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RESEARCH ARTICLE

The influence of prey density and fish size on prey consumption in common sole (*Solea solea* L.)

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Abstract – We examined the influence of prey density and fish size on prey consumption in common sole (*Solea solea* L.) foraging on buried ragworm *Alitta virens* (Sars) (formerly known as *Nereis virens* (Sars)). The tested prey densities of 0.8, 2.2, 4.3 and 6.5 individuals dm^{-2} were exposed to common soles of either 100 g or 300 g. At each prey density common sole foraged for 48 h. At both common sole classes studied, a positive correlation between prey consumption and prey density was observed ($P < 0.001$). Relationships however differed between 100 and 300 g common sole. In 300 g common sole the relationship between prey consumption and prey density was linear ($P < 0.001$), whereas in 100 g common sole the relationship between prey density and prey eaten was polynomial ($P = 0.018$). Small common sole reached satiety prey consumption rates at nearly every prey density while large common sole did not reach satiation rates even at highest prey densities. The data suggest that in nature, polychaetes such as *A. virens* may contribute to the diet of small common sole even when they are only moderately abundant. In contrast, polychaetes may not be an ideal prey for larger common sole as indicated by the absence of satiety regardless of prey density.

Keywords: *Alitta virens* / prey density / *Solea solea* / foraging / functional response

1 Introduction

Prey density may explain a considerable part of diet composition in opportunistic fish species. In fishes foraging on exposed prey (e.g. free swimming prey) the consumption of prey is positively correlated with prey density which has been confirmed in numerous studies for numerous species (Rice and Cochran, 1984). This correlation is explained by a decreased effort/time to search for prey at higher density. In contrast, the response of predator prey consumption towards densities of buried prey has received little attention and has mainly been studied in crabs foraging on bivalves. Density affected blue crab predation on a variety of bivalve species, including the soft clam, in Chesapeake Bay (Blundon and Kennedy, 1982; Lipcius and Hines, 1986). In contrast, density had no influence on prey consumption in lesser Scaup foraging on the clam *Macoma baltica* (Richman and Lovvorn, 2004).

In contrast, no information was found on this topic for other benthic predator-prey relations. The Common sole,

Solea solea has been described as a polychaete feeder (Yazdani, 1969; De Groot, 1971). *S. solea* including some species such as *Arenicola marina* (L.), *Nereis diversicolor* (Müller) or *Alitta virens* (Sars) (formerly known as *Nereis virens* (Sars)) known to bury below the first few centimeters (Kristensen, 1984; Zwarts and Wanink, 1993; Caron et al., 1996). A burial depth between 5 and 10 cm was considered a safe refuge towards most benthic predators (Esselink and Zwarts, 1989). There are several factors such as sea temperature and to a lesser extent day length and body condition, sediment type (Esselink and Zwarts, 1989) or size/age of polychaetes (Esselink and Zwarts, 1989; Caron et al., 1996) which are known to alter burial depth in polychaetes. All of these factors may contribute to an increasing abundance of this prey type in common sole diet in nature. The influence of prey density on prey consumption has to our knowledge not yet been studied. Density may be of particular importance considering the numerical dominance of some polychaetes within benthic communities. In the present study prey consumption of two common sole size classes (100 g vs. 300 g) in relation to the density of a burying prey (ragworms, *A. virens*, Sars) was investigated.

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2 Material and methods

Common sole were obtained from a commercial fish farm (Solea BV, IJmuiden, Netherlands). The benthic polychaete, *A. virens* (subsequently referred to as "prey") was used as prey and was obtained from a commercial producer (Topsy Baits, Wilhelminadorp, Netherlands). Experiments were conducted at the research facilities of Wageningen Imares in Yerseke, the Netherlands.

Prior to as well as after arrival at the experimental facilities, the common sole used in this study were exclusively fed with a commercial pelleted feed, thus being naïve to eating live prey. Therefore, prior to starting the experiment common sole were adapted for 7-d to accept the live prey type (e.g., polychaetes) and to a system in which prey were enabled to bury freely (20 cm sediment thickness). During this adaptation, prey of mixed size was used. As a result of consumption prey densities declined and were re-stocked once during the adaptation phase to maintain a theoretical density of $1.5\,\mathrm{kg\,m^{-2}}$. Prey was re-stocked during day-time when no feeding activity of common sole was observed. Avoiding active feeding on unburied prey was important to assure adaptation of common sole to forage on buried prey. Fish were adapted in a separate system (not the experimental system) consisting of 6 square plastic tanks connected to a recirculation system equipped with a drumfilter, trickling filter, ozone and UV. Conditions, i.e. sediment type, sediment depth, sediment settling time and water quality were the same as in the experimental system.

3 General experimental conditions

In this experiment, 16 square plastic tanks ($1\,\mathrm{m^2}$ bottom area and a total water volume 300 L per tank) were used. These experimental tanks were connected to one recirculation system, which was equipped with a beadfilter. Outflow pipes of the tanks were covered with screens to prevent prey from escaping. Seven days prior to the experimental period tanks were filled with pre-washed Metsel sand to a depth of 20 cm. One prey size was used (mean initial body weight ± SD $2.4 \pm 0.29\,\mathrm{g}$). Conditions were kept constant throughout the experiment (photoperiod 12L:12D; water flow $5\text{--}6\,\mathrm{L\,min^{-1}}$; temperature $18.6 \pm 0.7\,°\mathrm{C}$; salinity 32.3 ± 0.9; TAN $< 0.8\,\mathrm{mg\,L^{-1}}$; NO_2-N $< 0.55\,\mathrm{mg\,L^{-1}}$ and NO_3-N $< 17.1\,\mathrm{mg\,L^{-1}}$, pH > 7.7). Oxygen (DO) was kept above $> 7.8\,\mathrm{mg\,L^{-1}}$.

4 Experimental design

In the experiment, the following factors and levels were used: prey density (0.8, 2.2, 4.3 and 6.5 individuals of prey per $\mathrm{dm^2}$); common sole size (mean initial body weight ± SD of the 2 common sole sizes was $111.3 \pm 15.6\,\mathrm{g}$ and $315.8 \pm 57.4\,\mathrm{g}$, subsequently referred to as 100 g vs. 300 g). One density of prey was stocked per tank and the number of prey stocked in each tank was counted. Earlier observations showed that prey needed 20–23 h to reach their maximum burying depth of approximately 12 cm (Ende et al., 2018). Therefore, common sole was introduced to the tanks 24-h after stocking the prey. An additional 100 individuals were weighed individually to determine the mean initial body weight. In total, 32 common sole (16 common sole per size class) were individually weighed and distributed randomly (except for size class) over 16 tanks (4 fish tank^{-1}) resulting in 2 replicates for each prey density and fish size class. Each group of common sole was used four times, once at each of the four prey densities, thus four groups at each prey density. After being starved before each feeding period for 24 h, each group of fish was introduced at random to the next prey density treatment. This procedure was repeated until each group of fish was subjected to all prey density treatments once. The feeding period lasted 48-h after which common sole were removed. During this feeding period unburied prey was removed daily, weighed and counted during working hours between 09 and 17 h. Removing unburied prey was necessary to assure that feeding took place on buried prey. Common sole fed during the night time, hence removal procedure during day time (working hours) are unlikely to have interfered with their feeding behaviour. After 48 h, remaining prey was recovered from the sediment by sucking water, sediment and prey out of the tanks and separating prey by running the homogenate through a rotating drum. Prey was counted and total biomass was recorded.

5 Calculations and statistical analysis

Number of prey consumed per fish^{-1} d^{-1} was calculated per tank as the initial number of prey − final number of prey − numbers of unburied prey divided by the number of fish per tank divided by the number of experimental days. Statistical evaluations of data were performed using the statistical analysis systems statistical software package version 9.2 (SAS Institute, Inc., Cary, NC, USA). Data were normally distributed, therefore parametric tests were applied. The effect of fish size was determined by a one-way analysis of variance (ANOVA) using the procedure general linear model (GLM). The GLM was chosen because it allows testing for significant differences in responses between fish sizes.

In order to test if the linear relationship between prey consumption and prey density was different between the two common sole size classes the following model was used:

$$Y_{ijk} = \mu + S_i + e_{1ij} + \beta X_k + \beta_i X_k + e_{2ijk},$$

where Y_{ijk} = number of prey eaten by common sole size class i in group j at prey density k; μ = overall mean; S_i = the effect of common sole size class i (i = 1, 2); e_{1ij} = error term 1, which represents the random effect of group j within common sole size class I (j = 1,..,4); X_k = the measured prey density at the start of the feeding period within group j (k = 1,..,4); β = overall regression coefficient of Y on X; β_i = regression coefficient of Y on X within common sole size class i, which represents the interaction effect between common sole size and prey density; and e_{2ijk} = error term 2. The effect of common sole size was tested against error term 1 and the other effects against error term 2. Moreover, within common sole size class, it was tested if the relationship between prey consumption and prey density was polynomial. In all tests, the statistical significant difference between groups were considered when $P < 0.05$.

6 Results

Prey consumption was significantly affected by prey density ($P < 0.001$) and by common sole size ($P = 0.008$). At

both common sole classes studied, a positive correlation between prey consumption and prey density was present (Fig. 1). The linear relationship between prey density (x, in No. dm^{-2}) and prey eaten (y, No. fish^{-1} d^{-1}) was

$$y = 1.71(\text{SE}0.68) + 0.91(\text{SE}0.17)x \quad \text{(for 300 g common sole)},$$

$$y = 2.20(\text{SE}0.68) + 0.32(\text{SE}0.16)x \quad \text{(for 100 g common sole)}.$$

The intercepts did not differ between the two common sole size classes ($P > 0.05$), but the regression coefficient was significantly higher for the 300 g than for the 100 g common sole ($P = 0.02$). At low prey densities (0.8 and 2.2 prey dm^{-2}) worm intake was similar between common sole sizes, but at higher prey densities the intake of 300 g common sole was larger than that of 100 g common sole. Within the 300 g common sole class, the relationship between prey consumption and prey density was linear within the measured prey density range ($P > 0.001$). However, within the 100 g common sole class, the quadratic function between prey density (x, in No. dm^{-2}) and prey eaten (y, No. fish^{-1} d^{-1}) was significant ($P = 0.018$) being:

$$y = 1.2\,(\text{SE}0.43) - 11.2\,(\text{SE}0.30)x - 0.116\,(\text{SE}0.04)x^2,$$

with a R^2 of 99%. This curvilinearity indicated that above prey density of 2.2 worms per cm^2 the prey intake of 100 g common sole levelled off at about 3.7 prey eaten per fish per day (Fig. 1).

The number of unburied prey increased with prey density ($P < 0.001$, data not shown). However, the fraction of unburied prey did not alter with increasing prey density when expressed as percentage of the number of prey stocked ($P = 0.30$; Fig. 2). The percentage of unburied prey was higher in tanks stocked with 100 g common sole compared to those containing 300 g common sole, being 1.15% versus 0.22% ($P < 0.001$).

7 Discussion

This study assessed the prey consumption of two common sole size classes (100 g vs. 300 g) in relation to the density of a burying prey (ragworms, *A. virens*, Sars). Ragworms bury deeper than the top sediment layer, the first few centimeters (Kristensen, 1984; Zwarts and Wanink, 1993; Caron et al., 1996; Ende et al., 2018). Such a depth is considered a safe refuge from most predators including flatfish (Esselink and Zwarts, 1989). In addition, increasing density does did not significantly affect burial depth in *H. diversicolour* (Duport et al., 2006). Therefore it was expected that prey density of ragworms would have minor impact on the prey consumption in common sole. However, the prey (i.e., ragworms) density influenced prey consumption of common sole (Fig. 1). The current finding is paralleling the observed positive correlation between prey consumption and prey density in foraging on exposed prey (e.g. free swimming prey) (Rice and Cochran, 1984).

At both common sole classes studied, a positive correlation between prey consumption and prey density was present, but the relationships differed between 100 and 300 g common sole.
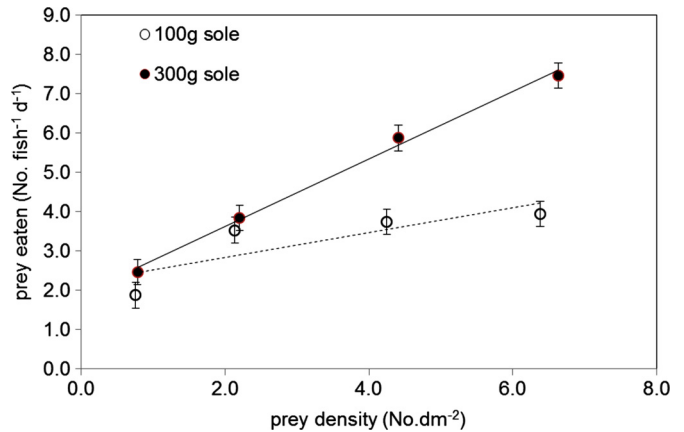

Fig. 1. Linear relationship of prey density (No. dm^{-2}, x-axis) and numbers of prey eaten (No. fish^{-1} d^{-1}, y-axis) in 100 g (broken line, empty circles) and 300 g common sole (solid line, solid circles). Presented values are means ($n = 4$) with error bars showing the standard error of mean.
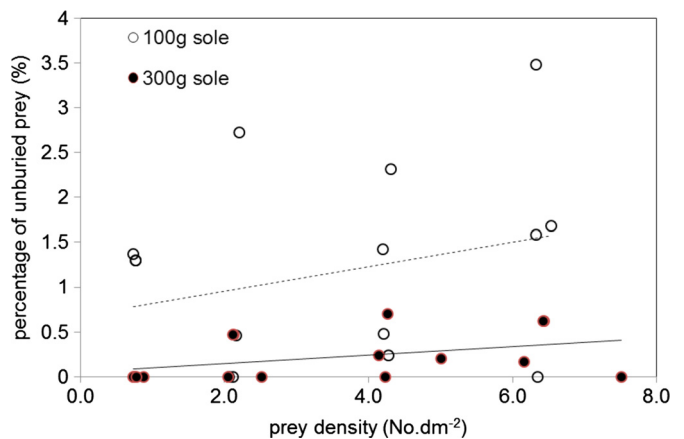

Fig. 2. The relationship of prey density (in No. dm^{-2}, x-axis) and numbers of unburied prey expressed as percentage of intial prey stocked (%, y-axis) in 100 g (broken line, empty circles) and 300 g common sole (solid line, solid circles).

The straight line response in 300 g common sole suggests that prey consumption was limited by all prey densities; the polynomial response in 100 g common sole in contrast suggests that at higher prey densities prey consumption was limited by other factors than prey density. The differences in prey consumption between predator size in response to prey density could be related to differences in physiological (satiation), physical (handling of prey size) or ecological (access to prey) capacities of the fish.

Besides the physiological capacity (satiation), ecological or morphological factors may constrain prey consumption differently between the two predator sizes. For example, the time required to ingest and handle prey increases when prey size approaches the fish's physical capacity limits (Werner, 1974; Kislalioglu and Gibson, 1976; Hoyle and Keast, 1987; Gill and Hart, 1994). Capacities to ingest and handle prey generally increase with increasing predator size

([Chattopadhyay and Baumiller, 2009](#)). Therefore smaller fishes require more time to ingest and handle prey than larger fishes which may be reflected by a lower prey consumption in smaller fish. However, our results suggest that differences in prey consumption between the two common sole sizes were not related to limitations in overall time budget. If time would have limited prey consumption in 100 g common sole prey consumption would have been lower than in 300 g common sole at all prey densities. In contrast, prey consumption was identical for 100 g and 300 g common sole at the lower densities.

The levelled-off prey consumption in 100 g common sole indicates that at the plateau-level, prey consumption in 100 g common sole was limited by satiation. On average, 100 g common sole ate 1.4% dry matter per unit body weight (% dm BW^{-1}; dry matter content of prey was 0.18 g g wet weight^{-1}, unpublished data). This value is higher than consumption values previously reported in unrestrictedly fed common sole (1.1% dm BW^{-1} ([Ende et al., 2016](#))). This suggests that consumption of prey in 100 g common sole was limited by satiation at prey densities higher than 2.2 individuals of prey per dm^{-2}. In contrast, the straight line response in prey consumption in 300 g common sole suggests that 300 g common sole did not reach satiation. Even at the highest prey density prey consumption (0.9% dm BW^{-1}) remained below the value of 1.1% dm BW^{-1} previously reported for this species. In addition, the higher intake in the present study compared to the intake values in the previous study ([Ende et al., 2016](#)) we chopped the ragworm into smaller pieces allowing unrestricted handling. This indicates that the levelling off cannot be related to increased handling time. The different influence of satiation between the two fish sizes is further supported by the differences in percentage of unburied prey found in the two fish size treatments. The lower percentage of unburied prey found in tanks with 300 g common sole (0.22%) compared to 1.15% of unburied prey found in tanks with 100 g common sole suggests that 300 g common sole ate relatively more unburied prey than the 100 g common sole that was presumably satiated already.

Mean burial depth of *A. virens* was at 11 cm in an experimental study using the same size class of *A. virens* (1–1.5 g), sediment type and sediment depth as in the present study ([Ende et al., 2018](#)). A burial depth between 5 and 10 cm was considered a safe refuge towards most benthic predators ([Esselink and Zwarts, 1989](#)). *H. diversicolor* remained at depth of around 7 cm even at high densities of 1153 individuals m^{-2} ([Duport et al., 2006](#)), This assumption has recently been validated in an experimental study which showed that prey consumption especially in larger common sole was lower when prey was at a mean depth of 7.7 cm compared to prey consumption in a setup when ragworm depth was restricted to the top 2 cm of sediment ([Ende et al., 2018](#)). Increasing prey consumption with increasing density could be related to reduced burial depth of *A, virens*. Present high densities of *A. virens* are also found in nature ([Kristensen, 1984](#)) suggesting that *A. virens* is naturally exploited.

In conclusion, other than expected prey density influenced prey consumption in common sole. Small common sole reached satiety prey consumption rates at nearly every prey density while large common sole did not reach satiety prey consumption rates even at highest prey densities exceeding those in nature. Results suggest that polychaetes such as *A. virens* can contribute to the diet of small common sole even at low/moderate densities. In contrast, the absence of satiety prey consumption in large common sole indicates that polychaetes such as *A. virens* are not an ideal prey type for larger individuals. These assumptions are in line with ecological data showing that polychaetes are an important prey type in the diet of small common sole but nearly absent in the diet of large individuals.

References

Blundon JA, Kennedy VS. 1982. Refuges for infaunal bivalves from blue crab, *Callinectes sapidus* (Rathbun), predation in Chesapeake Bay. *J Exp Mar Biol Ecol* 65: 67–81.

Caron A, Desrosiers G, et al. 1996. Comparison of spatial overlap between the polychaetes *Nereis virens* and *Nephtys caeca* in two intertidal estuarine environments. *Mar Biol* 124: 537–550.

Chattopadhyay D, Baumiller TK. 2009. An experimental assessment of feeding rates of the muricid gastropod *Nucella lamellosa* and its effect on a cost-benefit analysis. *J Shellfish Res* 28: 883–889.

De Groot SJ. 1971. On the interrelationships between morphology of the alimentary tract, food and feeding behaviour in flatfishes (pisces: pleuronectiformes). *Neth J Sea Res* 5: 121–196.

Duport E, Stora G, et al. 2006. Effects of population density on the sediment mixing induced by the gallery-diffusor *Hediste* (*Nereis*) *diversicolor* O.F. Müller, 1776. *J Exp Mar Biol Ecol* 336: 33–41.

Ende SSW, Kroeckel S, et al. 2016. Feed intake, growth and nutrient retention of common sole (*Solea solea* L.) fed natural prey and an artificial feed. *Aquac Res* 47: 681–688.

Ende SSW, Schrama JW, Verreth JAJ. 2018. The influence of prey size, sediment thickness and fish size on consumption in common sole (*Solea solea* L.). *J Appl Ichthyol* 34:111–116. DOI://doi.org/10.1111/jai.13520.

Esselink P, Zwarts L. 1989. Seasonal trend in burrow depth and tidal variation in feeding activity of *Nereis diversicolor*. *Mar Ecol Prog Ser* 56: 243–254.

Gill AB, Hart PJB. 1994. Feeding behaviour and prey choice of the threespine stickleback: the interacting effects of prey size, fish size and stomach fullness. *Anim Behav* 47: 921–932.

Hoyle JA, Keast A. 1987. The effect of prey morphology and size on handling time in a piscivore, the largemouth bass (*Micropterus salmoides*). *Can J Zool* 65: 1972–1977.

Kislalioglu M, Gibson RN. 1976. Prey "handling time" and its importance in food selection by the 15-spined stickleback, *Spinachia spinachia* (L.). *J Exp Mar Biol Ecol* 25: 151–158.

Kristensen E. 1984, Life Cycle, Growth and production in estuarine populations of the Polychaetes *Nereis virens* and *N. diversicolor*. *Holarct Ecol* 7, 249–256.

Lipcius RN, Hines AH. 1986. Variable functional responses of a marine predator in dissimilar homogeneous microhabitats. *Ecology* 67: 1361–1371.

Rice JA, Cochran PA. 1984. Independent evaluation of a bioenergetics model for largemouth bass. *Ecology* 65: 732–739.

Richman SE, Lovvorn JR. 2004. Relative foraging value to lesser scaup ducks of native and exotic clams from San Francisco Bay. *Ecol Appl* 14: 1217–1231

Werner EE. 1974. The fish size, prey size, handling time relation in several sunfishes and some implications. *J Fish Board Can* 31: 1531–1536.

Yazdani GM. 1969. Adaptation in jaws of flatfish (Pleuronectiformes). *J Zool* 159: 181–222.

Zwarts L, Wanink JH. 1993. How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. *Neth J Sea Res* 31: 441–476.