

Impact of a predator in the foraging behaviour of *Solea senegalensis*

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*Habitat modelling requires incorporation of both biotic and abiotic information. For juvenile flatfish the factors that most influence growth are water temperature, food abundance and predatory pressure. This study focuses on the impact the predator, the shore crab, *Carcinus maenas*, has on the foraging activity of sole, *Solea senegalensis*. The results show that in the presence of both prey (ragworm, *Nereis diversicolor*) and predator, $\approx 10\%$ decrease in foraging activity is observed when compared to the sole in the presence of only food. This suggests that when the shore crab is present, Senegalese soles are not only affected by direct predation but sub-optimal foraging is also found. Behaviours most correlated with foraging were crawling and tapping and these activities were also affected by the presence of the predator. This study also provides further support for visual recognition of predators and olfactory prey recognition in the Senegalese sole. Predator–prey encounters shape species behaviours profoundly and have to be looked at from different levels of ecology, behaviour and modelling.*

Keywords: *Carcinus maenas*, foraging, predator–prey, *Solea senegalensis*

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INTRODUCTION

Predator–prey interactions are commonly addressed through stomach content analyses and also predator–prey densities. However, little is known how the presence of a predator affects behaviour and induces foraging in sub-optimal habitat. Suitable habitats in estuarine systems high in prey abundance and lacking strong predatory pressures are rare, hence the predatory impact on prey to habitat usage, namely by foraging rate decrease, must be taken into account in habitat modelling.

For flatfish the key factors affecting growth and survival of juveniles are water temperature, food abundance and predation pressure (Gibson, 1994). Several studies have focused on the behaviour of flatfish in their natural conditions (e.g. Van der Veer & Bergman, 1987; Cabral & Costa, 1999; Cabral, 2000; Amezcua & Nash, 2001) and also under experimental conditions (Ansell & Gibson, 1993; Burrows & Gibson, 1995; Gibson *et al.*, 1995; Aarnio *et al.*, 1996; Fairchild & Howell, 2000; Kellison *et al.*, 2000; Hossain *et al.*, 2002; Taylor, 2004, 2005; Breves & Specker, 2005; Lemke & Ryer, 2006). However, none were able to quantify the impact of the presence of a predator on the feeding rate.

Predation is now recognized as one of the main factors influencing prey behaviour (review in Lima, 1990) and predator avoidance is known to lead to changes in the use of habitat, feeding, morphology and growth of prey (Jones & Paszkowski, 1997; Turner *et al.*, 1999). Also, despite the obvious fitness benefits of prey ingestion, antipredator behaviours can be

costly, negatively impacting activities such as feeding and breeding (Wong *et al.*, 2005). For plaice, *Pleuronectes platessa* L., predation by the crustaceans *C. crangon* and *Carcinus maenas* (L.) have been identified as key factors in regulation of density within the nursery areas (Van der Veer, 1986; Van der Veer & Bergman, 1987; Van der Veer *et al.*, 1990).

The Senegalese sole, *Solea senegalensis*, Kaup 1858, is a benthic fish distributed from the Bay of Biscay to Senegal and the western Mediterranean (Quero *et al.*, 1986). It is a species of increasing interest in aquaculture and is commonly cultured on the Portuguese and Spanish southern coasts (Dinis *et al.*, 1999). The ragworm, *Nereis diversicolor* is a common prey of *S. senegalensis* (Cabral, 2000). Habitat suitability index (HSI) models that included abiotic factors and polychaete abundance were the best predictors for this species distribution in the Tejo Estuary (Vinagre *et al.*, 2006b). Not much is known about the behaviour of this species (Cabral *et al.*, 2007) that is expanding its ranges north and possibly outcompeting *Solea solea* for resources (Desaunay *et al.*, 2006; Vasconcelos *et al.*, 2008). *Solea senegalensis* has further advantage over *S. solea* since both its growth and metabolic rates are higher (Vinagre *et al.*, 2007, 2008).

The first year of life is a key stage in fish development, particularly for species, like the soles, where large densities in estuarine and coastal nurseries are common and thus competition for space and food is problematic (e.g. Schoener, 1974; Ross, 1986).

The portunid shore crab *Carcinus maenas* (Linnaeus, 1758) has a wide distribution in coastal and estuarine shallow waters of temperate areas (Udekem d'Acoz, 1993). The shore crab preys heavily on juvenile Senegalese sole in Portuguese estuaries (Cabral, unpublished data) where they cohabit (Vinagre *et al.*, 2006a).

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This study focuses on 0-group juveniles of Senegalese sole, since this is when the individuals are most susceptible to shore crab predation and it is also when natural mortality is most common (Houde, 1987). It aims to investigate the interaction of the juvenile Senegalese sole with its natural predator shore crab and assess its impact on the sole's foraging behaviour.

MATERIALS AND METHODS

Eight month old juvenile Senegalese soles, *Solea senegalensis*, were used in this experiment from a hatchery (CRIP-Sul Aquaculture station, Portugal). Shore crabs, *Carcinus maenas*, were caught by trawl in the Tejo Estuary, Portugal (38°40'N 9°00'W) where they naturally co-occur with this species of sole. Ragworms, *Nereis diversicolor* Müller, 1776 were reared in aquaria at the laboratory.

Fish were kept in 160 l aquaria equipped with mechanical and biological filter units. Temperature was kept at $25 \pm 0.1^\circ\text{C}$ and salinity was $35 \pm 0.1\text{‰}$. These variables were monitored daily and fish were exposed to a 12:12 day/night cycle.

Prior to the experiment there were 45 hours of *ad libitum* observations to determine the baseline behaviours. Active behaviours included crawling on the substrate, swimming, 'head-up' movement, eating, rapid escape, tapping and burrowing. Crawling is characterized by the individual moving over the substrate keeping the body in contact with it; while in swimming, the individual moves by undulating its body, without touching the substrate. In the 'head-up' movement the individual lifts its head while remaining on the substrate. Burrowing is characterized by rapid undulation of the body in an attempt to bury itself. Rapid escape occurs when the individual dashes away from a threat and it is characterized by a strong acceleration. In tapping, the individual taps its head several times on the substrate. And finally, eating for this study included the time when the fish was biting or chewing food items.

For the behavioural experiments, fish were transferred into experimental aquaria (50 × 25 × 30 cm) (Figure 1). Soles used in this experiment ranged in size from 65 to 132 mm TL, averaging 94.9 mm. All soles were conditioned, two days

earlier, with 48-hour fasting, freely moving shore crab. They were therefore accustomed to this predator. They were also acclimatized to the experimental tank for a week where they were fed normally. Right before the experiment soles were subjected to a 24 hour fasting period.

For prey simulation, living ragworms were used, since this is one of their favourite prey items (Cabral, 2000) and soles had been reared with this diet.

Crabs ranged in size from 46 to 70 mm carapace width, with an average size of 55.2 mm and were subjected to 48-hour fasting prior to the experiment.

Four different treatments were used, termed: negative, interaction, positive or control treatments, considering food a positive stimulus and predator a negative one.

The negative treatment had one crab in the smaller compartment (Figure 1, compartment A) and one sole in the larger compartment (Figure 1, compartment B). The two compartments were separated by a fine mesh net, so the crab could not touch the sole.

In the interaction treatment there was one crab in the smaller compartment and one sole and one ragworm in the larger compartment. The ragworm was placed closer to the net.

The positive stimulus had no crab on the small compartment and ragworm and sole on the larger compartment. The control treatment included just the sole on the larger compartment. Each treatment had at least 12 replicates. To make sure the net was not a source of variability, the negative treatment was repeated 6 times with the crab and the sole on the same side of the net and no differences were found.

Observations were carried out for 10 minutes without stimulus and 30 minutes with stimulus, starting at dusk and under red dim light. The observer was positioned in a shadow corner. However, in order to accommodate for observer's disturbance the analysis was always compared with the pre-stimulus situation. These conditions were chosen based on other experiments conducted in Senegalese sole (Pais *et al.*, 2004) that show the species to be more active and to forage mostly at dusk. Every individual was used only once to avoid learned behaviours.

Per cent baseline activity for each individual was subtracted from the post-stimuli activity to accommodate for individual variability and analysed using the Mann-Whitney *U*-test.

Mean percentage of time spent in each of the seven most common behaviours and mean frequency (times per minute) was obtained for the four treatments. Due to non-uniformity of data and high variance, non-parametric ANOVA was used to test for differences in the treatments using both time and frequency of the most common behaviours.

RESULTS

The Senegalese sole spent a majority of its time in resting behaviour. Only 6.5% of activity was observed in the control group (Figure 2).

A decrease in the overall activity of soles was observed in the presence of shore crab and ragworm by 10% (Figure 2, $H(3, N = 80), P = 0.0096$), similar to the activity in the presence of only shore crab. Also significant, was the number of rapid escapes in the presence of crab, especially in the absence

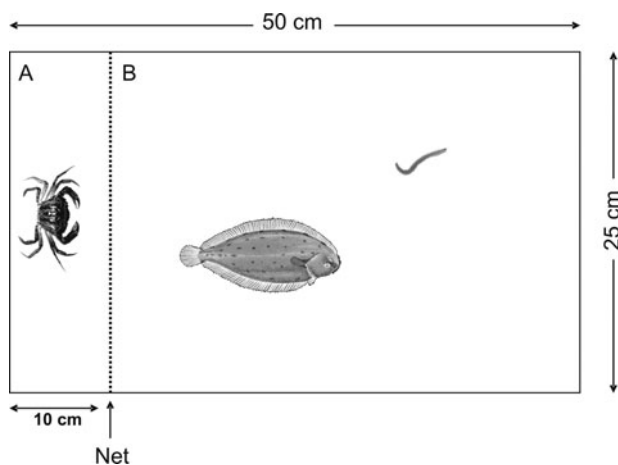


Fig. 1. Schematic representation of experimental setup. The negative stimulus, shore crab, *Carcinus maenas* was kept in compartment A, while Senegalese sole, *Solea senegalensis* and ragworm, *Nereis diversicolor* (positive stimulus) were in compartment B.

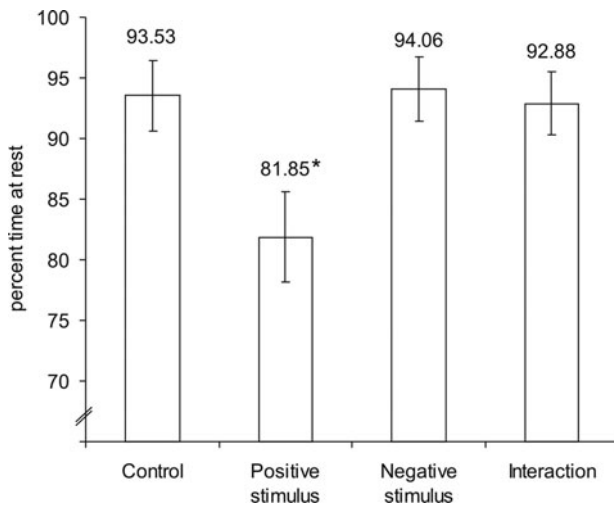


Fig. 2. Per cent time spent resting by Senegalese soles for the different treatments (control, positive stimulus, interaction and negative stimulus); whiskers represent standard error.

of ragworm ($H(2, N = 60), P = 0.0032$). On the contrary, tapping only occurred in the presence of prey (Figure 3, $H(2, N = 60), P = 0.014$).

When food was present and the predator was absent time spent crawling and burrowing was greater (Figure 3, $H(3, N = 80), P = 0.0042$) than in the control.

In terms of variation in activity prior and after stimulus, it can be observed that the negative stimulus is correlated with an overall decrease in activity; while the positive stimulus is associated with an increase in activity by 8% on average ($H(2, N = 17), P = 0.003$).

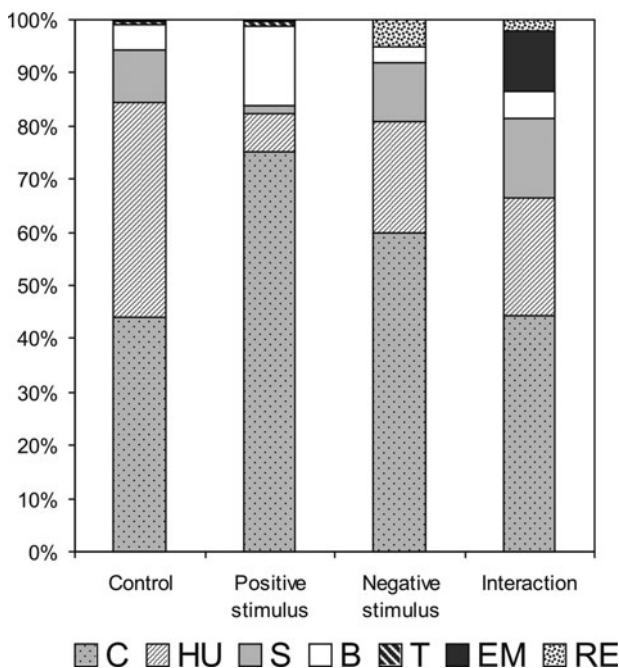


Fig. 3. Time (in percentage of total observed time) that Senegalese sole spent in each active behaviour (C, crawling; HU, head up; S, swimming; B, burrow; T, tapping; EM, eating movements; RE, rapid escape) for the four different treatments (control, positive stimulus, interaction and negative stimulus).

DISCUSSION

Low activity levels observed in this study are not surprising since soles are known to have a strong relationship with the benthos (De Groot, 1971). Furthermore, the great majority of flatfish have a low aerobic muscle content and low metabolism (Turner *et al.*, 1983).

Of the foraging behaviours observed, crawling, burrowing and tapping were the most frequent in the presence of food. Crawling was also related to the presence of predator and, this behaviour together with rapid escape and swimming, represents the typical predator avoidance behaviour. Less frequently, the sole attempted to bury itself to avoid the predator.

It was not possible to exactly ascertain if predator recognition was visual, chemical or both. However, all naïve soles were successful in avoiding predator attacks. Also the 'crab over fence' setup elicited predator-like escape behaviour, thus dismissing tactile recognition. In a study directed to investigate the feeding stimuli, De Groot (1971) found that the presence of an 8 cm ball elicited a flight response by the common sole, *Solea solea* (Linnaeus, 1758), suggesting visual predator recognition is important. It was also noted that an attack is not necessary to elicit rapid escape behaviour by the common sole and presence alone is enough to initiate this behaviour. That, along with the findings of Appelbaum & Schemmel (1983) which concluded that chemoreception in *S. solea* is not as important as previously thought through histology, indicates that predator recognition must be mainly visual. The lateral line system has been suggested to also be important for foraging behaviour (Appelbaum & Schemmel, 1983) and cannot be discarded. However, a motionless crab over the fence still elicits responses, which at a range of 20 cm makes sensing by the lateral line unlikely.

This study also allowed some insight into what is the main foraging pattern of the Senegalese sole. Prey recognition seems olfactory, similarly to what has previously been described for *Solea solea* (De Groot, 1971; Harvey, 1996), since the individual will increase its activity in the presence of food, moving randomly to the prey, searching in the substrate, as seen by the increase in tapping behaviour in the presence of just food. The tapping movement in relation to foraging has also been previously described for *S. solea* (De Groot, 1971). This behaviour might increase water circulation around the individual enhancing prey detection. Also, since *Solea senegalensis* is morphologically very similar to *S. solea*, the presence of taste buds in the oral cavity, pharynx, gill rakers and lips (Appelbaum & Schemmel, 1983) and the tapping behaviour would strongly enable the chemical food detection. However, lateral line detection cannot be excluded until experiments targeting this sense are implemented for this species.

There is a quantifiable impact on the Senegalese sole foraging by the presence of a predator. The 10% decrease in activity puts the interaction sole-crab-worm close to the sole-crab situation. It is well documented that shore crab impacts the population of other juvenile flatfish, especially *Solea solea* and *Pleuronectes platessa* Linnaeus, 1758 (e.g. Modin & Pihl, 1994; Fairchild & Howell, 2000). Recent sampling by beam trawl in Portuguese estuaries where *S. senegalensis* occur has shown evidence of intense predation by this crab species. Even when other juvenile fish (*Diplodus* spp. and *Dicentrarchus* spp.) are present the shore crabs seem to attack preferentially the soles (personal observation).

Apart from the direct risk of predation, the trade-off between escape from a predator and foraging has to be taken into account. Suitable nursery grounds for sole in terms of water temperature, salinity and food supply in Portuguese estuaries are also the areas where the shore crab is more abundant (Vinagre *et al.*, 2006a, b; Cabral, unpublished data on crab density). It is also important to note that shore crabs are generalist feeders and thus likely to compete with soles for food resources such as polychaetes and amphipods (Cohen *et al.*, 1995).

The next step will be to adjust the existing habitat models to incorporate this interaction of predator–sole–prey. This information is of the uttermost importance for delimiting marine reserves, since shore crab is a species with very high reproductive potential (Cohen *et al.*, 1995), and their numbers would likely increase to pose an even higher threat to soles. Future studies should focus on the comparison of sites with different crab densities and cross that information with soles' stomach contents.

In addition, knowledge of predator–prey behaviour is important for the release of hatchery reared fish for stock enhancement purposes (Fairchild & Howell, 2000), which is a growing practice throughout the world.

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