

Changes in Behaviour at Onset of Exogenous Feeding in Marine Fish Larvae

Anne Berit Skiftesvik

Institute of Marine Research, Austevoll Aquaculture Research Station, N-5392 Storebø, Norway

Skiftesvik, A. B. 1992. Changes in behaviour at onset of exogenous feeding in marine fish larvae. *Can. J. Fish. Aquat. Sci.* 49: 1570–1572.

The activity and swimming speed of fed and starved larvae of Atlantic cod (*Gadus morhua*) and turbot (*Scophthalmus maximus*) were measured from hatching to metamorphosis. The results indicate changes in behaviour over time, as well as differences between starved and fed larvae. It is suggested that determining the point at which activity increases and swimming speed during active periods decreases may be relevant as an indicator of the time of first feeding in marine fish larvae.

On a quantifié le niveau d'activité et la vitesse de déplacement de larves nourries et de larves privées de nourriture de morue franche (*Gadus morhua*) et de turbot (*Scophthalmus maximus*), de l'éclosion des oeufs à la métamorphose. Les résultats révèlent des variations du comportement selon le temps écoulé, ainsi que des différences entre les larves nourries et celles privées de nourriture. On formule l'hypothèse que la détermination du moment où l'activité augmente et la vitesse de déplacement pendant les périodes d'activité diminue pourrait servir comme indicateur du moment de la première prise de nourriture chez les larves de poissons marins.

Received August 2, 1990

Accepted February 26, 1992
(JA671)

Reçu le 2 août 1990

Accepté le 26 février 1992

Atlantic cod (*Gadus morhua*) and turbot (*Scophthalmus maximus*) are two species in commercial culture where the timing of the introduction of prey is essential for subsequent growth and survival. Experiments have shown that for cod, first feeding is 4–5 d after hatching at 5°C (Ellertsen et al. 1980), while for turbot, this point is about 3 d after hatching at 18°C (Jones 1972). Successful predation on small zooplankton gives both new energy reserves and increased energetic outlay (Houde and Schekter 1980) which the larvae must to some extent control for further survival. Thus, one would expect not only ontogenetic changes in behaviour patterns but also changes in response to the feeding environment, particularly starvation. The following experiments were conducted to reveal changes in the behaviour of cod and turbot larvae from hatching to metamorphosis in response to feeding and starvation.

Materials and Methods

Sources of Larvae

Cod

Naturally spawned eggs from several adult cod from the broodstock held at the Austevoll Aquaculture Research Station were collected according to Huse and Jensen (1983) and incubated in a 250-L incubator at mean temperatures between 3 and 5°C. The eggs were transferred to observation chambers before hatching and observations began at 50% hatching (day 0). One group of 1500 larvae was starved and died out by day 15. The other group of 1500 fed larvae was followed to day 42. The remaining larvae were healthy enough to be maintained in aquaria until day 68 by which time cannibalism had made an impact on mortality. The fed group of larvae was given cultivated rotifers (*Brachionus plicatilis*) and *Tisbe* sp. nauplii on days 4–35 and natural zooplankton thereafter. The

temperature was maintained at 5°C and salinity at 34 ppt. About 15% of the water was renewed daily. The light was 300 lx at the surface.

Turbot

Turbot eggs were delivered from the Ardtoe Research Station, Scotland, and hatched in the observation chambers. Observations began 1 d after 50% hatching for the 200 larvae in the starvation group and ended on day 7, when the last larvae died. Observations on the 600 larvae in the fed group began 2 d after 50% hatching and continued until day 18. The fed larvae were given *B. plicatilis* and *Tisbe* sp. nauplii from day 3. The temperature was maintained at 18°C and salinity at 34 ppt. About 15% of the water was renewed daily. The light was 1000 lx at the surface.

Observations

The behaviour of cod and turbot larvae was defined as swimming or resting. Activity was defined as the percentage of time spent swimming during the total observation time. Swimming speed during active periods was defined as the average speed from commencement of activity to its cessation and was measured in millimetres per second. This was measured for 10 randomly chosen larvae during each observation period, as were the activity measurements.

Behavioural studies of marine fish larvae were conducted using a computer-aided video system, allowing three-dimensional measurement of the larvae's position in 70-L observation chambers (for a more detailed description, see Huse and Skiftesvik 1985, 1990). Each of 10 randomly chosen larvae was tracked for 5 min and position and behaviour (swimming or resting) logged for each second. This was repeated during daylight hours until termination of the experiments.

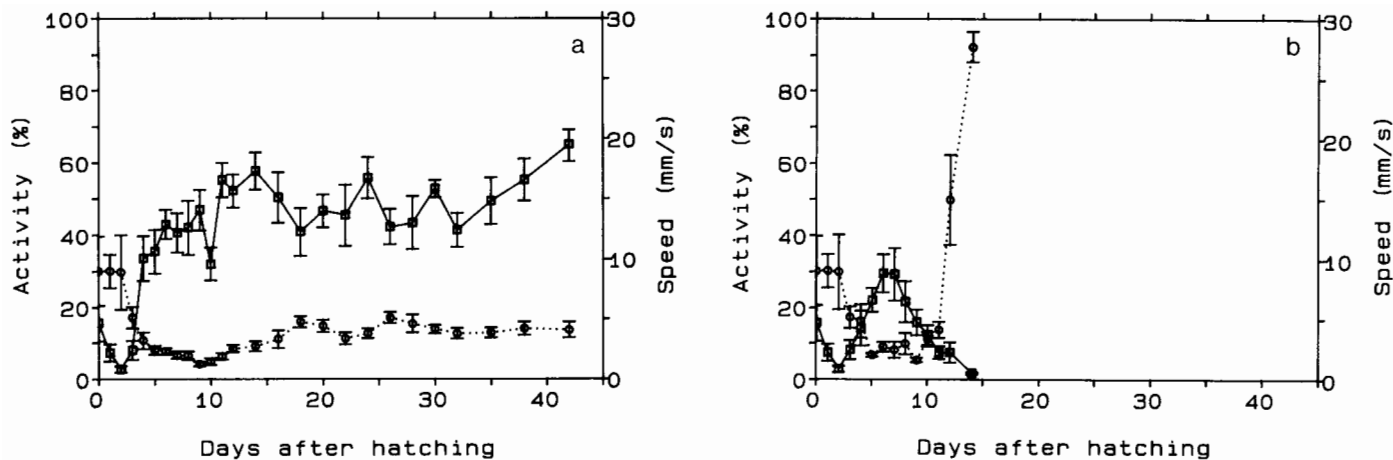


FIG. 1. Development of activity (solid line) and swimming speed (dotted line) in the active periods of (a) fed cod larvae and (b) starved cod larvae. Each point is the mean and standard error of 10 cod larvae.

Results

Cod

Activity

The activity of the two groups of cod larvae was the same throughout the first 3 d after hatching (under 10%) (Fig. 1). When prey were introduced to the fed group on day 4, the activity rose to over 30% and remained at that level for the remainder of the experiment (Fig. 1a).

The unfed group attained maximum activity of about 30% on days 6–7 but thereafter decreased within 4 d to under 10% (Fig. 1b). The last observation on d 14 shows an activity of about 2%.

Activity was significantly different between the two groups from day 4 onwards (robust *t*-test of medians; Hoaglin et al. 1983).

Swimming speed

The swimming speed during the active periods of both groups was identical during the first 4 d after hatching, being stable at 9 mm/s from day 0 to 3 and decreasing to 5 mm/s on day 4 (Fig. 1). In the fed group, the swimming speed during the active periods decreased further, remaining steady around 2 mm/s until about day 11 (Fig. 1a). Although the larvae developed in both length and morphology, the swimming speed during active periods did not exceed 5 mm/s for the rest of the experiment. The drop from day 3 to 5 was significant ($p < 0.0081$, Student's *t*-test).

The unfed group of cod larvae had comparatively elevated swimming speed during the entire observation period (Fig. 1b). On day 4, the mean speed during active periods was 5 mm/s. Speed dropped significantly ($p < 0.034$, robust *t*-test of medians; Hoaglin et al. 1983) on day 5 and remained at about the same level as in the fed group until day 10, when speed rose from about 4 to about 27 mm/s on day 14, the last day of observation.

Turbot

Activity

The activity was low (about 4%) for the first 3 d (Fig. 2) but rose on day 4, 1 d after the introduction of prey. No feeding was recorded on day 3. Thereafter, the turbot responded vigorously with activity higher than 70% from day 4 to 7 and over

90% for the remainder of the experiment (Fig. 2a). Activities of 100% were observed from day 16 to 18.

The unfed group had initially the same activity pattern as the fed group until the onset of exogenous feeding (Fig. 2b). Although activity rose on day 4, it was lower than in the fed group. Peak activity was on day 4 at about 55% and dropped to about 35% on day 7, the last day of observation.

Activity was significantly different between the two groups from day 5 onwards ($p = 0.0018$, Student's *t*-test).

Swimming speed

In contrast with the activity, the swimming speed in active periods was high during the initial observations (between 25 and 40 mm/s) (Fig. 2) but sank quickly to about 3.5 mm/s and increased slowly as larvae grow. The drop from day 3 to 4 was significant for both the fed and the unfed group ($p < 0.00005$, Student's *t*-test and $p < 0.00005$, robust *t*-test of medians (Hoaglin et al. 1983) for the fed and unfed group, respectively).

Discussion

The observations show a change in behaviour in both cod and turbot when they start feeding. Activity increases whereas swimming speed decreases. This change of swimming mode has also been found in larvae of other marine species when the energy source changed from endogenous to exogenous (Blaxter and Staines 1971; Hunter and Kimbrell 1980). Differences in activity were apparent at yolk absorption between fed and unfed larvae of black sea bream (*Acanthopagrus schlegeli*) (Fukuhara 1987). The swimming speed of these larvae also increased gradually as development proceeded and then slightly decreased after feeding began. Whereas fed larvae reduce their swimming speed, unfed larvae maintain less energetically conservative tempos when active, even exhibiting feeding behaviour until the day before mass mortality (Ellertsen et al. 1980).

The most obvious change in swimming speed between fed and unfed cod comes after day 10, a period near the point-of-no-return (days 8–10; Ellertsen et al. 1980). Turbot, according to Jones (1972), would have a point-of-no-return at day 7 at 18°C. However, a large change of swimming speed was not found for turbot. It is possible that some of the observed larvae in the fed group did not actually feed, although the narrow range of values for activity during the period would seem to

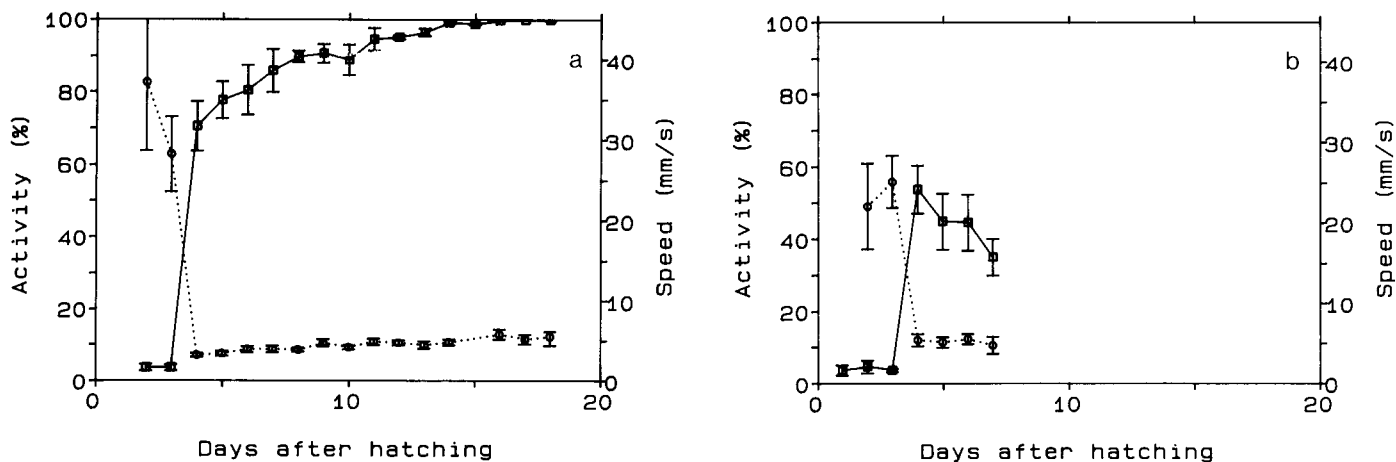


FIG. 2. Development of activity (solid line) and swimming speed (dotted line) in the active periods of (a) fed turbot larvae and (b) starved turbot larvae. Each point is the mean and standard error of 10 turbot larvae.

contradict this view. Thus it would seem that swimming speed alone is not sufficient as an early indicator of starvation.

Activity is correlated with the morphological development of the larva and may reflect the influence of predators. In both the fed and unfed groups of cod, activity rises between days 2 and 7, concurrent with the development of fins and the absorption of the yolk mass. If the activity of the unfed group is taken as baseline, then the presence of prey augments the activity levels by about 15% during days 4–7, during the changeover from endogenous to exogenous food. When the yolk supply has been exhausted, the unfed larvae conserve their energy by reducing activity after day 7 whereas the fed larvae maximize their contact probability by increasing their activity.

For both cod and turbot larvae, the activity was lower in the unfed group compared with the fed group after first feeding. Reduced swimming activity of unfed cod larvae was also found by Ellertsen et al. (1980). In studies cited by Sih (1987), reduced activity was a typical antipredator response that presumably reduces the frequency of contact with predators and the likelihood of detection and recognition as prey. Low activity also implies reduced consumption of energy; thus, reduced activity may delay the point-of-no-return.

From studies by Milinski (1986) and Jakobsen et al. (1988), it is known that fish that are starved, or by other reasons have an increased need for exogenous energy, will take higher risks. The buoyancy of starved larvae is different from that of fed larvae (Blaxter and Erlich 1974). Thus, starved larvae must have a vertical distribution different from that of fed larvae, as shown by Neilson et al. (1986). This may indicate that the demand for exogenous energy becomes more important than predator avoidance.

In summary, there is a change in the activity and speed of cod and turbot around the time of first feeding. This may reflect the increasing importance of energy acquisition as a motivator, in addition to ontogenetic changes. It is suggested that determination of the period during which activity increases and swimming speed decreases may be used to determine the time of first feeding in marine fish larvae.

Acknowledgements

The author would like to thank Karin Pittman (Department of Fisheries Biology, University of Bergen), Øivind Bergh, Jens Chr. Holm, and Ingvar Huse (Austevoll Aquaculture Research Station, Storebø)

for constructive contributions to the manuscript. The Norwegian Council for Fisheries Research (NFFR) supported the author financially.

References

- BLAXTER, J. H. S., AND K. F. ERLICH. 1974. Changes in behaviour during starvation of herring and plaice larvae, p. 575–588. In J. H. S. Blaxter [ed.] The early life history of fish. Springer-verlag, Berlin.
- BLAXTER, J. H. S., AND M. E. STAINES. 1971. Food searching potential in marine fish larvae, p. 467–485. In D. J. Crisp [ed.] Fourth European Marine Biology Symposium. Cambridge University Press, Cambridge.
- ELLERTSEN, B., E. MOKSNESS, P. SOLEMDAL, T. STRØMME, S. TILSETH, AND T. WESTGÅRD. 1980. Some biological aspects of cod larvae (*Gadus morhua* L.). Fiskeridir. Skr. Ser. HavUnders. 17: 29–47.
- FUKUHARA, O. 1987. Larval development and behaviour in early life stages of black sea bream reared in the laboratory. Bull. Jpn. Soc. Sci. Fish. 53(3): 371–379.
- HOAGLIN, D. C., F. MOSTELLER, AND J. W. TUKEY. 1983. Understanding robust and exploratory data analysis. John Wiley and Sons, New York, NY.
- HOUDE, E. D., AND R. C. SCHEKTER. 1980. Feeding by marine fish larvae: developmental and functional responses. Environ. Biol. Fishes 5(4): 315–334.
- HUNTER, J. R., AND C. A. KIMBRELL. 1980. Early life history of Pacific mackerel, *Scomber japonicus*. Fish. Bull. U.S. 78: 811–816.
- HUSE, I., AND P. A. JENSEN. 1983. A simple and inexpensive spawning and egg collection system for fish with pelagic eggs. Aquacult. Eng. 2: 165–171.
- HUSE, I., AND A. B. SKIFTESVIK. 1985. Qualitative and quantitative behaviour studies in starving and feeding turbot (*Scophthalmus maximus* L.) larvae. Counc. Meet. Int. Counc. Explor. Seas F:38.
1990. A PC-aided video based system for behaviour observation of fish larvae and small aquatic invertebrates. Aquacult. Eng. 9: 131–142.
- JAKOBSEN, P. J., G. H. JOHNSEN, AND P. LARSSON. 1988. Effects of predation risk and parasitism on the feeding ecology, habitat use, and abundance of lacustrine threespine stickleback (*Gasterosteus aculeatus*). Can. J. Fish. Aquat. Sci. 45: 426–431.
- JONES, A. 1972. Studies on egg development and larval rearing of turbot, *Scophthalmus maximus* L., and brill, *Scophthalmus rhombus* L., in the laboratory. J. Mar. Biol. Assoc. U.K. 52: 965–986.
- MILINSKI, M. 1986. Constraints placed by predators on feeding behaviour, p. 236–252. In T. J. Pitcher [ed.] The behaviour of teleost fishes. Croom Held Ltd., London and Sydney.
- NEILSON, J. D., R. I. PERRY, P. VALERIO, AND K. G. WAIWOOD. 1986. Condition of the Atlantic cod *Gadus morhua* larvae after the transition to exogenous feeding: morphometrics, buoyancy and predator avoidance. Mar. Ecol. Prog. Ser. 32: 229–235.
- SIH, A. 1987. Predators and prey lifestyles: an evolutionary and ecological overview, p. 203–224. In C. Kerfoot and A. Sih [ed.] Predation. Direct and indirect impacts on aquatic communities. University Press of New England, Hanover and London.