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Behavior of Sandeels Feeding on Herring Larvae

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Abstract: It is a common problem in ecosystem studies that information about predation on fish larvae is extremely sparse. There is little information about agents of mortality. This is likely to be because fish larvae are digested very rapidly in a predator's stomach. This study describes controlled experiments designed to evaluate the potential role of small low-trophic level fishes as predators on pelagic fish larvae. The study shows that sandeels, *Ammodytes marinus*, prefer herring larvae to copepods, their normal food items. When herring larvae are available the sandeels change behavior, their swimming speed increases drastically, and copepods are almost totally excluded from the diet. Once eaten, the herring larvae are only identifiable in the sandeel guts for 15-30 minutes using morphological criteria. It is concluded that abundant low-trophic level fishes potentially may have considerable impact on other fish species, even those that are normally not assumed to be predators on the low-trophic level fishes themselves.

Keywords: Fish predation, Clupea harengus, swimming speed, sand lance, cultivation-depensation.

INTRODUCTION

When working with ecosystem modeling, one of the notable challenges is to describe the causes of mortality, especially for fish larvae and juveniles [1]. We know that the mortality rates are very high, but rarely find such life stages in the stomachs of predators, and hence have little possibility for describing proper diet compositions for predators. It is often assumed that the lack of young stages in predator diet studies is likely to be because fish larvae are digested very rapidly, but there is little proof of such relationship.

This paper reports on a series of microcosm laboratory experiments conducted to examine the potential role of small low-trophic level fishes as predators on larvae of a fish species generally assumed to be a predator on the low-trophic level fish species itself. The study is focused of trophic interactions between two of the most common fish species in the North Sea: Lesser sandeel, *Ammodytes marinus* predating on larval herring, *Clupea harengus*. The paper seeks to answer one basic question: Are sandeel potential predators on herring larvae?

MATERIAL AND METHODS

Herring

The herring larvae were produced from two groups of ripe herring, both captured in fixed, encircling bottom nets, where they were kept alive until the nets were hauled. The herring were transported in chilled condition (at. 4-6 °C) to the laboratory. Here, the eggs were fertilized and incubated at 8-10 °C in seawater with salinity of approximately 31. The procedure of transportation and fertilization follows the procedure described by Munk and Rosenthal [2]. The larvae used for the experiments described below were up to 18 days old.

After hatching the herring larvae were transferred to 200 liter circular, black Polyethylene tanks where they were fed copepods at a concentration of approximately 100 copepods per liter. The copepods that were used for these experiments were reared from wild-caught plankton stored in a mixed copepod culture kept outdoors in a 30 m^3 concrete tank. The dominant species among the copepods was *Acartia tonsa*.

Sandeel

The sandeels were captured by a commercial trawler in Skagerrak, approximately 20 nautical miles west of Hirtshals, Denmark. They were kept alive, and transported to the laboratory at the North Sea Research Park in Hirtshals in a 100 liter tank. In the laboratory the sandeels were kept in a 3 m^3 tank (3 by 1 by 1 meter) without bottom substrate. The sandeels were captured two weeks before the first experiments to allow for a period of adaptation to the captive environment. During the adaptation period the sandeels were fed finely-chopped *Mysis* sp.

Before the experiments the sandeels were transferred to an 800 liter circular, black Polyethylene tank where they were acclimatized to feeding on copepods for at least two days. The tank used for this acclimatization was 1 meter in diameter and 1 meter deep. The tank was lit from above with four 40 Watt Cool-White light tubes for 12 hours a day. The water in the tank was renewed at a rate of approximately 2 liters per minute. The water temperatures were 10-11 °C and the salinity was approximately 31. The sandeels used for the experiments were 11.2 - 11.8 cm total length, with weights ranging from 3.41 - 4.01 g wet weight.

Consumption Experiments

A series of consumption rate experiments were performed in 800 liter tanks similar in material, shape and physical conditions to those used for the secondary acclimatization. The tanks were seeded some hours prior to the experiments with known numbers of copepods and herring larvae. At the start, one sandeel (zero in the control) was

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added to each tank. After the experimental period the sandeels were removed. The contents of the tanks were then filtered through an 80 μm plankton net, and the plankton retained was sorted to identify and count the remaining herring larvae.

Observation Experiments

The experiments were performed in a transparent, 800 liter cylindrical, acrylic tank. The shape and physical conditions were as described above for the Polyethylene tanks. Prior to each experiment, four to five sandeels were acclimatized to the tank for several days during which time they were fed copepods. At the onset of an experiment one sandeel, which swam freely in the water column, in other words it did not cling noticeably to the tank wall, was selected, and the others removed. Then copepods were added to a concentration of approximately 100 per liter, and the behavior of the remaining sandeel observed and recorded. After 30 minutes, 80 herring larvae (i.e. 0.1 per liter) were added, mixing the water gently, and the experiment was considered started (time = 0).

During the experiments two or three observers watched the behavior of the sandeels, and comments and time sequences related to swimming speed, prey attack and success, and estimated distances were recorded on tape. After the experiments the sandeels were removed, and their guts were examined immediately.

RESULTS

Consumption Experiments

Two experiments and one control were performed. The results of these are summarized in Table **1**. In the control experiment nearly all herring larvae were recovered after the experiment, while none were recovered in tanks with sandeels. This clearly indicates that the method of estimating consumption of herring larvae from the difference between numbers of herring larvae added and numbers recovered is an acceptable procedure. The results show that a sandeel on average was able to consume 80 larvae in an 800 liter tank in less than 5 hours.

Observation Experiments

During periods when no food was present the sandeels would swim in circles in the tank, typically against the weak water current, searching for food while maintaining a swimming speed of approximately 1 body length per second. The sandeels would form schools during the searches.

Once copepods were added to the observation tank the behavior of the sandeels changed markedly. They slowed down their swimming speed to around half a body length per second, and they snapped copepod after copepod using a stalk and strike sequence. The sandeels were able to and typically did catch 1-2 copepods per second. They did not pursue a copepod when an initial attack failed.

When the herring larvae were made available and had been discovered, the sandeels attacked and consumed them. After ingestion of from two to four herring larvae, the sandeel changed behavior abruptly. Their swimming speed increased approximately four-fold, up to around 2 body lengths per second. The sandeels then actively hunted for the herring larvae, and copepods were more or less ignored. The sandeels tended to move horizontally when they were hunting for the herring larvae, while when feeding on copepods they moved slowly, and changed their depth in the water column.

The sandeels reacted to herring larvae at a distance of usually one third to one half of their body length, which served as our distance measure for the experiments, but they occasionally responded when up to one body length away. If an attack failed, the sandeels always pursued the herring larvae until caught, which contrasted with their behavior when feeding on copepods. Larvae of the sizes used in these experiments only seldom reacted to the attacks.

The basic stimulus that primarily released an attack seemed to be the movement of the herring larvae. On several occasions sandeels hunting herring larvae, were observed to attack elongated objects, such as particles of dust, which were about the size of larvae. These objects would then be rejected immediately, after tasting. We did not observe this behavior with sandeels that did not have experience with herring larvae. Yolk sac larvae, which are not very active, were also eaten willingly by the sandeels.

The maximum catch rate was observed when a sandeel took twelve newly hatched larvae from the top of the tank in less than ten seconds. There were no noticeable lag times after the individual attacks.

Some of the basic characteristics of the feeding behavior of sandeels are summarized in Table **2**. The observations of schooling were performed in the 3 m^3 tank and in the observation tank. It is noticeable that when switching from feeding on copepods to herring larvae the sandeels change from stalkers to pursuers in the sense of Hunter [3].

In the Guts of Sandeels

No definite digestion experiments were conducted. However, from the observation experiments, estimates were made, based on morphological criteria, of the time during which a herring larvae remained identifiable in the sandeel guts. The intestine of sandeels is divided into a foregut, an

Table 1. Number of Herring Larvae Surviving in 800 Liter Tanks with 1 Sandeel (Zero in the Control)

Experiment no	Age of larvae (days)	Copepod density (per liter)	No. of sandeels	Duration (hours)	No. of larvae	
					Before exp.	After exp
1	3 + 7	120	1	18	80	0
2	6	194	1	5	80	1 (dead)
3	3 + 7	96	0	18	80	78

Table 2. Characteristics of the Feeding Behavior of Sandeel, *Ammodytes Marinus*

Food Item	Behavior	Swimming Speed (Body Lengths Per Second)	Stalker	Pursuer	Sandeel Schools
None	Searching	1	-	-	Well defined
Copepod	Feeding	½	Yes	No	Less defined
Herring larvae	Hunting	2	No	Yes	Disintegrate

appendix, and a hindgut. Larvae in the foregut were identifiable, even though the eyes most often were separated from the body and digestion was in progress. In the appendix, the bodies were disintegrated, and often only the eye pigments were left as identifiable items. In the hindgut, no identifiable remains were found, except occasionally for some eye pigments.

Fig. (**1**) gives the time sequences from three observation experiments. From the two experiments with sandeels starting with empty digestive systems, the time the larvae remained identifiable was estimated to be approximately 15 and 35 minutes. The estimates excluded the approximately five minutes that elapsed between ending the experiments and conducting the stomach analysis.

In the experiment with the sandeels that had been eating copepods before the experiment, the digestion of herring larvae was noticeably slower, and all larvae were recovered after 35 minutes. However, even here the larvae were in an advanced state of digestion, and only those in the foregut could be identified as herring larvae.

Predator/Prey Size Ratio

The wet weight of the sandeels used for the experiments were from 3.41 - 4.01 g, and the average weight of 3.7 g is used here for calculating predator/prey size ratio. The dry weights of the larvae were approximately 100 µg, corresponding to wet weights of approximately 0.5 mg. The adult *Acartia tonsa* weighs approximately 10 µg dry weight, corresponding to some 50 µg wet weight. The ratios of predator/prey weights are thus approximately 74,000:1 for sandeel and *Acartia*, and approximately 7,400:1 for sandeel and herring larvae.

The ratio of predator to prey weights for *Ammodytes* used by Andersen and Ursin [4] in their multispecies model of the North Sea was approximately 3,000:1. Herring larvae thus appear to be of a more appropriate size than copepods for sandeels of the size used in these experiments.

DISCUSSION

It is worth noting that the sandeel used in this experience were very unlikely to have had any previous experience with encounter and eating of herring larvae as there are no herring spawning areas within hundred of miles of where the sandeels were caught.

Food Items

The copepods used as food in these experiments are reported by several authors to be the most common prey organisms of sandeels. Macer [5] examined the stomach contents of sandeels from the Southwestern North Sea, and reports copepods to be the dominant prey item. Richards [6] examined 290 stomachs of *Ammodytes americanus* and found *Acartia* in 55%, while Meyer [7] reported zooplankton as the sole food for the species. Sekigouchi [8, 9] reported that *Ammodytes personatus* fed exclusively on *Acartia* in the spring, when *Acartia* was the dominant copepod in the plankton. The diet of *Ammodytes hexapterus* is reported to consist of zooplankton and zoobenthos [10].

Fish larvae were reported from the stomachs of *A. marinus* by Macer [5] and as contribution up to 0.6% of the stomach content for *A. dubius* by Bowman *et al.* [11]. Apart from these sources, very few records exist of fish larvae in the stomachs of *Ammodytes* spp. It should be noted though, that the chance of actually finding fish larvae in the guts is likely to be extremely small, as fish larvae are digested rapidly as demonstrated in this study. It is also a problem that there often are no spatial and temporal overlaps between occurrence of herring larvae and stomach sampling; often stomachs are not sampled where and when fish larvae are abundant. This would need to be the topic of a dedicated sampling program.

Volume Searched

The finding that the sandeels in the present experiments were able to catch the larvae offered in an 800 liter tank in less than five hours seems reasonable in view of the following calculations. From the observation-experiments the reactive distance (d) of the sandeels is estimated to be 1/2 body length. The areas searched (A) can be calculated [12] as the cross-sectional area a sandeel can search times the swimming speed (S),

$$A = \frac{2}{3} \cdot \pi \cdot d^2 \cdot S$$

where the swimming speed is 2 body lengths per second. The volume of water searched can then be estimated to 1.6 liter per second, corresponding to 6 m^3 per hour for a sandeel with the average length of 11.5 cm. The sandeels in the experiments can thus search 800 liter in less than 10 minutes.

It is, however, not possible to calculate the period of time the sandeels theoretically would need to encounter the eighty herring larvae in the 800 liter tank. To calculate this, several factors about which knowledge is incomplete would have to be taken into consideration. The most important factor involved is probably the search strategy of the sandeel. As noted earlier, sandeels tend to maintain their vertical position in the water column when hunting for larvae. This is likely an effective behavior in the sea, as herring larvae are not uniformly distributed vertically, and once a patch has been found, it may be efficient to search the given depth. However, in the tank, it means that the sandeels needs more time to search the volume of the tank.

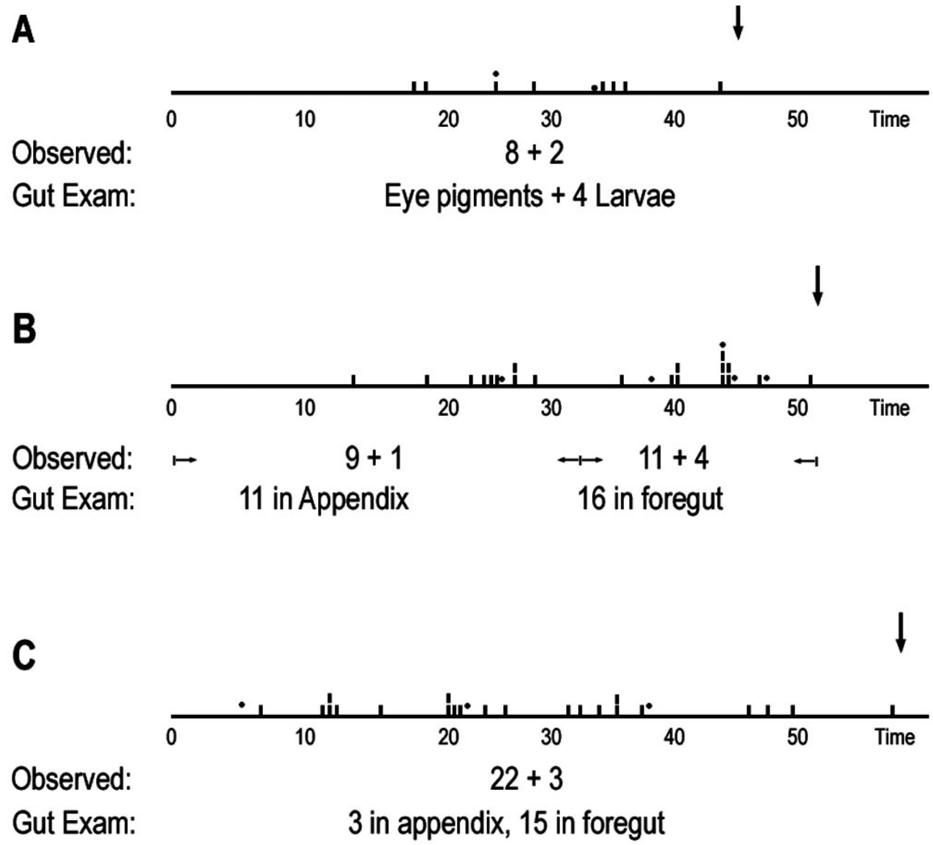

Fig. (1). Time sequences from three of the observation experiments. In A and C the gut of the sandeels were empty prior to the experiments. In B the hindgut of the sandeel was filled with copepods. The ages of the larvae were 11 days in A, 13 days in B, and 18 days in C. (**I**) denote observations of larvae captured, (●) observations of probable capture of larvae. "Observed" gives the number of certain plus uncertain observations during the time periods indicated, while "Gut Exam" gives the number of larvae found in the digestive system of the sandeels. The vertical arrows indicates the termination of each experiment.

Swimming Speed

Meyer *et al.* [7] estimated the swimming speed at sea of *Ammodytes americanus* with mean length of 18.2 cm to be 30-50 cm/sec when schools were swimming undisturbed, and not engaged in feeding. Schools exhibiting feeding behavior were usually found to swim at about half the speed of undisturbed schools, or about 15-25 cm/sec.

These swimming speeds are somewhat higher than those recorded in this study. The two main reasons to account for this are likely to be that the sandeels I used are smaller (11.5 cm versus. 18.2 cm), and that the sandeels in the laboratory experiments are restricted in their movement.

The changes in swimming speed with changes in feeding style are similar in the two studies. When the sandeels start feeding on copepods the swimming speed is halved. There does not seem to be any previous reports of a doubling in the swimming speed when fish larvae are prey.

Schooling

The present observations of schooling behavior resemble those of Meyer *et al.* [7] who found that the 'nearest-neighbor' distance between individuals of *Ammodytes americanus* when schooling, undisturbed and not feeding, was approximately one half to three quarter of their body length. Schools exhibiting feeding behavior spread out to a little over double the normal schooling distance, so that the nearest neighbor distance was approximately one to one and a half body lengths.

The observation in the present study that the schools disintegrate when hunting for larvae may complicate the sampling of sandeels feeding on larvae. Livingstone [13] documented on film that individuals and small schools of adult sandeels could easily escape a trawl net. In areas where abundance is high, the ability to avoid trawl nets may be less effective. Scott [14] found it unusual to catch adult sandeel in nets except in areas where they were very abundant.

CONCLUSION

Returning now to the question that was raised in the introduction: "Are sandeels potential predators on herring larvae?" the answer clearly must be that they can be, and even that they are likely to be efficient predators too. The implication of this is that, given the abundance of sandeel and other low-trophic level fishes, we must, especially in ecosystem modeling studies, consider that low-trophic level fishes could impact other fish species, which normally are considered predators on the low-trophic level fishes themselves. This is especially true of modeling studies of ecosystems. The result strengthens the call for modeling fish populations with explicit considerations of multiple age stages [15].

An important, potential consequence of interactions such as discussed here where abundant low-trophic levels fishes may be predating on the larvae of larger fishes is that it may cause depensation in the recruitment of the larger species. If the abundance of a dominant species (such as herring) declines drastically, a smaller species may increase in abundance and keep the previously dominating species trapped at the depleted level. This mechanism is often termed the 'cultivation-depensation' hypothesis [16].

While actual diet compositions may be difficult to obtain, we may meanwhile assume that small fish in the pelagic zone will feed on available fish larvae if present. To be able to actually assess the proportion of fish larval mortality attributable to predation by low-trophic level fishes, or specifically by sandeels, several investigations have to be made:

1. The prey size-selection of sandeels and other low trophic level fishes, and the upper and lower limits of selection as a function of the predator's size.
2. The prey species preferences of sandeels and other low-trophic level fishes when offered a variety of prey-organisms.
3. Estimation of the daily food intake from digestion experiments.

The experiments necessary should be carried out in a controlled environment with a minimum of stress factors. A medium scale enclosure (10-20 m^3) that can be sampled efficiently seems very appropriate. Comparative studies in systems of different sizes are, however, needed to assess the influence of the environment. Parallel to this series of studies, investigations on the co-occurrence and abundance of predators, larvae and other prey-organisms should be made.

A basic problem in the field studies is to be able to identify predators. The standard research sampling techniques with one-hour hauls are not very useful if larvae consumed by predators become unidentifiable in less than half an hour in the gut. To overcome the problems it will be worthwhile to develop non-morphometric methods, e.g., immuno-assay, fatty acid, or DNA techniques, and to use such as a routine in the diet studies.

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