

## Diel activity pattern and food search behaviour in cod, *Gadus morhua*

Svein Løkkeborg<sup>a</sup> & Anders Fernö<sup>b</sup>

<sup>a</sup>*Institute of Marine Research, Fish Capture Division, P.O. Box 1870, N-5024 Bergen, Norway*

(e-mail: svein.lokkeborg@imr.no)

<sup>b</sup>*Department of Fisheries and Marine Biology, University of Bergen, High Technology Center, N-5020 Bergen, Norway*

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### Synopsis

Food search behaviour in cod, *Gadus morhua*, was studied by means of a stationary positioning system. Six fish in a fjord in northern Norway were tagged *in situ* by allowing them to swallow bait-wrapped acoustic tags, and their swimming behaviour was continuously recorded. The fish exhibited a diel activity rhythm, with higher swimming speeds and a larger range during the day than at night. Chemically mediated food search was studied in periods of both high and low activity by setting a string of baits in the morning and at night. During the period of high activity, more fish localized the baits (70 versus 45% of the observations) and the time to localization was 50% shorter, indicating that high swimming activity increased the probability of encountering the odour plume and the odour source. No diel variations in the response threshold to olfactory stimuli were found, as the proportion of fish in the odour plume that responded rheotactically, and their response distances were similar in the two periods (240 and 227 m respectively). Cod performed area-restricted searches on encountering the string of baits during the day. The probability of cod detecting prey by taste receptors, encountering the odour plume of prey or localizing a stationary food source after olfactory stimulation should be relatively independent of light, and this could explain why cod were active throughout the 24 h cycle. On the other hand, the visual detection distance and the ability to capture active prey are influenced by the light level, resulting in higher activity during the day.

### Introduction

Animals can adapt to spatio-temporal variations in the environment by selecting locality and activity level. Many laboratory and field studies on fishes have demonstrated variations in activity throughout the 24 h cycle. The activity has been observed to peak during the day, at night or at dawn and dusk, and the activity pattern can be influenced by season, group size and social status (Thorpe 1978, Kavaliers 1980, Fernö et al. 1986, Løkkeborg et al. 1989, Fraser et al. 1993, 1995, Heggenes et al. 1993, Alanä-

rä & Brännäs 1997, Anras et al. 1997, Thetmeyer 1997). Although it is often assumed that diel rhythms are adaptations to temporal variations in predation pressure and food availability, our knowledge of the functional significance of activity rhythms is scanty (Helfman 1993).

Diel rhythms have also been observed in cod, *Gadus morhua*. Clark & Green (1990) observed both diel and seasonal variations in activity pattern and habitat selection of acoustically tagged juvenile cod. Shifts in activity were regarded to reflect an antipredator behaviour, but it was difficult to separate

the effects of predation, temperature and prey selection. To learn the functional significance of diel rhythms, it may thus be essential to study a situation where temporal variations in one factor mainly mould the behaviour. Adult cod experience a low predations risk (Palsson 1994), and outside the spawning season, the behaviour should thus reflect their feeding behaviour.

The success of searching for food depends on the search pattern, the efficiency of locating resources and the ability to adapt to changes in the environment (Bell 1990). There are at least three aspects of the searching behaviour that can vary over the 24 h cycle. The speed of movement and the search pattern (e.g. the tendency to turn between successive movement steps) can show diel rhythms. In addition, the tendency to react when exposed to various stimuli could show diel variations. The probability both to come into contact with various stimuli and to react to stimulation could thus show temporal variations.

In experiments in the North Sea, the activity of cod towards baited hooks peaked at dawn and dusk in September and at noon in December (Løkkeborg et al. 1989). The rhythms were believed to reflect variations in the feeding tendency, but in this study, it was not possible to separate diel variations in the tendency to react to olfactory stimuli from diel variations in other aspects of the food search behaviour. Variations in the long-distance attraction to food could have a strong influence on the activity level. Spiny lobsters, *Panulirus interruptus*, have been reported to respond to much lower concentrations of chemical attractants when being active than passive (Zimmer-Faust et al. 1996). On the other hand, animals may be generally passive when the chance to detect prey is low, yet have a strong tendency to react to chemical stimuli from the prey if the localization and capture success are high. To understand diel activity rhythms it is therefore essential to study the activity both during search with and without environmental cues.

Behavioural studies of cod when searching for and capturing prey items have provided information on the relative importance of the sensory modalities involved in food location and detection (Brawn 1969, Pawson 1977, Løkkeborg et al. 1989).

Both the visual and the chemical senses are important. Cod can be attracted to food by chemically mediated rheotaxis (Pawson 1977, Løkkeborg 1998). Cod in nature probably regulate activity level so as to maximize growth for a given prey availability (Kerr 1982). As the success of locating prey with different sensory modalities like vision and olfaction may depend on the light conditions, we hypothesized that the activity pattern and search style in cod may be related to time of day. Diel variations in stomach contents in cod with, e.g., more amphipods at night than during the day (Mattson 1990) also indicate changes in feeding styles over the 24 h cycle.

We used a stationary positioning system to study food search pattern of acoustically tagged adult cod outside the spawning cycle in a fjord in northern Norway, emphasizing diel variations in search for and localization of food. By setting a string of baits in the vicinity of the fish during the day and at night, respectively, diel rhythms both in the tendency to react to chemical stimuli and in other aspects of the food search behaviour could be investigated.

## Material and methods

The experiment was carried out in a small fjord in northern Norway in September–October 1996. The experimental site was at depths of 30–60 m in Ramfjord, a small side branch of the larger Balsfjord. Cod tagged with transmitters operating on various frequencies were tracked by means of a stationary positioning system (VRAP, Vemco Ltd.) that consisted of three hydrophone buoys anchored in a triangular configuration, at distances between the buoys between 405 and 820 m. The hydrophones received a series of pulses from the transmitter, and the time at which each pulse was received was registered by the buoys. The data were radio transmitted to a base station mounted on board a research vessel, and an average positional fix was calculated from the relative time delay of pulse arrivals at the hydrophones. A fix was made every 30 s, and its horizontal coordinates (x, y) and the real time were logged to disk. When tracking several fish simultaneously, one selected frequency (transmitter) was monitored at a time, and the in-

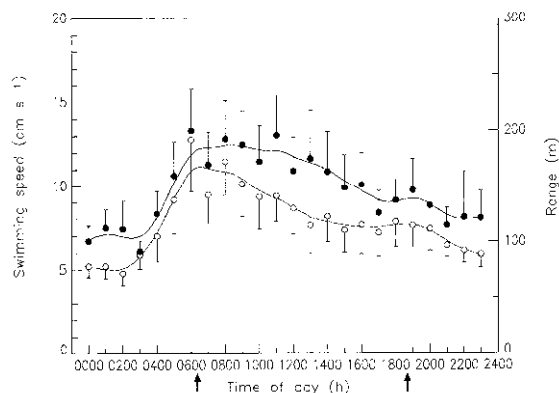


Figure 1. The mean swimming speed of cod (closed circles) during the 24 h cycle and the mean range within which cod swam within a period of one hour (open circles). Vertical bars denote standard error ( $n = 6$ ). Arrows indicate sunrise and sunset in the middle of the observation period (23 Sept).

Intervals between fixes on any one fish were multiples of 30 s.

Cod were tagged *in situ* by allowing them to ingest transmitters wrapped in mackerel baits. An underwater camera mounted in a frame was used to identify the fish that ingested the transmitter. The bait-wrapped transmitter was attached by a fine thread to the frame that was placed on the seabed. The frame had marks 10 cm apart to enable the observers to estimate the length of the tagged fish, and a bag filled with chopped mackerel was attached to the frame to attract fish more effectively. Transmitters of different sizes were used. All were 16 mm in diameter and were 48–80 mm long; they weighed 9–12 g in water. A more detailed description of the positioning system and tagging procedure is provided by Engås et al. (1996).

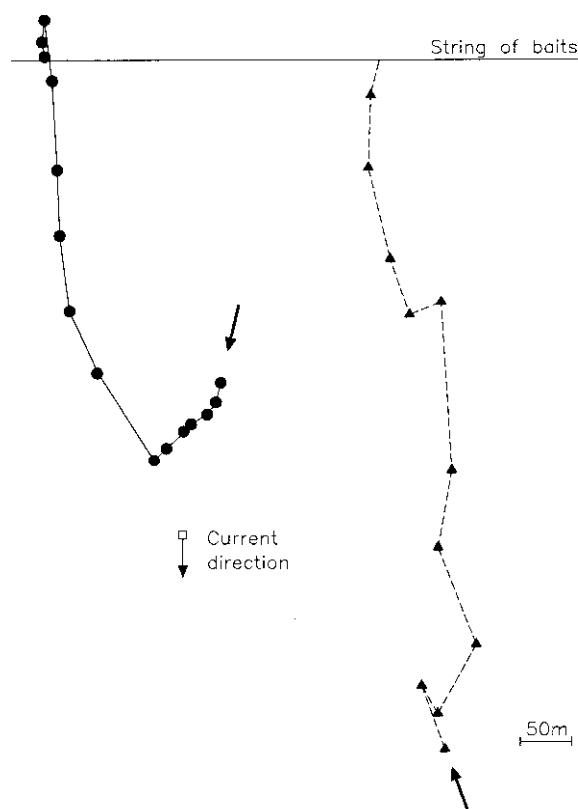
Six cod (estimated length: 40–55 cm) were tagged and their movements were tracked continuously for several days. One of the cod was tagged with a transmitter equipped with a depth sensor which provided three-dimensional fixes ( $x$ ,  $y$ ,  $z$  coordinates). All fish stayed in the study area, but two fish regurgitated their transmitters during the experimental period. Diel swimming activity rhythm, in terms of swimming speed and range of area occupied, was determined on the basis of six to eight days of tracking of individual fish. The tracks were visually inspected, and spurious fixes due to background noise or signals reflected from rocks were

manually removed prior to data analysis. Swimming speed was calculated by using the elapsed time and distance between successive fixes. When a fish was out of range of the positioning system for more than 10 min, the swimming speed recorded for this interval was not included in the analysis. The distance between the two fixes furthest apart was used as a simple estimate of the range of the area within which the fish were swimming over a period of one hour, i.e. the diameter of the circle within which the fish were swimming. Only periods during which at least one positional fix was recorded in each quarter of an hour were included in this analysis.

Search pattern and responses to food odour were studied by setting a string of mackerel baits over the seabed in the study area. The string had about 400 baits attached to a line at intervals of 1.2 m. To study diel variations in food search behaviour, baits were soaked during period of the day when cod activity was high and low, respectively. Periods of high and low activity were defined on the basis of diel rhythms in swimming speed and range of area occupied (see Results). A total of sixteen trials were conducted over a period of 11 days; seven trials were conducted in high-activity periods, and nine in periods of low activity. The behaviour of the two fish that regurgitated their transmitters was observed only in three and seven of the 16 trials.

Transmitters were attached to the string of baits in order to determine its position, and the string was set across the fjord with most but not all fish downstream of the baits. This allowed both chemically stimulated and random food searches to be studied. Current speed and direction were recorded by two current meters suspended one metre above the seabed, close to the locations of the string of baits and the majority of the fish. The width of the odour plume was defined by the projection of the string of baits along the current direction, e.g. with a current direction perpendicular to the string, the plume width was regarded to be equal to the length of the string. An odour plume is dispersed by the current because diffusion is low (Kleerekoper 1982), and the front of the plume was therefore regarded as moving at the speed of the current, which varied between  $< 2$  (the lower threshold of the current meters) and  $12 \text{ cm s}^{-1}$ .

a



b

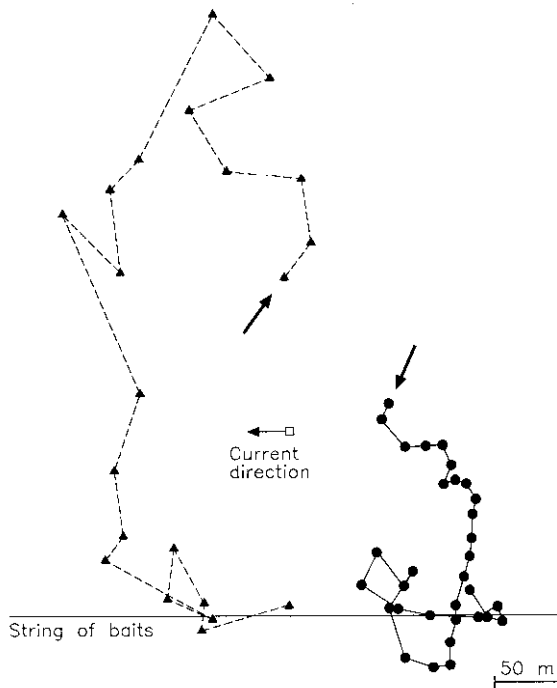


Figure 2. Tracks of four cod locating baits: a – two through chemically stimulated rheotaxis, and b – two through random search. The elapsed time between successive positional fixes was 3 min except for a few cases where the elapsed time was 6 min due to missing fixes. Note the increase in swimming speed when one of the cod (a) changed swimming direction and swam upcurrent towards the baits. Arrows indicate current direction and start of the track.

The ability of cod to locate baits was studied by comparing the tracks of the fish with the position of the baits in the period after the string of baits was set. The tendency to encounter baits and the time that elapsed until the fish located baits were compared between sets made during periods of high and low activity.

## Results

Cod exhibited diurnal activity rhythms both in swimming speed and area occupied (Figure 1). Activity increased in the morning between 4 and 6 h, remained high until 14 h and then gradually decreased throughout the afternoon and evening. At night the activity was relatively low. In order to

study differences in behavioural responses to food in periods of high and low activity the string of baits was therefore set between 6:15 and 8:45 h (mean swimming speed =  $13 \text{ cm s}^{-1}$ , mean range = 169 m) or between 21:00 and 23:30 h (mean swimming speed =  $8 \text{ cm s}^{-1}$ , mean range = 93 cm), and the pattern of movement of the fish was observed for a period of six hours. The cod tagged with a depth transmitter remained close to the bottom at depths ranging from 37 to 58 m during periods of both high and low activity, indicating that the fish did not exhibit vertical migration.

When the string of baits was set, the mean distance between the tagged fish and the string was 262 m (range: 23–768 m). Tagged fish that occupied the area where the baits were set (i.e. within a distance of 10 m from the string) were not included in

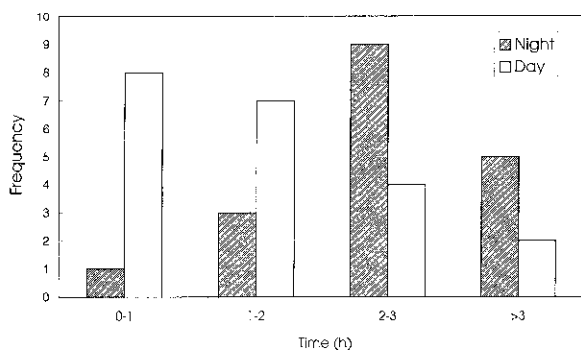


Figure 3. Elapsed time between setting a string of baits and location of the baits in the periods of high activity during the day and low activity at night.

the analysis. All six fish located the baits; the two that regurgitated their transmitters once and twice, the other four 6–12 times. The fish appeared to locate the baits through one of two different search patterns; encounter by random search or chemically stimulated rheotaxis (Figure 2). Fish that were downstream of the baits and swam upstream towards the bait source after the current had carried the odour released by the baits to them were classified in the latter category. The dispersion speed and direction of the odour plume were calculated from the records of the current meter nearest to the string of baits. All other fish were regarded as having located the baits by random search.

A higher level of swimming activity was expected to increase the probability of encountering food items. The six cod showed a higher tendency to encounter baits during periods of high (day) than low (night) activity (one-tailed sign test,  $p < 0.05$ ), and the proportions of observations during which cod encountered baits, regardless of search pattern, were 0.70 (21/30) and 0.45 (18/40) respectively. The time that elapsed until the fish located baits was shorter during the day (Figure 3; means: 81 and 166 min, respectively; paired-sample  $t$  test,  $p < 0.05$ ). Five of the six fish showed a higher tendency to locate baits when encountered by the odour plume than when staying upcurrent or out of range of the plume, whereas there was no difference for one fish. There was no significant difference between the two periods in the probability that fish in the odour plume would locate baits (13/15 = 0.87 during the day and 10/15 = 0.67 at night). Nor was there any

difference between day and night in the mean distance from which the fish responded during chemically stimulated rheotaxis (240 and 227 m respectively).

The range of the area within which the fish were swimming decreased when the fish encountered baits during the day. During a 30-min period prior to localization, the mean diameter of the area that the fish were occupying was 174 m compared with 87 m during the 30-min period immediately after locating baits (paired-sample  $t$  test,  $p < 0.01$ ). Swimming speed also decreased when the fish encountered baits during the day. The mean swimming speed was  $21 \text{ cm s}^{-1}$  during a 30-min period immediately before the fish responded to the baits and  $11 \text{ cm s}^{-1}$  when the fish stayed within the vicinity of the baits after locating them, i.e. within a range of 40 m defined as categories (a) and (b) below ( $p < 0.05$ ). At night there were no significant differences before and after locating the baits either in diameter of area occupied (78 and 70 m, respectively) or in swimming speed ( $9$  and  $15 \text{ cm s}^{-1}$ , respectively).

Upon encountering baits, the fish either (a) moved along or in the close vicinity of the string of baits (Figure 4a), (b) moved within a larger area around the string without showing any apparent reaction to the baits (Figure 4b), or (c) moved from the area in which the string was set. Fish were classified in these three categories on the basis of the distance within which they were moving perpendicularly to the string of baits, 0–15 m, 16–40 m and  $> 40$  m, respectively. To be classified in categories (a) and (b), the fish had to stay within these ranges for at least 10 min. During the day, (a) was the dominant behavioural category, whereas category (c) dominated at night (Figure 5; chi-square,  $p < 0.05$ ). Encounters classified in category (a) during the day occurred within a shorter time after the baits were set than encounters classified in categories (b) and (c) (means: 70 and 119 min, respectively;  $t$  test,  $p < 0.05$ ).

## Discussion

Rhythms in foraging behaviour ought to be related

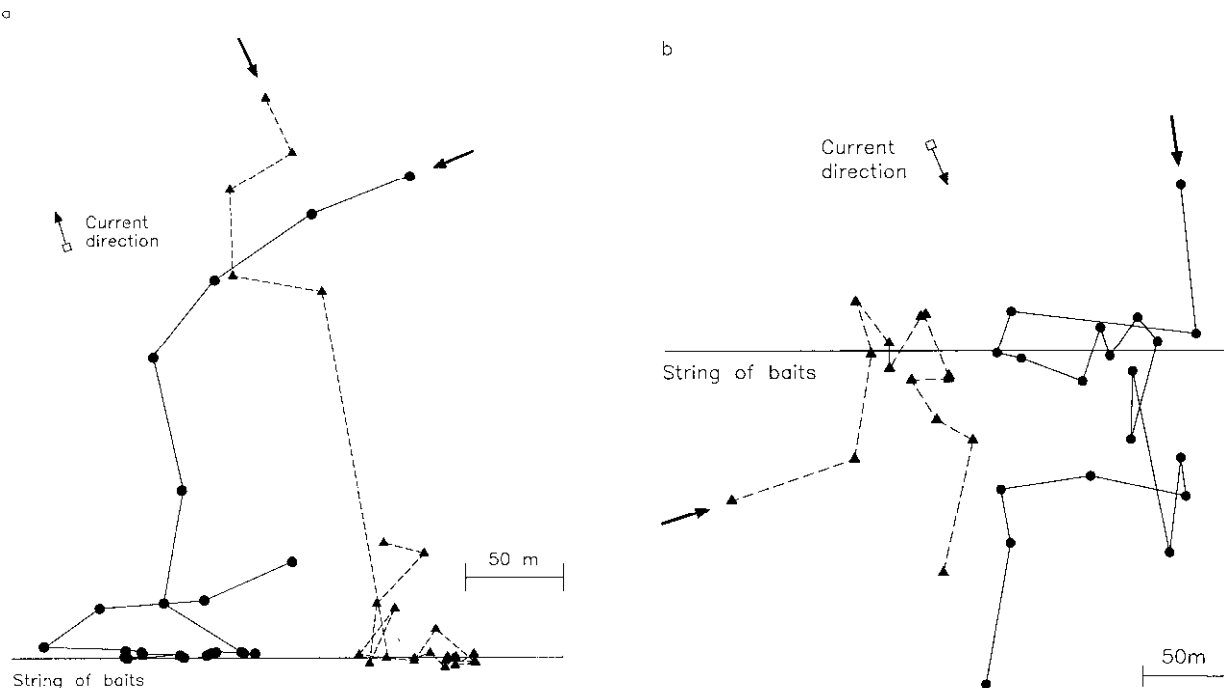


Figure 4. Behaviour of four cod on encountering baits: a – two that moved along the string of baits, and b – two that stayed within the area but did not show any apparent reaction to the baits. The elapsed time between successive positional fixes was 3 min except for a few cases where the elapsed time was 6 min due to missing fixes. Arrows indicate current direction and start of the track.

to diel variations in the probability of encountering prey and predation risk. The recorded swimming activity of cod in the present study is regarded as reflecting food search behaviour, as predation was assumed to be negligible, and spawning was not due until several months after these observations. Cod of the size tracked in this study experience low pre-

dation (Pálsson 1994), and no potential predations were observed, neither during the experimental period or in an ecosystem study conducted in this area (Klemetsen 1982).

Swimming speed of cod was observed to increase at dawn, with a decrease in activity at night. The range of movement varied in a similar pattern throughout the 24 h cycle. The higher swimming speed and greater range could explain why the proportion of fish that encountered the baits was higher and the time until the fish located the baits shorter during the day.

Comparing diel rhythms in a particular species in different seasons and localities may provide information on their adaptive significance. Although cod can feed throughout the 24 h cycle (Klemetsen 1982, Clark & Green 1990), their feeding behaviour might be expected to reflect a style that results in optimal energy gain. In this study, the activity of cod in September–October appeared to be related to light level, with a marked increased activity at dawn and a gradual decrease after noon. In a similar study in the same locality in late spring, with higher light

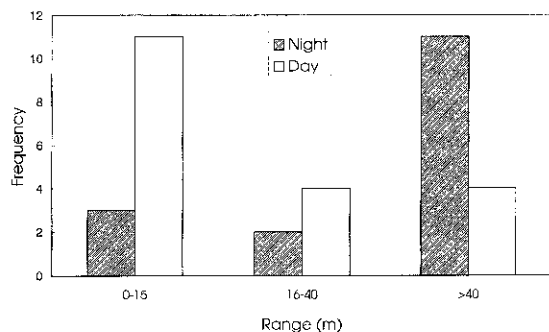


Figure 5. Range of area occupied by cod after locating baits. Upon encountering baits fish were classified in three categories on the basis of the distance (range) from the baits within which they were moving, and the frequency distributions of these categories are shown for the period of high activity during the day and low activity at night. See text for details.

levels at night, a similar but much less pronounced rhythm was observed (Løkkeborg 1998). This suggests that there exists a critical light level below which the activity decreases. In accordance with this suggestion, cod in the North Sea showed higher activity vis-a-vis baited hooks during the day in both September and December, but the increase in activity in the morning was observed later in December in connection with a change in the time of sunrise (Løkkeborg et al. 1989).

Cod can detect prey visually (Brawn 1969) and their reduced activity at night could be connected with poorer ability to detect visual stimuli. Cod have high visual sensitivity (Anthony 1981) and may also use vision under low light conditions, but the reaction distance in fish decreases with decreasing light level (Confer et al. 1978, Utne 1997), and the encounter radius has a great influence on encounter rate (Gerritsen & Strickler 1977). In particular, prey organisms that are active should be caught most effectively when visibility is good. With a reduced ability to locate prey by vision during the night, it might well pay less to search around without environmental cues provided by the prey.

However, in the present study area cod feed on both stationary and mobile prey such as fishes, crustaceans and polychaetes (authors' observations, Klemetsen 1982). A high capability for differentially adapted prey capture requires several sensory modalities, and cod use both their visual and chemical senses to search for and localize food (Brawn 1969). Detection of food by taste receptors on the barbel and the pelvic fins is not dependent on light. Although rheotactic responses observed in cod (Pawson 1977, Løkkeborg et al. 1989) are not regarded as permitting as accurate localization as tropotaxis (Atema 1980), they should enable cod to come into contact with a food source that produces an odour plume without using the visual system. The odour plume is narrow close to the source, and fish that lose contact with the plume may change swimming direction until they reenter the plume (Pawson 1977, see also Zimmer-Faust et al. 1995). Localization by chemical tropotaxis close to the stimulus source might also be possible (Bardach et al. 1967, Timms & Kleerekoper 1972, Atema 1980). The existence of a commercial long-line fishery for

cod in the winter in the Barents Sea (Bjorndal & Løkkeborg 1996) strongly supports the idea that cod are able to localize an odour source under non-visual conditions. Under certain conditions, vision may improve localization, but many organisms that produce olfactory stimuli may be difficult to detect visually. The probability of encountering and catching prey via chemical stimuli should thus be relatively independent of light in contrast to detection of prey by means of visual stimuli. This suggestion is supported by the present finding that the tendency to respond and reaction distance to an odour source in cod did not seem to be influenced by time of day. If cod do not depend on vision to localize odour sources, diel changes in their responsiveness to olfactory stimuli should not be expected.

Clark & Green (1990) observed diel and seasonal variations in the activity patterns and habitat selection of juvenile cod. The recorded inactivity nocturnally in the autumn is in agreement with the present study. However, shifts in activity in the study by Clark & Green were regarded as reflecting an anti-predator behaviour, and seasonal habitat shifts were explained by temperature changes. It was thus difficult to separate the effects of predation, temperature and prey selection. In the present study, cod remained within a limited area and the effect of predation was negligible. We therefore believe that the influence of diel light variations on foraging success could explain the activity pattern. That is, a chemically mediated search for stationary and odour releasing prey explains a light independent food search throughout the 24 h cycle, and increased encounter rate and ability to locate and capture active prey by vision explain the higher swimming activity during the day.

When they came into contact with the string of baits during the day-time, the fish tended to decrease their swimming speed and to stay in the vicinity of the baits, whereas there was no such tendency at night. This could be the first observation of area-restricted search after encountering prey in cod, an aspect of food search behaviour earlier described in sticklebacks, *Gasterosteus aculeatus* (Thomas 1974). Searching in the vicinity after encountering prey could produce net benefits, as prey items are often patchily distributed. Under condi-

tions of low visibility at night, fish may search more randomly and have a shorter giving-up time (Krebs et al. 1974), as prey in the vicinity are difficult to localize visually. This explanation may seem contradictory to the previous arguments that chemical rheotaxis alone permits localization of an odour source, but the visual sense may improve localization in situations in which food items are clearly visible. The fish may also have used the line to which the baits were attached to localize new baits by exploration of visual stimuli reinforced by consumption of baits. Cod attracted to the area at night may also have encountered fewer baits, as the elapsed time until contact with the baited string was longer at night, entailing a higher risk that the baits would have been consumed by scavengers, and without reinforcement the fish could soon leave the area. The negative relationship between the elapsed time until the fish encountered the string of baits and the tendency to stay in the area supports this idea.

The similar activity patterns among evolutionary related but ecologically dissimilar species of fishes suggest that diel rhythms do not have to be related to current biotic and environmental stimuli (Helfman 1993). The flexibility of the activity rhythm in cod, however, warrants functional explanations. Foraging costs probably comprise the major portion of average activity metabolism in cod, and it is reasonable to assume that cod in nature regulate the activity so as to maximize growth for a given prey availability (Kerr 1982). With reduced ability to locate prey by vision during the night, swimming speed when searching for prey may be explained by a light-dependent trade-off. Higher swimming speed will lead to higher energy gain resulting from more frequent prey encounters but higher energy expenditure (Jobling 1994). The swimming costs of cod may be relatively low (Soofiani & Priede 1985), but in addition to lowering energy costs, decreasing swimming speed could increase the probability of locating prey through the chemical senses. Visual feeders have been shown to decrease their swimming speed when searching for less conspicuous prey (Gentron & Staddon 1984, Ryer & Olla 1997). The localization of prey by olfaction and taste should not be dependent on light, and cod might thus benefit from active searching under non-visual

conditions too, but at a lower speed. A similar tendency to respond to olfactory stimulation observed during the day and at night supports the suggestion that important aspects of the food search behaviour of cod are independent of the visual system.

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