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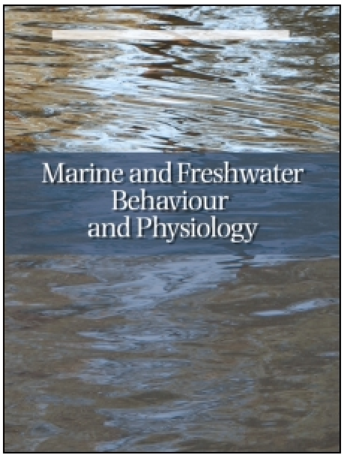

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Short Communication

DIFFERENCE IN SHOALING BEHAVIOUR BETWEEN OCELLATED (*SYMPHODUS OCELLATUS*) AND LONG-STRIPED (*S. TINCA*) WRASSES AND ITS RELATION TO OTHER BEHAVIOURAL PATTERNS

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Shoaling behaviour in fishes is acknowledged as an important adaptive mechanism (Radakov, 1972; Magurran, 1990; Pitcher and Parrish, 1993), and its benefit as a defence against predators is particularly well documented (see Magurran, 1990, for a review). However, as in other behavioural strategies, shoaling may have associated costs, namely increased competition for limited resources and, possibly, manipulation by conspecifics (Pitcher and Parrish, 1993; Metcalfe and Thomson, 1995).

In the present article we document differences in shoaling behaviour between two species of wrasses (*Symphodus* genus, Teleostei: Labridae) – ocellated, *S. ocellatus* Forskål and long-striped, *S. tinca* (L.). These fishes are common inhabitants of shallow waters throughout the Black Sea. Both maintain territories only during the reproductive period (Mochek, 1987),

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feed on benthos (mainly Harpacticoida and various molluscs) and exhibit pronounced niche overlap (e.g. Duka and Gordina, 1971, reported that they share as much as 86% of prey species at the age 1+). However, the body length of adult individuals of the long-striped wrasse is two to three times larger than that of the ocellated wrasse (Svetovidov, 1964). Such differences in the body size can lead to different costs and benefits of shoaling behaviour (Werner and Gilliam, 1984). Indeed, it has already been found (e.g. Mochek, 1987; Mochek and Budaev, 1993) that the long-striped wrasse is much less likely to shoal than the ocellated wrasse. In the present study we document further differences in shoaling and, more importantly, examine the correlations between shoaling and other behaviours to ascertain whether the two species employ dissimilar behavioural tactics, presumably to achieve the necessary balance between feeding and avoiding predators. However, the predation pressure has become low for both species during the last few decades, and such predators as large comber (*Serranus scriba*), elf (*Pomatomus saltatrix*) and predatory turbot (*Scophthalmus maeoticus macoticus*) are now rare. Despite this, anti-predator behaviour is typically very conservative and remains unchanged long after the predation stress has diminished (Magurran, 1990).

The observations took place during the non-reproductive period (July–August 1992) around the location of Maliy Utrish biological station (Black Sea, Northern Caucasus). The main study area was a gently sloping shallow area covered by dense weeds (mainly *Cistoseira* sp.) from 2 to 7 m depth. All underwater observations were made using a video camera operated by an experienced SCUBA diver. The observer, swimming quietly along a shore, selected one individual wrasse, immediately turned on his video camera-recorder and followed the fish for, approximately, 2 min. Unfortunately, it was generally impossible to trace the fish for longer periods of time as they sometimes swam out of the field of view of the camera and the observer tended to avoid sharp movements of the camera (all unusually short observations were discarded, resulting in the minimum observational period of 1.5 min). Also, one may expect the fish to be more afraid of an exceedingly tenacious observer, and individuals which do not permit observation over a long period would be perhaps more fearful. Because shyness is related to a higher schooling tendency (Budaev, 1997), very long observations would lead to biased data.

We were forced to be opportunistic in our haphazard selection of individuals, so the most fearful fish may have been under-represented in the data. However, the wrasses never demonstrated apparent fear or avoidance of the observer, as indicated by gathering to a polarised school, clear interruption of foraging, jerking or freezing when the diver approached (perhaps because skin-divers are quite common in this habitat and neither of the two species is an object of fishery or hunting). Yet, we cannot rule out more subtle changes in their behaviour (see below).

All observations were made between 10:00 and 13:00 h when both wrasses were most active in terms of locomotion and foraging (Budaev, personal observations). At other times of the day both species are usually less active, although the between-species differences in shoaling remain unchanged (Mochek, 1987; Mochek and Budaev, 1993). For example, while the ocellated wrasse typically form relatively large shoals (20–100 individuals), only singletons or small shoals (not more than 5 individuals) of the long-striped wrasse are usually observed (Mochek, 1987; Mochek and Budaev, 1993; Budaev, personal observations). To minimise possible artefacts, we recorded the behaviour of both species of wrasses in a randomized order during each particular diving session, and only one individual was selected from each shoal. In total, we observed 23 ocellated and 25 long-striped wrasses.

Later, the behaviour of fish was transcribed from the TV screen and ciphered onto a personal computer using specially written software which accepted keystrokes as codes for particular behaviour patterns (Budaev, 1995). The following behaviours were easily distinguishable on the TV monitor and recorded (percentages of the total time were analysed): (1) active locomotion (swimming), (2) obvious feeding on benthos, and (3) hiding in shelters and among weeds. Holding station in midwater was also recorded, but not included in the present analysis since it was not so easily interpretable. In addition, 3–4% of the total time the observed individuals swam behind various obstacles, such as weeds, which was recorded as 'not seen' (there was no significant difference between species in this variable: Mann–Whitney test, $U = 249$, $p = 0.4$).

The gross percentages of time that individual fish spent in shoals, i.e. within 0.5 m of other conspecifics, were also recorded. This distance corresponded to approximately 3 body lengths of the long-striped wrasse and 6 body lengths of the ocellated wrasse, and was the distance at which the shoal, from which the observed individual dropped out, shifted from the TV monitor as the video camera moved following the fish. That the criterion for shoaling was different for the two species when expressed in the body length was rather unimportant in the present investigation because, when leaving shoals, individuals of both species swam for the most time at much larger distances from other conspecifics (no shoal was seen on the monitor). The inverse of schooling, the time spent alone, was defined as

100% minus the time spent in shoals minus the time spent hiding. It was highly correlated with schooling in the ocellated wrasse ($R_s = -0.91$, $t_{21} = 10.13$, $p < 0.0001$) but not in the long-striped wrasse ($R_s = -0.28$, $t_{23} = 1.38$, $p = 0.18$).

The size of the observed fish was also measured directly on the TV monitor. Thus measured, fish size depends on the distance from fish to the camera. For example, a fish swimming closer to the observer would appear larger on the TV screen. This potential source of error made it impossible to conduct an analysis of intraspecific correlations between fish size and behaviour, but did not preclude the comparison of the average size of the two species (provided they swam, on average, at the same distance from the observer, which was roughly the case). Unfortunately, it was not possible to determine the sex of the observed fish. The Mann–Whitney U test and Spearman's correlation coefficient (Sokal and Rohlf, 1981) were used for the statistical analyses. The statistics are expressed in sequel as mean ± standard error.

As the measurements of the body length revealed, individuals of the long-striped wrasse were significantly larger than ocellated wrasse (respectively 15.4 ± 0.7 cm and 7.6 ± 0.2 cm, Mann–Whitney test, $U = 5$, $p < 0.0001$). Also, the behaviour of the two wrasse species differed markedly. While the ocellated wrasse frequently formed relatively large shoals (20–50 individuals), only singletons or small shoals (not more than 5 individuals) of the long-striped wrasse were observed. Furthermore, long-striped wrasses shoaled for much less time than ocellated wrasses, the differences being highly significant (see Table I). The former species also showed significantly higher tendency to hide in weeds and devoted much less time to obvious feeding.

Shoaling and feeding were highly positively correlated while shoaling and hiding were negatively correlated in the ocellated wrasse (see Table II). Long-striped wrasses showed a different pattern – significant positive

TABLE I The differences in behaviour between the two wrasse species. Individual behaviour patterns are expressed as percentages of the total time observed

Behaviour pattern	*S. ocellatus* ($N = 23$)	*S. tinca* ($N = 25$)	*Mann–Whitney test*	
			U	*p*
Shoaling	71.6 ± 5.9	3.6 ± 1.7	18	< 0.0001
Alone	15.7 ± 4.5	51.4 ± 4.0	65	< 0.0001
Swimming	36.0 ± 3.6	22.7 ± 2.7	149	0.004
Hiding	11.0 ± 2.1	42.4 ± 3.9	40	< 0.0001
Feeding	37.7 ± 4.9	10.8 ± 2.4	121	0.0006

TABLE II Spearman rank correlation coefficients between individual shoaling tendencies (the percentage of time spent in shoals) and other behavioural units

Behaviour pattern	R_s	t	p
S. ocellatus ($N=23$)			
Swimming	−0.28	−1.35	0.193
Hiding	−0.76	−5.34	< 0.0001
Feeding	0.70	4.47	< 0.0001
S. tinca ($N=25$)			
Swimming	0.46	2.50	0.020
Hiding	−0.12	−0.56	0.582
Feeding	−0.07	−0.32	0.748

correlation ($R_s = 0.62$, $t_{23} = 3.83$, $p < 0.001$) between feeding and the time spent alone. The time spent alone was analysed in the latter species, because it accounted for the large proportion of time hiding (but did not correlate well with the time schooling, see above): it was unclear whether the fish fed while hiding or not. There was also a significant, although moderate, positive correlation between shoaling and active swimming in the long-striped wrasse. Ocellated wrasses exhibited an opposite, albeit nonsignificant trend.

Pronounced variability (0–100% of time in shoals) of shoaling behaviour was observed in the ocellated wrasse, suggesting an equilibrium between shoaling and solitary strategies (see Budaev, 1997). However, this was not characteristic for the long-striped wrasse, in which the percentage of time spent shoaling ranged from 0% to 32%.

Our present data confirm the results of Mochek (1987) and Mochek and Budaev (1993), in that the ocellated wrasse exhibits a much more pronounced tendency to shoal than the long-striped wrasse. Furthermore, it was found that the relationships between shoaling and other behaviours differ in these two species.

What possible adaptive mechanisms favour the differences in behaviour between the two species of wrasses? Obviously, body size may play an important mediating role and, indeed, the size difference itself may evolve as a part of the overall adaptive strategies. As a rule, smaller fish have higher vulnerability to potential predators (Peters, 1983; Werner and Gilliam, 1984; Werner and Hall, 1988) and therefore anti-predator benefits of shoaling would be more important for the ocellated wrasse. In addition, competition for food resources may be more intense among larger individuals (Weatherley, 1972; Peters, 1983), which would increase the cost of shoaling for the long-striped wrasse, even though it might be balanced in some circumstances by easier detection of more profitable food patches due to the 'many eyes' of the shoal members (Pitcher *et al.*, 1982; Clark and Mangel, 1986). Furthermore, the low percentage of both shoaling and ostensible feeding in the long-striped wrasse might suggest that the large amount of time these fish were hiding in weeds helped them to conceal possible profitable patches from competing conspecifics, rather than serving an anti-predator function.

The shoaling behaviour of the ocellated wrasse thus bestows a relatively higher anti-predator benefit and results in a lower probability of resource competition. The behaviour of the long-striped wrasse, on the other hand, shows a reverse pattern. However, the profound variability of shoaling behaviour in the ocellated wrasse would indicate that there may still be certain benefits of being solitary, even in this smaller fish, and that it is close to a pay-off equilibrium between the solitary and schooling strategies. Furthermore, no significant differences in size between the solitary and schooling ocellated wrasses have previously been found (Budaev, 1997).

The high correlation between shoaling and feeding that is characteristic of the ocellated wrasse may provide a good illustration of the anti-predator advantages of shoaling. Namely, that individuals can reduce the amount of time spent being vigilant and devote more time to feeding. Similarly, the inverse correlation between shoaling and hiding agrees with the typical observation when a normally shoaling fish drops out of a shoal, it is likely to hide and remain relatively immobile, because it would be exposed to a greater risk of being eaten (Magurran and Pitcher, 1987). In contrast, individuals of the long-striped wrasse strongly preferred to forage alone, suggesting that shoaling might indeed increase the probability of food competition. The positive correlation between shoaling and active locomotion observed in this species is also worth noting. This would imply that, when explicit competition is not primarily involved, the anti-predator and, possibly, patch detection benefits of shoaling may still remain crucial. We cannot rule out the possibility that individuals of the long-striped wrasse respond to the diving observer as to a potential predator (although strong avoidance responses were not observed, see above). In this case shoaling is the appropriate adaptive response to the immediate threat (e.g. Magurran and Pitcher, 1987).

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