *M. surmuletus* preferentially feeds on a suite of benthic invertebrates over an unstructured bottom (Labropoulou *et al.*, 1997; De Pirro *et al.*, 1999), and is less likely to forage in habitats with high coverage of vegetation like *Caulerpa taxifolia* and *Posidonia oceanica* (Levi & Francour, 2004), this species and its relatives are highly mobile and thus encounter both hard (*i.e.* reef) and soft substrata during foraging (McCormick, 1995; Tserpes *et al.*, 2002; Uiblein, 2007). No studies, however, have characterized the dynamics of *M. surmuletus* foraging behaviour as this species traverses a mosaic of benthic habitats. Previous studies have either examined behavioural associations in mesocosms (Tipton, 2008), or have focused solely on single habitat effects on *M. surmuletus* foraging behaviour alone (De Pirro *et al.*, 1999; Levi & Francour, 2004). Thus, the ability to identify critical substrata important to this fisheries species remains limited. Furthermore, no studies have quantified associations of attendant species that may interact with *M. surmuletus*, and the potential role of habitat in generating these heterospecific aggregations.

A short-term observational study was conducted to characterize the dynamics of *M. surmuletus* assemblage composition and foraging behaviour across a variety of benthic habitats in shallow waters of the western Mediterranean Sea. The study goals were to: (1) characterize *in situ* the heterospecificity and behaviour of *M. surmuletus* assemblages and (2) assess the potential impacts of location and benthic habitat structure on these parameters.

Field sampling was performed off Santa Pola del Este, Spain, in the western Mediterranean Sea (38.2° N, 0.51° W). Three sites, covering a variety of benthic habitats (sandy bottom, rock, macroalgae and seagrass), were chosen for analysis. Two sites were located within the Tabarca Marine Reserve 7 km to the south-east of the town of Santa Pola, Spain. The reserve was subdivided into three areas based on different levels of protection described in Ojeda-Martinez *et al.* (2007) and Forcada *et al.* (2008). Two sampling locations were chosen in the reserve and included a site where fishing was completely prohibited (TB II), and a site where limited pound net fishing for silversides *Atherina* spp. and amberjack *Seriola dumerili* (Risso 1810) as well as trolling for *S. dumerili* were allowed (TB III). The third site was located offshore of Santa Pola (SP) and experienced heavy fishing pressure from bottom trawlers and purse seines (Forcada *et al.*, 2010).

Underwater sampling *via* haphazard roving video transects was used to document *M. surmuletus* assemblages at study sites (see Video S1, Supporting information). Two observers snorkelled a parallel along-shore transect (0.5–1.5 m depth; 300–400 m in length), and diverted to follow any solitary *M. surmuletus*, *M. surmuletus* groups (homoaggregation) or *M. surmuletus* and attendant species groups (heteroaggregation). During an encounter, observers conducted a 1 min focal-follow and recorded the assemblage composition, size and behaviours as well as underlying benthic habitat with a video camera (Panasonic Pro AG-DVC30 3-CCD MiniDV Camcorder with 16x Optical Zoom, NTSC; www.panasonic.com). During observations, the video camera was held c. 1–2 m away from the fish shoal. Each transect survey generally lasted 1.0–1.5 h for a total of 12.2 h in 11 surveys. All underwater surveys were conducted from 3 to 11 September 2009, between 0930 and 1830 hours local time, under clear skies and sunny conditions.

Videos were analysed in the laboratory for the presence of aggregating species with the behaviours of all individuals (*M. surmuletus* and aggregates) in the assemblage documented. During this interval, *M. surmuletus* and other aggregates were enumerated and the presence and absence of five main behaviours was recorded by two readers: (1) searching, exhibiting behaviours in search of food in the benthos (e.g. manipulating substrate with barbels); (2) feeding, visible ingestion of prey material, whether along the benthos or in the water column; (3) cruising, swimming in a single direction without any interaction with the benthos (*M. surmuletus* only); (4) resting, lying stationary on the benthos (*M. surmuletus* only); (5) following, moving in the same direction as the *M. surmuletus* (attendants only). Video readers also classified the underlying benthic habitat (<1 m radius of the event) from all observations into proportions of sand, rock, *Caulerpa prolifera*, *Cymodocea nodosa* or *P. oceanica*. For some statistical analyses, these values were used to create dominant habitat categories based on the substratum that encompassed >50% cover of the benthos during an encounter: (1) sand, (2) rock, (3) vegetated (*C. prolifera*, *C. nodosa* or *P. oceanica*) or (4) mixed, for instances in which none of the previous dominant habitats comprised >50% coverage.

Mullus surmuletus assemblage patterns were assessed using univariate and multivariate methods. First, a Kruskal-Wallis test was run on the numbers of attending species to assess variation in richness by habitat type. Multivariate methods were then used to assess compositional changes in species assemblages. For each observation involving a *M. surmuletus*, count data for all species within the assemblage were $\log_{10}(x + 1)$ transformed and used to develop a Bray-Curtis dissimilarity matrix. A two-way permutational analysis of variance (PERMANOVA) was used to assess differences by site (TB II, TB III and SP) and dominant benthic habitat. Since every habitat type was not available at all sites, this factor was nested within site and thus considered a random factor in the PERMANOVA. Pairwise comparisons were conducted for significant factors where $\alpha < 0.05$ to determine the source of fish assemblage variation. A similarity percentage (SIMPER) analysis was employed to identify the species driving the disparity among various levels of a factor.

To better identify substratum impacts on assemblages, benthic habitat composition data were normalized to build a Euclidean distance-based resemblance matrix to relate to the Bray-Curtis-based biological resemblance matrix. These data were exposed to a non-parametric form of a Mantel test (RELATE) to assess agreement in the multivariate pattern between matrices using a suite of random permutations. Following RELATE, a BEST analysis (i.e. Bio-env) was used to determine the habitats most greatly explaining fish assemblage patterns. Lastly, principal components analysis (PCA) was employed to visually represent the composition of benthic samples in multivariate space. All analyses were conducted in Primer V6 (www.primers-e.com).

Mullus surmuletus or *M. surmuletus* and aggregating species were encountered a total of 122 times, with the behaviour of 446 total fishes observed. *Mullus surmuletus* were 10–16 cm total length (L_T) (i.e. sub-adults) and observed as solitary individuals (26%), homoaggregations (9%), and predominantly heterospecific aggregations (65%). Homoaggregations generally included two individuals, though there were single instances of 20 and 25 *M. surmuletus*. Heterospecific aggregations were generally led by a solitary *M. surmuletus* (75%), followed by pairs (15%), groups of three (8%) and a single instance of four individuals. Aggregation characteristics varied by habitat type; homoaggregations were mainly observed over sand (63%), whereas solitary *M. surmuletus* and particularly heteroaggregations were more common in

all other habitat types. Solitary and homoaggregated *M. surmuletus* behaviours were dominated by feeding (30 and 33%) and searching (46 and 47%), but were additionally encountered resting (2 and 7%) and cruising (22 and 13%). *Mullus surmuletus* in heteroaggregations were only observed feeding (46%) and searching (54%).

Over half (65%) of the *M. surmuletus* observations involved at least one attendant species, and included as many as five species at a time. Attendant richness was significantly affected by dominant benthic habitat (Kruskal-Wallis Test, $H = 14.952$, $P < 0.01$). Dunn's multiple comparisons revealed significantly lower numbers of attendant species in sand (mean \pm s.e. = 0.4 ± 0.5 species) compared to rock (1.0 ± 0.15 species; $Q = 2.872$, $P < 0.05$), vegetated (0.8 ± 0.12 species; $Q = 2.872$, $P < 0.05$) and mixed (1.1 ± 0.12 species; $Q = 2.872$, $P < 0.05$) habitats. Throughout the study period, seven total attendant fish species were observed with *M. surmuletus*, which included representatives from the families Labridae ($n = 3$), Sparidae ($n = 3$) and Serranidae ($n = 1$). Overall, the most commonly observed attendant species was Mediterranean rainbow wrasse *Coris julis* (L. 1758) (34%), followed by two-banded seabream *Diplodus vulgaris* (Geoffroy Saint-Hilaire 1817) (27%), peacock wrasse *Symphodus tinca* (L. 1758) (22%), white seabream *Diplodus sargus* (L. 1758) (9%), and three species that were only observed once: painted comber *Serranus scriba* (L. 1758), red porgy *Pagrus pagrus* (L. 1758) and ornate wrasse *Thalassoma pavo* (L. 1758) (collectively 2.5%).

Mullus surmuletus was observed feeding in 70% of the encounters (Table I). *Mullus surmuletus* fed the least (61% of observations) and cruised the most (16% of observations) in rocky habitats, and was observed feeding the most in vegetated habitats (85% of observations). Collectively, attendant species were observed feeding 30% of the time (Table I). *Symphodus tinca* was the species most commonly observed feeding (36%), followed by *D. sargus* (25%), *D. vulgaris* (22%) and lastly *C. julis* (16%). Attendants rarely searched for food themselves (<1% of observations) and followed *M. surmuletus* in >90% of the observations.

Mullus surmuletus assemblages were consistent across sites (PERMANOVA, $F_{2,121} = 1.3434$, $P > 0.1$), although significant variability was observed by dominant benthic habitat (PERMANOVA, $F_{7,121} = 3.3546$, $P = 0.001$). Subsequent pairwise comparisons indicated that habitat effects were evident at TB III and SP (Table II). At both sites, significant differences in assemblages were observed between sand and vegetated habitats, which SIMPER analysis showed to be driven by higher amounts of *M. surmuletus* on sandy habitats and *S. tinca* on vegetated habitats. Both sites also demonstrated significant differences between vegetated and mixed habitats, again mainly driven by higher amounts of *S. tinca* on vegetation, but also *D. vulgaris* on mixed habitats. At TB III, significant assemblage differences were observed between sand and rock habitat, as well as sand and mixed habitat. Rocky habitats were mainly characterized by higher proportions of *S. tinca*, as well as contributions from *C. julis*, *D. sargus* and *D. vulgaris*. Mixed habitats had higher proportions of *D. vulgaris* and *C. julis* than sand.

Statistically significant agreement was found between fish assemblage and benthic composition resemblance matrices (RELATE test, $\rho = 0.101$; $P < 0.01$). The subsequent BIO-ENV test found that the combination of sand and *C. prolifera* ($\rho = 0.142$) provided the highest Spearman rank correlation value among the possible combinations of the five variables. PCA qualitatively confirmed this result (Fig. 1), as overlays of the fish assemblage data on the PCA scatterplot demonstrated a shift from

TABLE 1. Frequency of occurrence of behaviours for the top five species observed in heteroaggregations. For each species, the sample size (n) of observations is provided for all encounters (overall) and per habitat type






Species	Behaviour	n	Habitat				
			Overall	Sand	Rock	Vegetated	Mixed
<i>Mullus surmuletus</i> 	Resting	122	25	44	13	40	
	Cruising	0.02	0.04	0.00	0.00	0.03	
	Searching	0.10	0.04	0.16	0.00	0.10	
	Feeding	0.87	0.80	0.89	0.85	0.90	
<i>Coris julis</i> 	Feeding	0.70	0.76	0.61	0.85	0.73	
	Following	42	3	22	2	15	
	Searching	0.95	1.00	0.91	1.00	1.00	
	Feeding	0.00	0.00	0.00	0.00	0.00	
<i>Symphodus tinca</i> 	Feeding	0.17	0.00	0.23	0.00	0.13	
	Following	27	1	10	8	8	
	Searching	0.93	0.00	1.00	1.00	0.88	
	Feeding	0.04	0.00	0.00	0.00	0.13	
<i>Diplodus vulgaris</i> 	Feeding	0.37	1.00	0.30	0.38	0.38	
	Following	25	5	6	0	14	
	Searching	0.92	0.80	0.83	–	1.00	
	Feeding	0.04	0.00	0.00	–	0.07	
<i>Diplodus sargus</i> 	Feeding	0.24	0.20	0.33	–	0.21	
	Following	8	0	4	0	4	
	Searching	1.00	–	1.00	–	1.00	
	Feeding	0.13	–	0.00	–	0.25	
		0.25	–	0.00	–	0.50	

TABLE II. Pairwise comparisons between dominant habitats from two-way nested permutational analysis of variance. The highest contributing species (from similarity of per cent contribution analysis) for each significant pairwise comparison is listed with its associated habitat

Site	Habitat 1	Habitat 2	<i>t</i>	<i>P</i> (perm)	Unique perms	Contributing species (%)	Group
TB III	Sand	Rock	2.046	0.009	908	<i>Symphodus tinca</i> (33.34)	Rock
	Sand	Vegetated	2.174	0.018	77	<i>Symphodus tinca</i> (72.92)	Vegetated
	Sand	Mixed	2.673	0.001	972	<i>Diplodus vulgaris</i> (39.68)	Mixed
	Rock	Vegetated	1.158	0.333	127	–	–
	Rock	Mixed	1.662	0.065	981	–	–
	Vegetated	Mixed	2.389	0.006	159	<i>Symphodus tinca</i> (54.72)	Vegetated
SP	Sand	Vegetated	3.082	0.001	577	<i>Symphodus tinca</i> (61.20)	Vegetated
	Sand	Mixed	0.911	0.513	570	–	–
	Vegetated	Mixed	2.510	0.011	522	<i>Symphodus tinca</i> (71.55)	Vegetated

Bold values are significant at $P < 0.05$.

M. surmuletus dominated assemblages in 100% sand habitats to assemblages dominated by *D. vulgaris* and *D. sargus* along intermediate (mixed) habitats, and *S. tinca* dominated assemblages in higher percentages of *C. taxifolia*. Rock-dominated habitats were characterized by consistently diverse assemblages, with nearly all attendant species observed there. While not typically observed in numbers as high as *S. tinca* when encountered, *C. julis* was the most frequent attendant in rocky habitats (50% of encounters).

The observations of heterospecific aggregations led by *M. surmuletus* confirm previous reports of these assemblages elsewhere in the Mediterranean Sea (De Pirro *et al.*, 1999; Tipton, 2008). The attendant species most likely form these heteroaggregations due to increased food availability; heteroaggregations were only observed when *M. surmuletus* was actively excavating or feeding along the benthos. Interestingly, despite the high occurrence of these aggregations, common attendant species were only observed feeding 17–37% of the time. This observation suggests that attendants may be selective in their prey choice while attending *M. surmuletus*, or that there are additional reasons for attendants to form heteroaggregations such as an antipredator behaviour (Lukoschek & McCormick, 2000). Further field and laboratory studies are clearly needed to better understand the nature of this relationship as the present study period was temporally restricted and habitats were not evenly sampled.

As far as is known, this is the first attempt to quantify *in situ* associations of *M. surmuletus* and attendant species across a continuum of habitat types. The findings suggest that this is a dynamic aggregation, with species membership potentially driven by the proportion of underlying sand and vegetated (*i.e.* *C. prolifera*) substratum. In the western Mediterranean Sea, elevated habitat complexity appears to disperse *M. surmuletus* homoaggregations and increase the occurrence of attending *S. tinca* in areas of high rock or vegetation cover, while aggregations over more mixed benthic mosaics appear to be driven by *D. vulgaris*. As such, *M. surmuletus* probably plays a large role in mediating habitat connections between bare substrata and more complex habitats in this region. More long-term tracking approaches are needed to support this notion as the present study monitored individuals for very short periods (1 min).

Mullus surmuletus sandy habitat homoaggregations and foraging observations further emphasize this species' adaptation for feeding in these softer substrata where

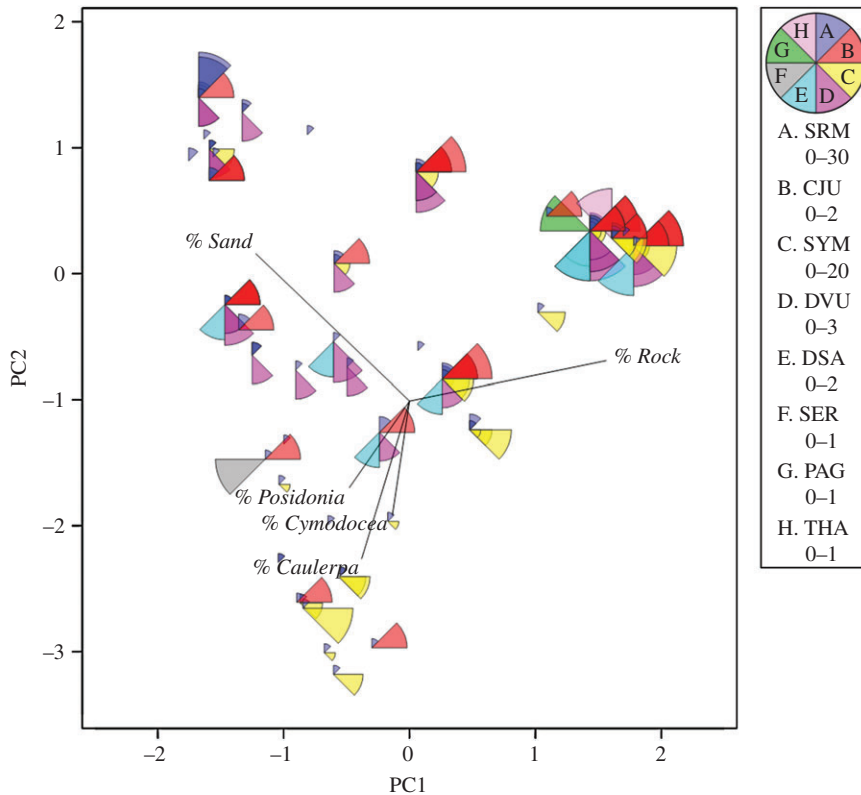


FIG. 1. Principal components analysis showing the distribution of samples based on benthic habitat composition. *Mullus surmuletus* (SRM) assemblages are overlain as pie charts on the plot, with a colour code for species: CJU, *Coris julis*; SYM, *Symphodus tinca*; DVU, *Diplodus vulgaris*; DSA, *Diplodus sargus*; SER, *Serranus scriba*; PAG, *Pagrus pagrus*; THA, *Thalassoma pavo*.

sensory barbels can deeply penetrate the benthos and probably best detect prey (De Pirro *et al.*, 1999). Homoaggregations, while the rarest of the three aggregation types observed, are hypothesized to maximize foraging efficiency, vigilance (*i.e.* antipredator strategy) and spawning activities (Helfman *et al.*, 1997). As *M. surmuletus* were encountered in other types of habitats such as rocky or vegetated bottoms, attendant richness significantly increased. These more speciose aggregations could be a response to the ambient diversity of fishes associated with more complex habitats as documented elsewhere (Friedlander & Parrish, 1998; Gratwicke & Speight, 2005; Kovalenko *et al.*, 2012). Concurrent abundance surveys of all species, stratified by benthic habitat, could help better clarify the role of ambient attendant densities in forming heteroaggregations.

The efforts here represent an important initial step in defining trophic linkages between a heavily targeted fishery species, *M. surmuletus*, and other components of Mediterranean nearshore ecosystems. As such, these data should prove useful to resource managers interested in implementing ecosystem-based approaches. At least seven different species appear to interact with *M. surmuletus* in these shallow coastal waters. Moreover, the high proportion of heteroaggregations across several

habitats suggests that *M. surmuletus* may have considerable ecological importance to this region. While overall attendant richness was lower than described in analogous mullid assemblages in tropical ecosystems (Lukoschek & McCormick, 2000; Sazima *et al.*, 2006), it is worth noting that three of the attending species observed are also locally exploited: *D. vulgaris*, *D. sargus* and *P. pagrus*. In conclusion, the dynamical nature of *M. surmuletus* assemblages and foraging behaviour with substratum type reinforces the need for benthic habitat composition to be considered when developing management plans for highly interactive demersal species like *M. surmuletus*.

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Supporting Information

Supporting Information may be found in the online version of this paper:
Video S1. Underwater video of a heteroaggregation led by striped red mullet (*Mullus surmuletus*) off Tabaraca, Spain.

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