THE INFLUENCE OF VISUAL AND CHEMICAL STIMULI FROM COD *GADUS MORHUA* ON THE DISTRIBUTION OF TWO-SPOTTED GOBY *GOBIUSCULUS FLAVESCENS* (FABRICIUS)

ANNE CHRISTINE W. UTNE & BIANCA BACCHI

SARSIA

UTNE, ANNE CHRISTINE W. & BIANCA BACCHI 1997 08 15. The influence of visual and chemical stimuli from cod *Gadus morhua* on the distribution of two-spotted goby *Gobiusculus flavescens* (FABRICIUS). – *Sarsia* 82:129-135. Bergen. ISSN 0036-4827.

Detection of a potential predation risk and its influence on patch choice was measured by examining the spatial distribution of 10 two-spotted gobies *Gobiusculus flavescens* (FABRICIUS) between two feeders, at one of which the presence of a predator was introduced either visually, chemically or both visually and chemically. Without predation influence the gobies were distributed according to the Ideal Free Distribution (IFD). However, as the chemical and / or visual stimulus from a predator cod (*Gadus morhua* L.) was introduced together with the food at one of the feeding sites, the gobies avoided the affected site. The avoidance persisted during feeding sessions for 1 or 2 days after the introduction. Although image had the most pronounced effect at the time of introduction, odor had a stronger effect on the gobies persistence in avoiding the affected site. Introduction of odor from an injured conspecific (alarm substance) at one of the feeding sites, had no significant influence on the gobies' distribution.

Anne Christine W. Utne and Bianca Bacchi, University of Bergen, Department of Fisheries and Marine Biology, Bergen High-Technology Center, N-5020 Bergen, Norway.

KEYWORDS: Predator odor; visual cue of a predator; *Gobiusculus flavescens*; fright persistence; alarm signal.

INTRODUCTION

Optimal foraging theory predicts how animals should behave to achieve a maximal energy intake, given the types of food and their distribution (MACARTHUR & PIANKA 1966; CHARNOV 1976a, b). According to the theory foragers will occupy the habitat where they can achieve the highest energy. However, obtaining food in the most economical way is only one of many subgoals for maximising fitness. Another important goal is to avoid being eaten oneself. Many experiments have shown that animals' feeding behaviour changes when they are aware of the presence of a predator (reviews by DILL 1987; SIH 1987). Fish are known to change their behaviour in various ways in response to presence of a predator (LIMA & DILL 1990; MAGURRAN 1990). Studies have shown that predators do not have to be seen by their prey to produce altered behaviour as they can be sensed chemically by their odor, or by an alarm substance (Schreckstoff) from an injured prey fish (VON FRISCH 1941; PFEIFFER 1974; JAKOBSEN & JOHNSEN 1989; SMITH 1992). Chemical cues inform the prey of the potential danger and studies have shown that the prey fish alter their behaviour in a similar manner as when they detect a predator physically. Some species decrease their activity level when exposed to predator odor (MATHIS & SMITH 1993), others quit feeding and start to school or hide (MAGURRAN 1990), or they avoid the dangerous area (MATHIS & SMITH 1992; KEEFE 1992; PETTERSSON & BRÖNMARK 1993; JACHNER 1995). Studies done on chemical cues from predators or wounded conspecifics (Schreckstoff) have so far, with few exceptions (PFEIFFER 1977; SMITH 1989), been performed on freshwater species. Fish that possess the alarm substance fright reaction, are mostly social, lack defensive structure (i.e. spiny fins or gills), and are generally non-predaceous (PFEIFFER 1977).

Gobiusculus flavescens live in small social groups in the littoral zone. They lack defensive structures, and their prey is mainly zooplankton. It is therefore possible that *G. flavescens* also possess an alarm substance.

The turbidity is often high in the littoral zone due to runoffs from land. Furthermore *G. flavescens* have relatively poor light sensitive vision (UTNE 1995). Yearling (0-group) cod (*Gadus morhua*) is known to be a major predator on *G. flavescens* (NORDEIDE & SALVANES 1991). Cod use olfactory organs while searching for prey (BRAWN 1969), which gives them the ability to hunt also when visibility is poor: at night, during twilight (BLEGVAD 1917), and in high turbidity. The gobies can therefore not rely on vision alone to detect their adversary and need an alternative way of sensing danger. The use of the olfactory sense in the detection of a predator odor and / or the possession of an alarm system are possible abilities with which the two-spotted goby might gain an early warning of a predator attack. We wanted therefore by this study to: 1) clarify the importance of chemical stimuli compared to visual stimuli in *G. flavescens* predator recognition behaviour; 2) reveal whether *G. flavescens* has an alarm system (reacts on water conditioned by an injured conspecific). Furthermore it is known from the literature that both wild and cultivated cod have a very low migratory activity (ca 87 % of both reared and wild cod were recaptured, two years later, in the same area as released (SVÅSAND 1990)). 3) We therefore wanted to test if the avoidance of the affected area by the gobies persisted, as a possible adaptation to the stationary behaviour of their major predator.

MATERIALS AND METHODS

Experimental method

The influence of the different factors (predator image, predator odor and alarm substance) on habitat choice and feeding behaviour of the gobies were quantified by studying the deviation from an Ideal Free Distribution (IFD, FRETWELL & LUCAS 1970). It has been demonstrated earlier (UTNE & al. 1993) that male *G. flavescens* as several other fish species (MILINSKI 1979; GILLIS & KRAMER 1987; PITCHER & al. 1988) are distributed according to the IFD in the presence of a resource. When a group of individuals is distributed according to the IFD in the presence of a resource (here food), it is possible to investigate the influence of other factors (e.g. predation risk) by measuring the deviation from the IFD when individuals are exposed to such factors (ABRAHAMS & DILL 1989). By the use of this method earlier studies have shown that *G. flavescens* avoid a feeding patch containing cod and choose to feed in the safe / predator free patch (UTNE & al. 1993; UTNE & AKSNES 1994). We used the same method (deviation from IFD) in this study, this time to clarify whether cod odor, odor of an injured conspecific (alarm substance) or the image of a predator have any immediate or long-time effects on the feeding behaviour or habitat choice of the *G. flavescens*.

Experimental procedure

Gobiusculus flavescens was collected with a beach seine in July and December over a hard bottom covered with *Fucus* spp. in Raunefjorden close to Bergen (western Norway). During the summer months *G. flavescens* are highly infected by ectoparasites. To kill any ectoparasites the gobies collected in July were treated for thirty minutes in a formaldehyde bath of 1:5000 ratio, the same day that they were caught. Ten gobies were transferred into each experimental aquarium (0.8 x 0.4 x 0.2 m). Only male gobies of equal size (ca 45 mm) were used in the experiments. The gobies were acclimatised in the experimental aquaria for eight days before the experiments. Live copepods were offered daily. No feeding was undertaken in the 24 h prior to the experiments. The experiments were done at a temperature of 14 ±1 °C in July and 10 ±1 °C in the December experiments. The experimental aquaria had water running through them at all times except during the trials. The aquaria were divided in two equal parts by a net, with one feeding site on each side of the net. The total experimental arena was 0.32 m^2. During a trial (10-12 minutes), the same number of zooplankton suspended in water (water taken from the tank where the gobies where fed) were supplied through two inlets at the opposite sides of the aquarium. This design was used earlier in UTNE & al. (1993) and UTNE & AKSNES (1994). The gobies could swim freely through the net between the two feeding sites in the aquarium. The net, however, seemed to delayed the mixing / advection of the two zooplankton suspensions added at each side of the net. The mixing delay was confirmed prior to the experiments by adding dye ($KMnO_4$) to one of the zooplankton suspensions.

The distribution of the gobies was recorded on videotape. Artificial light, with 12 h light, 12 h dark and a dusk and dawn simulation, was used. The experiments were always initiated at midday, when the light was at a maximum of ca 80 mmol m^{-2} s^{-1}. Zooplankton (mainly copepods) used as prey, was collected with plankton nets and kept alive in containers at low temperature (5-6 °C) for a maximum of three days. Zooplankton in size range 0.5-2 mm was used as food for the gobies. The species composition can be considered to be the same at the two different sides of the aquarium within each experiment, but not among all experiments (due to the use of natural plankton).

Experiments with predator

0-group (length 15-17 cm) cultivated cod (*Gadus morhua*) were used in the experiment where the effects of predator odor and / or image on the distribution of gobies were investigated. The individuals used were kept in the same tank, they were from the same cohort (siblings) and had the same treatment history. Prior to the experiment the cod were kept in a storage tank (1 x 1 x 0.9 m) where they were fed dried pellets daily.

To create a zooplankton suspension with cod odor, one randomly picked cod was moved from the storage tank to a 30 litre tank where it was kept for 24 hours. During the 24 hours the tank-water was aerated but not changed, and the cod was not fed. One of the two zooplankton suspensions was then made by suspending plankton in water taken from the 30 litre tank (which had held a starved cod for 24 hours) instead of water taken from the experimental aquarium.

During the testing of visual stimuli, the cod was placed in a transparent plastic container adjacent to one of the to feeding sites.

To test the combined effect of both smell and vision, the cod was placed in a perforated plastic container at the feeding site where zooplankton suspension with cod odor was introduced. After the treatments with predator odor and / or image, the gobies were fed for the next 2 days without any stimulus from a cod, to reveal if there was any effect of memory. Three experiments were performed with an empty plastic container, to determine whether the container had any influence on the distribution of the gobies.

Inspection activity was analysed in the two experimental set-ups with a visual cod stimulus (image, and image and odor combined). Inspection was characterised in accordance with PITCHER & al. (1986).

Introduction of alarm substance

This time we added water that had contained an injured conspecific (alarm substance) to one of the two zooplankton suspensions. Alarm substance was obtained by making 50 cuts in the skin of a freshly killed (by a knock on the head) goby, which had been soaked in 20 ml of sea water for 3 minutes. This water was thereafter added to one of the two food suspensions. The same method was used by SMITH (1989) in his studies of alarm substance in the two goby species *Asterropteryx semipunctatus* and *Brachyogobius sabanus*. We first performed the alarm substance experiments in July, no positive results in this period led to repeated experiments in December, as the lack of reaction in July could be an adjustment to an abrasive breeding behaviour (SMITH 1973; 1976).

Statistical methods

The food ratio of 1:1 was used to see whether the gobies distributed themselves according to the food, in the absence and presence of alarm substance, predator odor and / or image. We recorded the number of fish located at both sides of the aquarium every 30 seconds during the 10-12 minute trials, providing 20-24 pairs of observations for each trial. We began the recording 90 seconds after a trial had started as the gobies needed some time to investigate the profitability of the two feeding sites (UTNE & al. 1993). We then used the mean of the 20-24 observations to characterise the distribution in each of the experimental set-ups. The mean and standard deviation were calculated on the basis of the four replicates. Comparison was done by the use of ANOVA with arcsin square root transformed proportions (number of fish present at one side divided by the total number of fish used in the experiment) as the raw data. As there was no difference (ANOVA $p > 0.05$) between alarm substance experiments performed in July and those performed in December the two data sets were pooled.

The plastic container's (box) and alarm substance's influence on the distribution was tested by a one-way ANOVA against the control distribution (the IFD). Accordingly one-way ANOVA was used to reveal any difference in inspection activity between the two experimental set-ups containing a visual stimulus from a predator (between image and image combined with odor).

A two-way ANOVA was used to analyse any combined or linked effects between the introduced effects (image and odor) and time (days after introduction of effect).

Level of difference between the different experimental set-ups (IFD, cod odor and/or image) were tested by two-way ANOVA Post Hoc test (Newman Keults test).

Fish that were inactive, lying at the bottom or in the corners of the tank during the experiments, were excluded from the analysis as they were not actively feeding. Consequently, the results are sometimes based on fewer than 10 fish. An experiment was considered invalid if more than two fish were inactive during the whole trial.

RESULTS

When food alone was introduced in the two patches in equal amounts (the IFD experiments), the gobies were distributed according to the food availability (Fig. 1a). Introduction of a plastic container (box) had no influence on the gobies' distribution (ANOVA, Table 1 and Fig. 1a).

Experiments with predator

When a cod was present in the plastic container (image) there was a significant avoidance of this side of the aquarium (ANOVA, Table 1 and Fig. 1a). Introduction of cod odor from one of the feeders also led to a significant avoidance of that feeder (ANOVA, Table 1 and Fig. 1a). Accordingly the introduction of a combined stimulus (plastic container with a cod and cod odor in feeder) led to a significant avoidance of the affected site (ANOVA, Table 1 and Fig. 1a). The previously affected side of the aquarium was also avoided ($p < 0.05$) the following day during feeding treatment (Table 1 and Fig. 1b). The second day after treatment the avoidance was no longer significant. There was a difference between the odor and image treatments concerning the persistence of avoidance (Table 2 and Fig. 2); odor had a stronger effect (Table 1, Fig. 2), than image.

Inspection was significantly higher in the experiment with image compared to the experiments with both odor and image (Table 2).

Introduction of Alarm substance

When alarm substance was introduced in one of the feeders, there was no significant (Table 2 and Fig. 1a) side preference, although fewer fish were represented at the 'alarm substance' side of the aquarium.

DISCUSSION

Immediate effects

In correspondence with the earlier findings (UTNE & al. 1993), the ten gobies were distributed according to the input match (PARKER 1978) or Ideal Free Distribution (FRETWELL & LUCAS 1970), when only food was introduced at the two feeding sites. Introduction of chemical, visual or combined stimuli from a predator at one of the feeding sites produced a significant change in the gobies' habitat choice, with an overuse of the unaffected feeding site. Their reaction to the chemical, visual or combined stimuli from a predator was similar to their reaction when detecting a predator physically (UTNE & al. 1993).

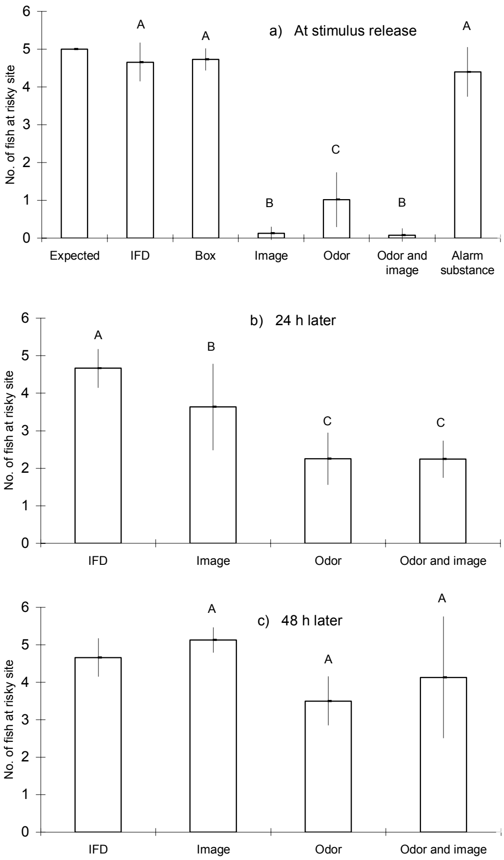

Fig. 1. Average number of *G. flavescens* on the stimulus affected feeding side of the aquarium. At the time of stimulus introduction (a), the day after stimulus had been introduced (b) and two days after stimulus had been introduced (c). Standard errors are indicated. Significant relations between treatments are indicated (A, B and C) on top of the bars.

Expected: expected distribution according to the Ideal Free Distribution (IFD) theory; *IFD*: distribution in the IFD experiments. *Box:* number of fish at side of the aquarium adjacent to an empty box; *Image*: number of fish on the side where a predator was presented visually (in a box); *Odor*: mean number of fish on the side where a predator odor was presented; *Odor and image*: mean number of fish on the side where a predator was presented both visually and chemically; *Alarm substance*: mean number of fish on the side where chemical cues from an injured conspecific were presented.

Earlier studies of antipredator behaviour triggered by chemical stimuli, have been performed with wild caught predators which had been feeding on the tested prey. We used cultivated cod which had only been fed pellets. A study done on juvenile brook trout (*Salvelinus fontinalis*) showed that the trout avoided water conditioned by Atlantic salmon fed on fish, but not water conditioned by salmon fed on mealworms (Keefe 1992). The pellets given to our cod, contained fish meal. However, the cod was starved for 24 hours before being moved to the tank, and it was never fed in the tank where it was kept overnight to produce cod scented water. The gobies' reaction was therefore most probably a result of scent released from the cod's skin or mucus (Peters & al. 1989).

The visual cue of a predator led to an avoidance of the feeding site closest to the predator. Earlier studies, with the exception of Jachner (1995), have also revealed an antipredator response among prey fish at the introduction of visual cues of a predator (e.g. Segers 1974; Magurran 1986; Smith & Smith 1989). Accordingly visual and chemical cues combined also significantly affected the distribution of gobies.

The avoidance effect was significantly stronger at the introduction of a cod image (image alone and image and odor combined) compared to the introduction of cod odor (Fig. 1a). The cause of this difference was probably that in the experiment with odor alone, the gobies had to attend the affected feeding site to sense the predator, while in the image studies the gobies could see the

Table 1. Two-way anova Post Hoc test (Newman - Keults test), expressing level of difference (p-value) between the different stimulus treatments (ideal free distribution, image, odor, and odor and image) at day of treatment, one day after and two days after the treatment (see Fig. 1a, b and c).

	IFD	Image	Image / Odor
At the time of effect introduction (Fig. 1a):			
IFD	———	0.000*	0.000*
Image	0.000*	———	0.721
Odor	0.000*	0.002*	0.002*
Image / Odor	0.000*	0.721	———
1 day after (Fig. 1b):			
IFD	———	0.044*	0.000*
Image	0.044*	———	0.025*
Odor	0.000*	0.010*	0.984
Image / Odor	0.000*	0.025*	———
2 days after (Fig. 1c):			
IFD	———	0.445	0.392
Image	0.445	———	0.251
Odor	0.153	0.064	0.290
Image / Odor	0.392	0.251	———

* significant difference

predator from a distance. The number of registered fish at the chemically affected site therefore became higher in the experiments without visual cues.

Jachner (1995) found that bleak (*Alburnus alburnus* L.), showed a significantly lower feeding activity (time at feeding site) when both seeing and smelling a predator than when just seeing one. In the present study there was a slight, but not significant, difference in number of fish present in the affected patch in the image alone (mean 0.13 fish) compared to in the combined (mean 0.08) study. This slight increase in number of gobies at the affected site during the image treatment compared to in the combined treatment, was probably due to a significantly higher inspection activity in the image alone treatment. A possible explanation to this phenomenon, is that chemical cues enhance the gobies' ability to quickly retrieve information about their potential predator, thus reducing the overall inspection activity. The paradise fish (*Macropodus opercularis* L.) used more time to inspect an intruding species when their olfactory nerves were put out of function than when their olfactory nerves were functioning (Miklósi & Csányi 1989). Olfactory recognition of cod should be particularly valuable to the gobies as cod is a predator that can hunt in conditions where visibility is poor (Brawn 1969).

When alarm substance was introduced the gobies showed no significant preference for feeding side. The way the alarm substance was collected could have been insufficient, and therefore could have affected the results. However, we followed the same procedure as Smith (1989) used when he discovered a response to alarm substance in the two goby species *Asterropteryx semipunctatus* and *Brachyogobius sabanus*. The gobiid species *Gobius niger* (L.), *Pomatoshistus microps and P. minutus* all being neighbours of *G. flavescens* in the littoral zone, were tested both histologically and behaviourally for the presence of alarm substance by Pfeiffer (1977). None of the tested gobiid species seemed to have an alarm substance system, which makes it likely that *G. flavescens* does not posses such a system either.

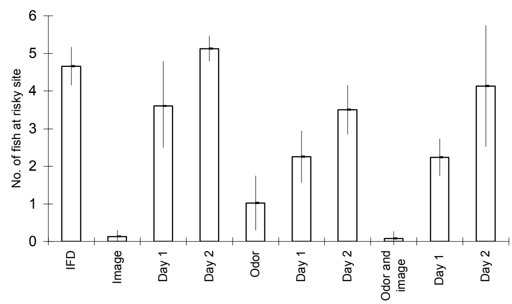

Fig. 2. Average number of *G. flavescens* on the stimulus (image, odor or combined) affected feeding side of the aquarium, at the time of stimulus introduction, and the following two days (Day 1 and Day 2).

Table 2. One-way ANOVA; testing effect of box, alarm substance (compared with their ideal free distribution) and inspection activity (the image and the combined image and odor studies are compared). Two-way ANOVA; testing for relations between time and type of stimulus (image, odor and combined image and odor).

Effect	df-effect	df-error	*F*-value	*P*-value
Effect of box:				
Box / IFD	1	9	2.76	0.131
Alarm substance:				
Alarm substance / IFD	1	17	2.97	0.103
Inspection:				
Image / odor and image	1	14	5.09	0.041*
Time and type of stimulus:				
Stimulus type	2	31	4.531	0.019*
Time	2	31	85.607	0.000*
Time / Stimulus type	4	31	4.426	0.006*

* significant difference

Furthermore, cod is the most common predator on *G. flavescens* (Nordeide & Salvanes 1991). Experimental studies have shown that cod swallow gobies in one piece (pers. commn Salvanes). Alarm substance may therefore be of little help in avoiding predation by cod. Minnows, however, who possess a Schreckstoff reaction, are frequently hunted by pike which uses its teeth while catching its prey, skin tearing is therefore more common in minnow predation.

Time effect

The gobies avoided the area previously affected by visual, chemical or combined stimuli for 1-2 days. Few (Gotceitas 1990; Metcalf 1987) earlier studies have been done on the persistence of the avoidance behaviour after the predator has vanished. Gotceitas (1990) found that foraging rate of bluegills decreased at a decreasing rate during the first 15 minutes after seeing a predator. Metcalf (1987) found that salmon parr's feeding motivation decreased up to one hour after seeing a predator. In comparison with the results presented by Gotceitas and Metcalf a 1-2 day persistence in feeding site avoidance is quite dramatic. CSÁNYI & LOVÁSZ (1987) tested whether paradise fish learn to avoid the dangerous patch or the source of the key stimulus, a predator dummy. They treated some of the fish entering an area with electric shocks and some with a predator dummy. Only those treated with electric shock avoided the area after the treatment had finished, and not those treated with a predator dummy. Csányi & Lovász concluded that only the stimulus and not the place of the stimulus elicits an avoidance behaviour. Our results, however, showed that gobies avoided the area where they had previously observed a predator either visually, chemically or both. Cod presence seems to have the strongest effect on the gobies ability to remember and recognise the area of cod detection. This behaviour could be a response to the stationary behaviour of their major predator.

After 1-2 days, however, the gobies returned to the earlier affected feeding patch. At this time the chance of meeting the cod again at the very same site is small, and the gobies' hunger has increased, which will push the gobies' optimal strategy more towards feeding than avoiding predation.

Odor either alone or introduced together with image led to a longer persistence of avoidance of an earlier affected site than did predator image alone (Fig. 1b). This indicates the importance of odor in the identification of a possible predator. A significantly higher inspection activity in the predator image studies where no predator odor was introduced, also emphasises the importance of odor for the gobies' evaluation of a predator. Altogether the introduction of predator odor alone seemed to have the strongest time effect on the gobies' avoidance behaviour (Fig. 1c). When odor is introduced alone (without any image) inspection, which contributes to valuable information about the predators aggressiveness, would not be possible. The gobies could therefore have chosen to be extra cautious.

ACKNOWLEDGEMENTS

We thank the ERASMUS program for a grant to Bianca Bacchi, and the Department of Fisheries and Marine Biology, University of Bergen for providing the facilities. Thanks to Professor Dag L. Aksnes for financial support, Cand.scient. Gunnar Nyhammer for providing us with cod, and Ståle Kolbeinson for correcting the language.

REFERENCES

Abrahams, M.V. & L.M. Dill 1989. A determination of the energetic equivalence of risk of predation. – *Ecology* 70:999-1007.

Blegvad, H. 1917. Om fiskens føde i de danske farvande inden for Skagen. – *Beretning fra den danske biologiske station* 24:19-72.

Brawn, V.M, 1969. Feeding behaviour of cod (*Gadus morhua*). – *Journal of the Fisheries Research Board of Canada* 26:583-596.

Charnov, E.L. 1976a. Optimal foraging: the marginal value theorem. – *Theoretical Population Biology* 9:129-136.

— 1976b. Optimal foraging: attack strategy of mantid. – *American Naturalist*. 110:141-151.

Csányi, V. & F. Lovász 1987. Key stimuli and the recognition of the physical environment by the paradise fish (*Macropodus opercularis*). – *Animal Learning and Behaviour*. 15:379-381.

Dill, L.M. 1987. Animal decision making and its ecological consequences: the future of aquatic ecology and behaviour. – *Canadian Journal of Zoology*. 65:803-811.

von Fischer, K. 1941. Über einen Schreckstoff der Fischhaut und seine biologische Bedeutung. – *Zeitschrift für vergleichende Physiologie* 29:46-145.

Fretwell, S.D. & H.L. Lucas Jr. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. 1. Theoretical development – *Acta Biotheoretica* 19:16-36.

Gillis, D.M. & D.L. Kramer 1987. Ideal interference distributions: population density and patch use by zebrafish. – *Animal Behaviour*. 35:1875-1882.

Gotceitas, V. 1990. Foraging and predator avoidance: a test of a patch choice model with juvenile bluegill sunfish. – *Oecologia* 83:346-351.

Jachner, A. 1995. Changes in feeding behaviour of bleak (*Alburnus alburnus* L.) in response to visual and chemical stimuli from predators. – *Archiv für Hydrobiologie* 133:305-314.

Jakobsen, J. & G. H. Johnsen 1989. The influence of alarm substance on feeding in zebra danio fish (*Brachydanio rerio*). – *Ethology* 82:325-327.

Keefe, M.L. 1992. Chemically mediated avoidance behaviour in wild brook trout, *Salvelinus fontinalis*: the response to familiar and unfamiliar predaceous fishes and the influence of fish diet. – *Canadian Journal of Zoology*. 70:288-292.

Lima, S.L. & L.M. Dill 1990. Behavioural decisions made under the risk of predation: a review and prospectus. – *Canadian Journal of Zoology* 68:619-640.

MacArthur, D.J. & E.R. Pianka 1966. On the optimal use of the patchy environment. – *American Naturalist* 100:603-609.

Magurran, A.E. 1986. Predator inspection behaviour in minnow shoals: differences between populations and individuals. – *Behavioral Ecology and Sociobiology* 19:267-273.

— 1990. The adaptive significance of schooling as an anti-predator defence in fish. – *Annales Zoologici Fennici*. 27:51-66.

Mathis, A. & R.J.F. Smith 1992. Avoidance of areas marked with a chemical alarm substance by fathead minnows (*Pimephales promelas*) in a natural habitat. – *Canadian Journal of Zoology* 70:1473-1476.

— 1993. Fathead minnows, *Pimephales promelas*, learn to recognize northern pike, *Esox liucius*, as predators on the basis of chemical stimuli from minnows in the pike's diet. – *Animal Behaviour* 46:645-656.

Metcalf, N.B., F.A. Huntingford & J.E. Thorpe 1987. The influence of predation risk on the feeding motivation and foraging strategy of juvenile Atlantic salmon. – *Animal Behaviour*. 35:901-911.

Miklósi, Á. & V. Csányi 1989. The influence of olfactory behaviour in the paradise fish (*Macropodus opercularis* L.). – *Acta Biologica Hungarica*. 40:195-202.

Milinski, M. 1979. An evolutionary stable feeding strategy in sticklebacks. – *Zeitschrift für Tierpsychologie* 51:36-40.

Nordeide, J.T. & A.G.V. Salvanes 1991. Observations on reared newly released and wild cod (*Gadus morhua*) and their potential predators. – *ICES Marine Science Symposia* 192:139-146.

Parker, G.A. 1978. Searching for mates. Pp. 214-244 in: Krebs, J.R. & N.B. Davies (eds). *Behavioural Ecology*. Blackwell Scientific Publications. Oxford.

Peters, R.C., K. Kotrschal, W.-D. Drautgartner, & J. Athema 1989. A novel chemosensory system in fish: electrophysiological evidence for mucus detection by solitary chemoreceptor cells in rocklings (*Ciliata mustela*, Gadidae). – *Biological Bulletin. Marine Biological Laboratory, Woods Hole, Mass*. 177(2):329

Pettersson, L.B. & C. Brönmark 1993. Trading of safety against food: state dependent habitat choice and foraging in crucian carp. – *Oecologia* 95:353-357.

Pfeiffer, W 1974. Pheromones in fish and amphibia. – Pp. 269-296 in: Birch, M.C. (ed.). *Pheromones*. North Holland, Amsterdam.

— 1977. The distribution of fright reaction and alarm substance cells in fishes. – *Copeia* 1977:653-665.

Pitcher, T.J., S.H. Lang & J.R. Turner 1988. A risk-balancing trade-off between foraging rewards and predation risk in shoaling fish. – *Behavioral Ecology and Sociobiology* 22:225-228.

Pitcher T.J., D.A. Green & A.E. Magurran 1986. Dicing with death: predator inspection behaviour in minnow shoals. – *Journal of Fish Biology* 28:439-448.

Segers, B.H. 1974. Geographic variation in the response of guppies (*Poecilia reticulata*) to aerial predators. – *Oecologia* 14:93-98.

Sih, A. 1987. Predators and prey lifestyles: an evolutionary and ecological overview. – Pp. 203-224 in: Kefoot, W.C. & A. Sih (eds). *Predation: Direct and indirect impacts on aquatic communities*. University of New England Press, Hanover, New Hampshire.

Smith, R.J.F. 1973. Testosterone eliminates alarm substance in the male fathead minnows. – *Canadian Journal of Zoology* 51:873-876.

— 1976. Seasonal loss of alarm substance cells in North American cyprinoid fishes and its relation to abrasive spawning behavior. – *Canadian Journal of Zoology* 54:1172-1182.

— 1989. The response of *Asterropteryx semipunctatus* and *Gnatholepis anjerensis* (Pisces, Gobiidae) to chemical stimuli from injured conspecifics, an alarm response in Gobies. – *Ethology*, 81:279-290.

— 1992. Alarm signals in fishes. – *Reviews in Fish Biology and Fisheries* 2:33-63.

Smith, R.J. & M.J. Smith 1989. Predator-recognition behaviour in two species of gobiid fishes, *Asterropteryx semipunctatus* and *Gnatholepis anjerensis*. – *Ethology* 83:19-30.

Svåsand, T. 1990. Comparisons of migration patterns of wild and recaptured reared coastal cod, *Gadus morhua* L., released in a small fjord in western Norway. – *Aquaculture and Fisheries Management* 21:491-495.

Utne, A.C.W. 1995. *Experimental investigations of habitat choice in fish*. – Dr.scient. dissertation. Department of Fisheries and Marine Biology, University of Bergen, Norway. 121 pp.

Utne, A.C.W. & D.L. Aksnes 1994. An experimental study on the influence of feeding versus predation risk in the habitat choice of juvenile and adult two-spotted goby *Gobiusculus flavescens* (Fabricius). – *Journal of Experimental Marine Biology & Ecology* 179:69-79.

Utne, A.C.W., D.L. Aksnes & J. Giske 1993. Food, predation-risk and shelter: An experimental study on the distribution of adult *Gobiusculus flavescens*. – *Journal of Experimental Marine Biology & Ecology*. 166:203-216

Accepted 12 February 1997