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Food, predation risk and shelter: an experimental study on the distribution of adult two-spotted goby *Gobiusculus flavescens* (Fabricius)

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Abstract: Adult two-spotted gobies *Gobiusculus flavescens* (Fabricius) distributed themselves according to the Ideal Free Distribution (IFD) when 10 individuals were offered equal amounts of prey items at two sites in aquaria. As ratios between the prey supply at the two sites increased, however, increasing deviations from the IFD were observed. It is suggested that perceptual constraints within the time scale of the experiments hampered optimal foraging at increased food supply ratios. Introduction of a predator caused a pronounced deviation from the IFD. It is suggested that in the trade-off between food availability and predation risk more emphasis is put on survival than feeding. Introduction of shelter at one of the sites had little or no effect on the observed distribution of gobies when a predator was absent. In the presence of a predator, however, shelter had a pronounced effect on goby distribution. *G. flavescens* spent up to five times more time in the vicinity of the predator when shelter was present.

Key words: Feeding; *Gobiusculus flavescens*; Predation risk; Trade off

INTRODUCTION

According to the ideal free distribution (IFD; Fretwell & Lucas, 1970) individuals distribute themselves so that every individual gets the same resources. Assuming only one kind of resource, such individuals should distribute themselves in a way that is proportional to the distribution of the resource itself (Abrahams & Dill, 1989) and individuals will not benefit by moving along the resource gradient. An IFD is expected when each individual is free to move anywhere, the survival expectancy is the same for all individuals and all individuals have the same needs and equal competitive abilities (Milinski, 1987). Equal competitive ability, however, is not an ultimate requirement (Sutherland & Parker, 1985).

IFD of fishes has been demonstrated several times in aquaria (Milinski, 1979; Gillis & Kramer, 1987; Pitcher et al., 1988). When individuals of a species are known to distribute according to the IFD in the presence of one resource (e.g., 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.

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In the present study, we have studied the distribution of *Gobiusculus flavescens* (Fabricius) in response to food availability, presence of a predator and shelter. In nature, *G. flavescens* is found in dense concentrations among or close to the macrovegetation in the marine sublittoral area (Fosså, 1991). Its prey (zooplankton), however, is produced in open water outside the *G. flavescens* habitat. In the near-shore coastal habitat, zooplankton is patchily distributed in both space and time (Magnesen, 1988; Aksnes et al., 1989; Fosså, 1991), and zooplankton availability is believed to be heavily influenced by the physical renewal rate of the near-shore water as well as by downwelling and upwelling events along the Norwegian coast (Aksnes et al., 1989; Giske et al., 1991). When *G. flavescens* abundance is high and sublittoral water renewal (i.e., zooplankton supply) is low, the fish may increase its food intake by moving outside its normal habitat. Here, however, the visibility to predators, and thereby the predation risk, is probably increased. In contrast, macrovegetation may serve as a shelter from visual predation. Accordingly, we conducted experiments to see if macrovegetation had any influence on the distribution of *G. flavescens* in the presence and absence of a predator.

MATERIALS AND METHODS

G. flavescens was collected in Raunefjorden close to Bergen, western Norway, where the depth was 2–5 m and *Fucus vesiculosus* L. was the dominant macroalga. A trap made of transparent plastic placed 0.5–1 m off the bottom was used and we believe that the fish were trapped by “accident” rather than by active search for shelter or other means. Several fish (shoals), swimming along two transparent leading plates and further into the trap through a small hole, were observed to be caught simultaneously. The gobies were kept for 14 days under laboratory conditions (30–40 ind in 150-l aquaria) before experiments were done. Living copepods were offered daily.

1 day before each experiment, 10 gobies were transferred into the experimental aquaria (Fig. 1). Here, no feeding was undertaken before initiation of the experiment. Only males of equal size (≈ 45 mm) were used in the experiments. During the experimental period (10 min), zooplankton were supplied suspended in water through two inlets at opposite sides of the aquaria (Fig. 1). 1 l of zooplankton suspension was supplied at each side during the experimental period. Different ratios at the two sides of the aquaria were achieved by adjusting the zooplankton concentration (Table I). The two concentrations were adjusted, however, so that the total number of zooplankters offered was kept at ≈ 600 ind in all experiments. *G. flavescens* could freely swim through the net between the two feeding sites of the aquarium (Fig. 1). The predator (when present), however, could not pass this net. This design was similar to that used by Abrahams & Dill (1989). The distribution of the gobies was recorded on video tape, and no one was present in the laboratory during the experiments. Artificial light was used and the irradiance was $12 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ in all experiments.

Copepods were used as prey. They were collected with a plankton net and kept alive

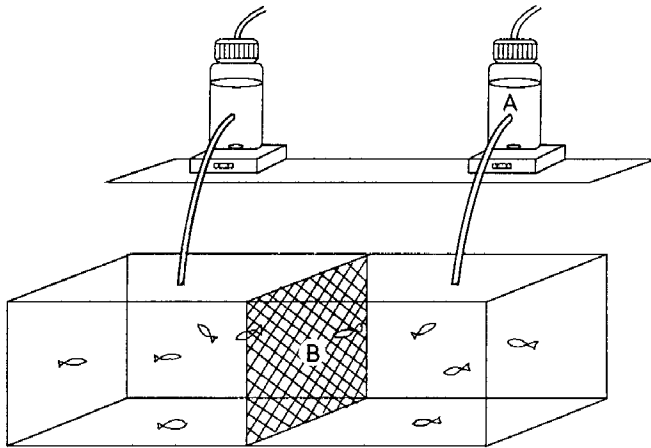


Fig. 1. Experimental design: A, zooplankton medium; B, net that allows *G. flavescens*, but not cod (when present), to swim through.

in containers for a maximum of 2 days. Samples were filtered through a 0.5-mm sieve and organisms in the size range 0.5–2 mm were used as food for the gobies. The main species were *Calanus finmarchicus* (Gunnerus), *Acartia* spp. and *Metridia longa* (Lubbock). The species composition can not be considered constant in all experiments. The relative difference between the ratios at the two sides of the aquaria, however, was not influenced by this constraint. To avoid over-feeding, the total ration of ≈ 600 ind (for 10 gobies) was chosen according to feeding capacity experiments (Table 1) where six gobies were allowed to eat freely at high zooplankton concentration ($40 \text{ ind}\cdot\text{l}^{-1}$). After 20 min, and a consumption of ≈ 60 ind, feeding ceased.

TABLE I

Summary of experiments with *G. flavescens*: combinations, number of experimental combinations of factors investigated; *n*, number of replicates for each experimental set-up; total, total number of experiments (combinations $\times n$). All experiments, except feeding capacity experiments, were carried out with 10 *G. flavescens*.

Factors investigated	Combinations	<i>n</i>	Total
Feeding capacity	1	6	6
IFD			
at feeding ratios 1:1, 1:2, 1:5 and 1:8	4	3–5	15
Influence of predator at feeding ratios 1:5 and 5:1	2	3	6
Influence of shelter at feeding ratios 1:5 and 5:1	2	3	6
Influence of predator and location of shelter at feeding ratios 1:5 and 5:1	8	3	24
Total			57

Cod *Gadus morhua* was used in experiments where the effects of predator presence on the distribution of gobies were investigated. This species has proved to be the main predator on *G. flavescens* (Nordeide & Salvanes, 1991). One 23-cm cod was collected with an eel-trap at the same locality as the gobies and was used in all experiments. Initially, the cod was kept in a separate aquarium, but the gobies soon realized that it did not represent any threat. The smell of the cod may perhaps affect the behaviour of the gobies. Consequently, it was decided to locate the cod in the same aquaria as the gobies. The cod chased the gobies, but no goby was caught during the experiments.

Simulated macroalgal vegetation was used to determine the effect of shelter on the distribution of gobies. Plastic material was selected in favour of real macroalgae to eliminate possible influence of epizoites and metabolites on goby behaviour. Furthermore, the synthetic shelter could be used in all experiments to minimize differences between experiments.

In addition to the feeding capacity observations, a total of 51 experiments were done (Table I). The food ratios 1:1, 1:2, 1:5 and 1:8 were used to see how gobies distributed themselves when neither predator nor shelter was present (denoted "IFD experiments"). We wanted to investigate the influence of predator, shelter and the combination of both when different amounts of food were offered at the two sides of the aquaria, and the food ratio 1:5 (and 5:1) was chosen for this purpose (Table I). In all trials, the numbers of fish located at both sides of the aquaria were recorded every 30 s for 12 min, providing 24 pairs of observations in each trial. The first 90 s of the experiment were excluded from the analyses as the gobies needed some time to "measure" the profitability at the two feeding sites. The mean of the 24 observations was used to characterize the distribution in each of the particular trials. Three trials (five in IFD 1:5 experiments) were repeated for each experimental set-up (i.e., for each combination of predator, shelter, etc.), each time with a new group of gobies. The mean and standard deviation were then calculated on the basis of these three (or five) replicates. Experiments with a predator were compared with the experiment without a predator (IFD 1:5) to determine the influence of the predator on the distribution of gobies. Influence of shelter (in the absence of a predator) was also assessed by comparison with the IFD 1:5 experiment. Influence of shelter, in the presence of a predator, however was assessed by comparison with the experiment with a predator, but no shelter. All comparisons were made using the two-tailed *t* test (Sokal & Rohlf, 1981). Supplementary to the observations of the number of fish at each feeding site, the number of passages through the net between the two sites was also noted.

All experiments were conducted between 1200 and 1500 in the nonreproductive period from August to December. In five out of the 59 experiments, one or two fish were observed inactive, lying at the bottom during the experiments. These individuals were excluded from the analysis. Consequently, the results are sometimes based on a total number of fish, that is slightly less (as the results are based upon at least three replicates) than 10.

TABLE II
Influence of feeding ratio on distribution of *G. flavescens*.

Feeding ratio	1:1	1:2	1:5	1:8
Number of fish at most profitable side predicted by IFD	4.48	6.32	8.27	8.84
Mean number of fish at most profitable side in experiments	4.46	6.30	7.86	7.81
SD	0.40	1.27	0.27	0.30
Number of experiments	3	4	5	3

RESULTS

EXPERIMENTS WITHOUT PREDATOR AND SHELTER

At food ratios of 1:1 and 1:2 the average numbers of fish at the two sites during the experiments were 1:1.01 and 1:1.98 which are very close to predictions from IFD theory (Table II). At food ratios of 1:5 and 1:8, however, there were some deviations

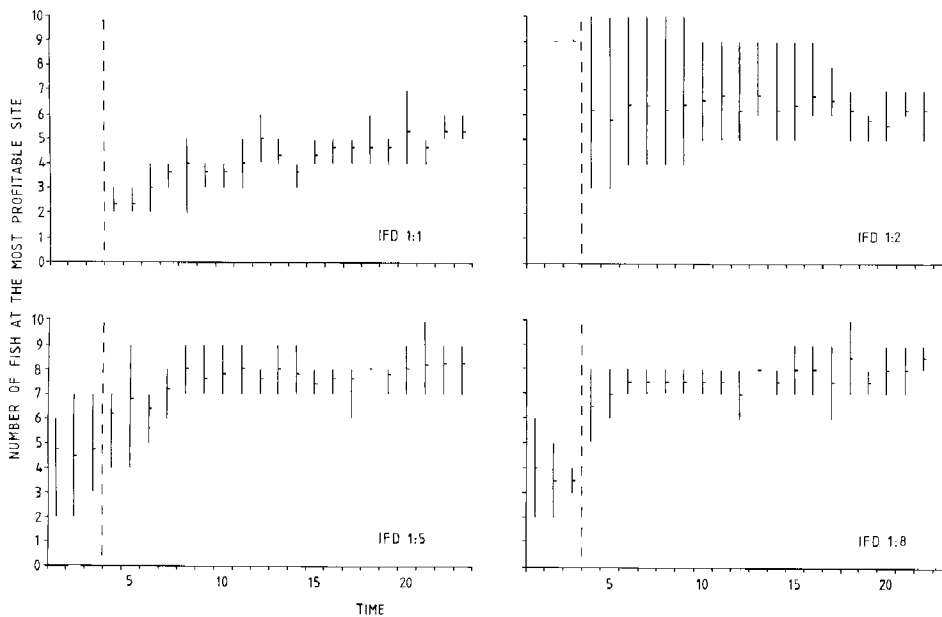


Fig. 2. Time course of distribution of *G. flavescens* in IFD experiments. x axis gives numbers of observations (30 s between each), while y axis indicates number of fish at most profitable site. Vertical bars indicate maximum and minimum of replicates (four in 1:1, five in 1:5 and three in two others). Feeding was initiated after 90 s (vertical lines).

TABLE III
Distribution of *G. flavescens* in presence of shelter.

Feeding ratio 1:5	Most profitable patch on shelter side	Least profitable patch on shelter side
Mean number of fish at shelter side	8.40	1.85
SD	1.10	0.49
Number of experiments	3	3
<i>t</i> test: comparison with IFD 1:5 (Table II)		
<i>t</i>	-1.10	0.80
<i>P</i>	0.40	0.50
df	6	6

from the IFD. The largest deviations were observed during the first minutes when gobies had least experience of the two sites, and inspection of the time courses of the experiments indicated that *G. flavescens* improved their distribution during the experiments (Fig. 2).

EXPERIMENTS WITH SHELTER

In these and later experiments, the 1:5 food ratio was used. Introduction of shelter at the site with most food did not seem to influence the preference of *G. flavescens*. Although a weak tendency for preference of the shelter-site was observed, the results did not differ significantly from the experiment without shelter (Table III). The same conclusion was drawn from the experiments where shelter was placed at the site with least food (Table III).

TABLE IV
Distribution of *G. flavescens* in presence of a predator.

Feeding ratio 1:5	Most profitable patch on predator side	Least profitable patch on predator side
Mean number of fish at predator side	0.79	0.06
SD	0.42	0.06
Number of experiments	3	3
<i>t</i> test: comparison with IFD 1:5 (Table II)		
<i>t</i>	27.81	11.83
<i>P</i>	0.001	0.01
df	6	6

EXPERIMENTS WITH PREDATOR

Introduction of cod at the site with the most food had a pronounced effect on the distribution of *G. flavescens* (Table IV). On average, <1 preferred the site with most food (and the predator), while >7 preferred this site when the predator was absent (Table II). The same effect was found when the predator was placed at the site with least food. On average, <0.1 (or <1% of available time) preferred this site, while <2 preferred the same site in the absence of the predator.

EXPERIMENTS WITH SHELTER AND PREDATOR

The distances between shelter, feeding site and predator are probably of significance when the goby decides where to stay. Therefore, the shelter was placed at different

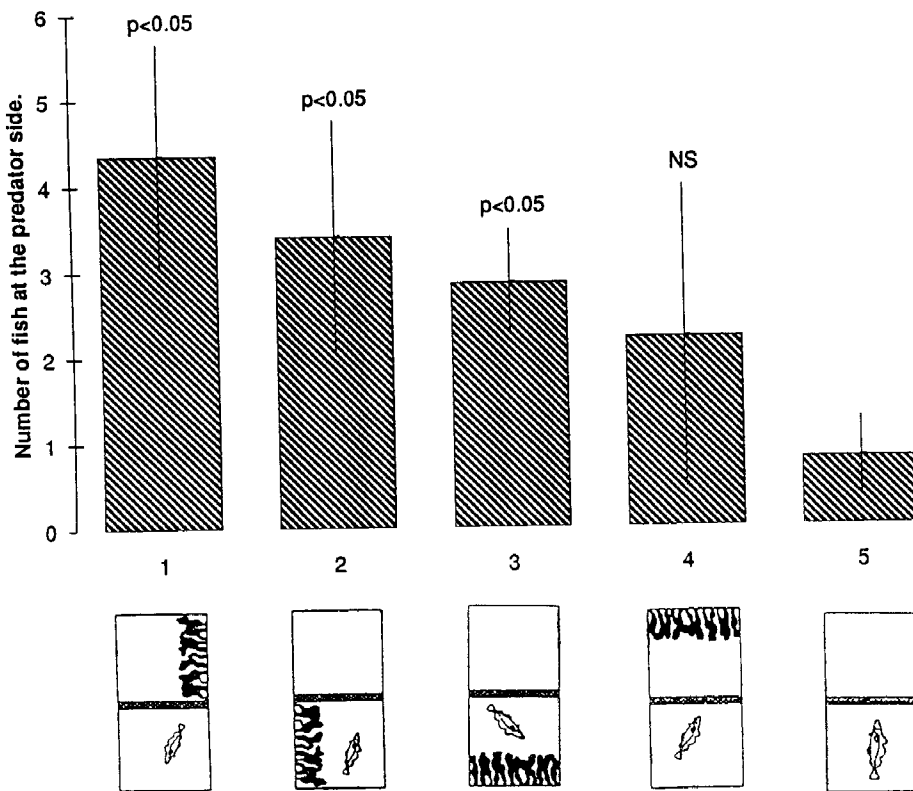


Fig. 3. Distribution of *G. flavescens* in presence of both shelter and predator (except Column 5, which is experiment of comparison, where no shelter was present). Illustrations below indicate locations of cod and shelter in aquarium as seen from above. Shelter had a significant effect on distribution of *G. flavescens* when shelter was close to predator (three bars to left), but not when shelter was placed at largest distance from predator (Bar 4).

TABLE V
Distribution of *G. flavescens* in presence of both shelter and a predator

Feeding ratio 1:5	Column number in Fig. 3				
	1	2	3	4	5
	Experiment of comparison (Table IV)				
Mean number of fish at predator side	4.34	3.40	2.86	2.21	0.79
SD	1.31	1.34	0.61	1.76	0.42
Number of experiments	3	3	3	3	3
<i>t</i> test: comparison with experiment with most profitable patch on predator side and no shelter (Table IV)					
<i>t</i>	-4.46	-3.20	-4.69	-1.76	
<i>P</i>	0.05	0.05	0.05	0.20	
df	4	4	4	4	

locations in the aquarium (Fig. 3). More time was spent with a predator when shelter was placed close to the net that prohibited predator passage between the two sites (Fig. 3). Least time was spent with a predator when shelter was placed at the maximum distance from the predator. Here also, the shelter seemed to reduce the fear of the cod, although the outcome of this experiment was not statistically different from the corresponding experiment with cod, but without shelter ($P = 0.2$, Table V). At the three other shelter locations (Columns 1–3 in Table V and Fig. 3), the results differed significantly ($P = 0.05$) from the experiment without shelter. The presence of shelter did not over-ride the fear of the cod in any of the experiments, however, because fewer individuals (2.21–4.34, Table V) were located at the site with most food (and the predator) than in the experiments without a predator at this site (8.40, Table III).

MOVEMENTS BETWEEN FEEDING SITES

The activity of the gobies, measured as the number of passages between the two sites, was highest (a mean of $0.52 \text{ passages} \cdot \text{fish}^{-1} \cdot \text{min}^{-1}$, $\text{SD} = 0.025$) in the IFD ex-

TABLE VI
Activity of *G. flavescens* during experiments measured as mean number of passages between two sites.

Experiments	Passages $\cdot \text{fish}^{-1} \cdot \text{min}^{-1}$	SD
Without predator and without shelter	0.52	0.025
With shelter	0.32	0.071
With predator located at site with		
Most food	0.27	0.047
Least food	0.05	0.017
With predator and shelter. Predator located at site with		
Most food	0.23	0.090
Least food	0.10	0.038

periments (Table VI). Presence of shelter seemed to decrease the activity ($0.32 \text{ passages} \cdot \text{fish}^{-1} \cdot \text{min}^{-1}$, $\text{SD} = 0.071$). The most pronounced decrease in activity was observed in the presence of a predator, especially when the predator was located at the site with least food ($0.1 \text{ passages} \cdot \text{fish}^{-1} \cdot \text{min}^{-1}$, $\text{SD} = 0.038$).

DISCUSSION

IFD AND DEVIATIONS FROM IFD

G. flavescens distributed themselves close to the IFD when food ratios between sites were 1:1 and 1:2. At the higher ratios of 1:5 and 1:8 fewer individuals than predicted by IFD-theory were found at the site with highest food availability (Table II). This finding means that the site with the highest food input was under-utilized and that the reward (in terms of number of food items per fish) was highest at this site. This deviation from the IFD was highest at the 1:8 ratio (Fig. 4). Increased deviation from the IFD, with increased difference in feeding between sites, has also been observed in several other published experiments where continuous feeding has been applied (Fig. 4). Such deviation from the IFD is expected from models of perceptual constraints (Abrahams, 1986) and despotism (Harper, 1982). Furthermore, differences in competitive abilities may also cause an apparent deviation from the IFD. This means that although the ratio between the number of fish at each site differs from the food input ratio, the individual food intake corresponds to IFD theory (Sutherland & Parker, 1985; Parker & Sutherland, 1986). However, despotism and unequal competitive abilities are unlikely here, as an IFD was observed at a food ratio of 1:2. Perceptual constraints seem to be a more likely explanation, although the other explanations can not be excluded. As observed by Milinski (1979), individuals need time to test out the two feeding sites and thereby to establish an IFD (Fig. 2). When input rates at the two sites differ considerably, exact assessment of differences in profitabilities may be difficult (Abrahams, 1986). Furthermore, use of > 10 fish might have been given a closer fit to the IFD because ratio estimators (the ratio between the number of fish at each site) are likely to be imprecise and biased when they are based upon small discrete counts rather than continuous numbers. Thus, we believe that the deviation from the IFD in our experiments may be a result of perceptual constraints (at least the deviations within the time course of the experiments; Fig. 2) and probably also experimental constraints (at least in the IFD 1:8 experiment). Hence, the experimental design (both duration and number of fish) may interfere with the results, and this calls for caution in interpretations and comparisons of results from these kinds of behaviour experiments.

TRADE-OFF BETWEEN PREDATION RISK AND FOOD AVAILABILITY

Introduction of a predator (cod) had a highly significant effect because little time was spent in the side of the aquarium containing the predator (Table IV). Fraser & Hunt-

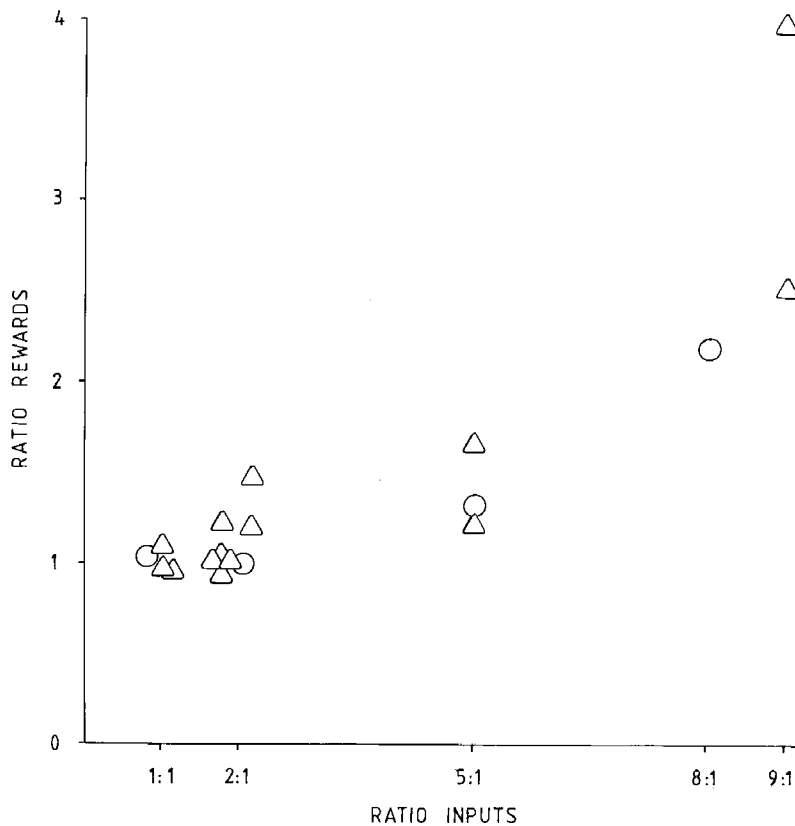


Fig. 4. Deviation from IFD at increasing ratios between food at two sites. A ratio reward of 1 means that food per fish is equal at two sites (IFD). Increase in reward at most profitable patch (y axis) with increased input ratio is caused by under-utilization of most profitable patch, i.e., fewer individuals than predicted by IFD are aggregating at this patch. Results from present investigation are marked with open circles. Other observations are taken from Milinski (1979, 1984), Harper (1982), Godin & Keenleyside (1984), Shingler (1985) and Sutherland et al. (1988). Modified after Sutherland et al. (1988).

ingford (1986) list four different reactions to predation risk; risk reckless, risk avoiding, risk adjusting and risk balancing. To balance risk, individuals take a higher risk if more food becomes available. This corresponds to the behaviour of *G. flavescens* because we observed a clear tendency to take higher risks when more food was offered on the side of the aquarium with the predator (Table IV). If predation risk is measured as the number of goby visits to the predator's side, the risk was about five times higher in the experiments with a high food level on the predator's side compared with those with a low food level on the predator's side (Table IV).

Although the experiments did not have the appropriate design to reveal quantitative formulated decision rules for habitat shifts, it is indicated that *G. flavescens* increases

its predation risk if the relative increase in feeding availability is higher than the relative increase in risk exposure. The reward associated with risk exposure can be assessed by comparing the individual food availability at the sites. This food availability may be inferred from the feeding rate at the site divided by the average number of fish at the site. It may then be calculated that in the experiment with predator at the site with most food (Table IV), the food availability for the one choosing the predator site (5 food units: 1 ind = 5) could increase, relative to those staying at the safe site (1 food unit: 9 ind = 0.11), by a factor of ≈ 50 . On the other hand, in the experiment with a predator at the site with least food, the food availability for the one choosing the predator site (1 food unit: 1 ind = 1) increased only by a factor of ≈ 2 relative to those staying at the safe site (5 food units: 9 = 0.56). Thus, in terms of food availability, it was ≈ 25 times more profitable to choose a site with a predator in the first experiment. This relative increase in reward was apparently also reflected as increased risk exposure because a mean of 0.79 ind aggregated at the predator site in the first experiment while only 0.06 did so in the second experiment (Table IV). Due to the high standard deviations, however, these figures are not reliable estimators of the risk exposure. Using the passage rate as an alternative measure of risk exposure (Table VI), it can be inferred that the risk exposure was increased by a factor of 5.4 (0.27/0.05) in the high food predator experiment compared to the low food predator experiment. Thus, although somewhat speculative, it is indicated that the increase in exposure risk (≈ 5 times) was associated with a higher increase in food availability (≈ 25 times). In other words, increase in predation risk is given more weight than increase in feeding availability when the decision on where to stay is taken. This is in accordance with the theoretically derived "clutch-manipulator" strategy of Aksnes & Giske (1990), where, the ratio between predation risk and the logarithm of feeding rate should be minimized or kept constant in order to induce a habitat shift. This strategy is likely to apply to adults, and to organisms unable to increase fitness by reduction in time to next spawning (i.e., fixed time to spawning is assumed). For "time manipulators", the ratio between predation risk and feeding rate should be minimized or kept constant to induce a habitat shift (Aksnes & Giske, 1990). This strategy corresponds to that derived by Werner & Gilliam (1984) in which an increase in predation risk may be compensated for by the same relative increase in feeding opportunity. According to this rule, a 25-fold increase in predation risk may be accepted if the feeding availability is increased 25 times.

Our experiments were conducted on adult *G. flavescens* that spawn yearly. Due to the strong environmental seasonality at the coast of Norway, any reduction in time to next spawning (such as winter spawning) will most probably lead to a mismatch between the survival requirements of the offspring and the conditions offered by the environment. As a result of such seasonality, a fixed time between spawnings gives a fitness reward, and the clutch manipulator strategy is to be expected. Whether this strategy applies to juvenile depends, according to the theory of Aksnes & Giske (1990), on how fitness is affected by a possible food-induced shortening of the juvenile period.

More experimentation is needed to test for quantitative formulated decision rules. Our preliminary results clearly indicate, however, that it is possible to make quantitative comparison of food opportunities and predation exposure. By altering the experimental design it should be possible to quantify the trade-off between the two by varying the food availability (adjusting the zooplankton concentration in the outflowing water, as in the IFD experiments) and the predation risk (adjusting the location of the shelter).

INFLUENCE OF SHELTER ON PREDATOR AVOIDANCE

The introduction of shelter had only a negligible effect, if any, on the distribution of gobies at the two feeding sites when a predator was absent. The number of passages between the two sites, however, seemed to decrease when shelter was introduced (Table VI). Presence of shelter may have induced an increase in perceived safety, which in turn resulted in more time spent at each visit to a site (shelter was visible from both sites). As stated above, however, this did not significantly affect the average number of individuals present at each site (Table III). Introduction of a predator, however, induced increased preference for the shelter site (Fig. 3). The average number of individuals present close to the predator increased by a factor of 2.8–5.4 when compared with experiments without shelter (but with predator). The distance between shelter and predator seemed to be decisive for predator avoidance as the gobies spent more time on the predator side when shelter and predator were close (Fig. 3). Such behaviour has also been observed in mammals (Lima et al., 1985) and birds (Lima, 1985).

Our experiments indicate that *G. flavescens* is able to utilize shelter as a function of perceived predator risk. Hence, we could hypothesize that they should extend their distribution out from their habitat of nearshore macroalgae when predation risk and food concentrations are low. Dense aggregations, exceeding $150 \text{ ind} \cdot \text{m}^{-3}$ have been observed within macroalgae (Fosså, 1991) and the local zooplankton availability is thus likely to be depleted within this safe habitat. Reduction or elimination of predation risk outside the macroalgal habitat is therefore expected to induce a shift to a more pelagic habitat as zooplankton availability is likely to be higher there. This is in accordance with Werner & Hall (1988), who, by comparing five lakes, found pelagic habitat use of juvenile bluegill sunfish to be correlated with pelagic predation risk. Werner et al. (1983) also found that juvenile bluegill sunfish moved into open water to feed in the absence of predators.

G. flavescens is a major link between pelagic secondary production and production of near-shore and benthic fishes (Fosså, 1991; Giske et al., 1991; Nordeide & Salvanes, 1991). From an ecosystem perspective two contrasting effects may be postulated from its potential shifts between two habitats: (1) Oscillations in zooplankton abundance will be reduced by gobies, giving their predators a more even food regime: at reduced food availability, the gobies may tend to compensate for low growth conditions by moving more frequently to the pelagic, thus exposing themselves to increased predation. When feeding opportunities are good, gobies may remain hidden to a greater extent. (2) Dur-

ing periods of poor feeding conditions the goby population may be exposed to such intense predation that the population density of their predators will be reduced, because the predation rate has reduced their prey to such low levels that a large predator population can no longer be sustained.

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