

NOTE

Adaptive mass formations in fish shoals founded in conflicting motivation

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ABSTRACT: The organising principles behind adaptive collective formations in animals are not well understood. Here we document that persistent vertical hourglass formations occur during the critical spawning period in huge shoals of the herring *Clupea harengus* spawning demersally. We compared individual maturity stage between the upper and lower components of the formations and found the proportion of spawners to pre- and post-spawners to be significantly higher in the lower than in the upper components. Our results provide empirical support for the hypothesis that these formations are a collective output of individual risk assessment in a compromise between survival and reproduction, where non-spawners minimise the time spent in the demersal zone, where density of gadoid predators was found to be highest. Conflicting individual motivation may thus be an organising principle behind mass formations in fish shoals.

KEY WORDS: Herring · Spawning · Hourglass formation · Motivation

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INTRODUCTION

Among the most impressive collective formations in nature are those displayed in free-ranging marine fish shoals, but little is known about the underlying mechanisms of such formations (Parrish & Edelstein-Keshet 1999, Krause et al. 2000). The herring is an obligate collective species which lives in a permanent state of social interaction throughout all stages of life (Blaxter & Hunter 1982) and displays a wide range of schooling patterns and dynamics dependent on its life-cycle stage and the ecological context (Nøttestad et al. 1996, Pitcher et al. 1996). During the spawning period, herring migrate from the non-feeding wintering areas to the spawning sites and complete the annual spawning event within a few days and resume feeding shortly thereafter (Nøttestad et al. 1996). Unlike most fish adapted to a life in the pelagic, herring are bottom spawners and are dependent on a habitat associated with a high density of gadoid predators for reproduction (Stensholt et al. 2002). The optimal behaviour in a

compromise between reward and risk, e.g. maximising reproduction and avoiding predators, is state-dependent (Milinski 1993). Axelsen et al. (2000) hypothesised that the group behaviour of a small isolated school of spawning herring reflected a trade-off between survival and reproduction, as the school showed partial vertical splitting, forming an hourglass shape. They speculated that pre-spawners and post-spawners stayed in the pelagic above bottom-dwelling spawners to minimise the time spent in an area with an assumed high predation risk.

Here, we use extensive time series of acoustic data from herring spawning surveys to investigate whether partial vertical splitting is a collective behaviour also displayed by huge aggregations of herring in the main spawning areas. If so, we aim to use biological data to test the hypothesis of Axelsen et al. (2000) that a reproductive state-dependent trade-off between survival and reproduction can explain the formations with different individual depth preferences. If such a trade-off exists, we expect the ratio of pre- and post-spawners to

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spawners to be lowest in the low component of the hourglasses and the density of predators to be highest near the bottom.

MATERIALS AND METHODS

We analysed time series of acoustic data from the Norwegian spring spawning (NSS) herring *Clupea harengus* spawning areas along the Norwegian coast, where each spring herring are found in some of the largest known animal aggregations on the globe. The acoustic data material was acquired in February and March 1994 to 2006 (except for the years 1996 and 2002) in part as abundance estimate surveys of NSS herring, and in part as distribution mapping and/or behavioural studies within selected herring spawning sites (Fig. 1). In total, 260 trawl stations were available, and acoustic data were collected during 170 d at sea for an area covering roughly 30 000 nautical miles (n miles).

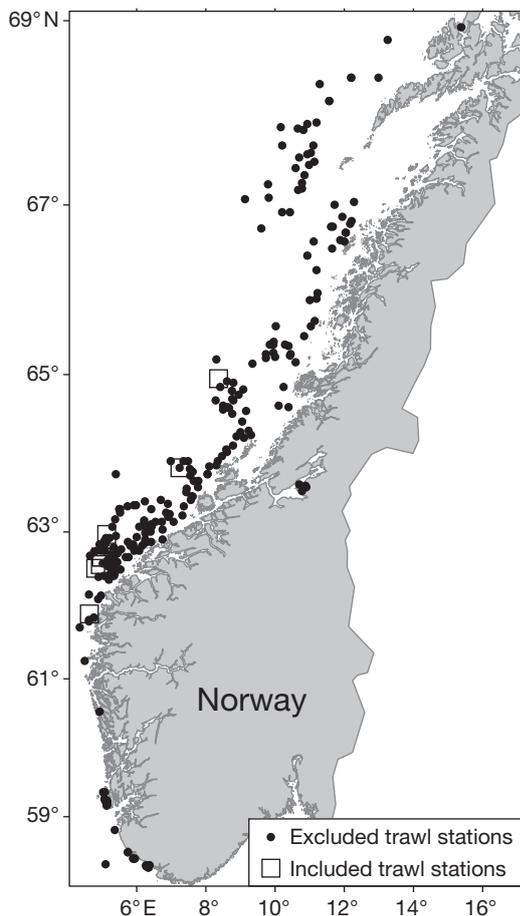


Fig. 1. Trawl stations of the Norwegian spring spawning herring acoustic surveys in 1994 to 1995, 1997 to 2001 and 2003 to 2006. □: stations included in the present study

The collection of data was carried out by experienced personal and followed a standard scheme: Acoustic recording was done with a 38 kHz SIMRAD EK 500 echo sounder and integrator (replaced with EK 60 in 2005) and post-processed using the Bergen Echo Integrator (BEI) (Foote et al. 1991). Acoustic signal characteristics combined with trawl catches were used for reference when allocating acoustic densities to species. All biological samples were obtained by pelagic trawl upon recordings of herring and not at random or fixed stations. If permitted by the size of the catch, 100 herring were randomly sampled from each trawl haul. Herring with maturing and mature gonads were categorised as 'pre-spawners', individuals with running gonads as 'spawners' and individuals with empty or quasi-empty gonads as 'post-spawners'. The acoustic density values were stored by species in nautical area scattering coefficient (NASC) units (MacLennan et al. 2002) in a database with a horizontal resolution of 1 n mile and a vertical resolution of 10 m, referenced to the surface.

In order to distinguish potential hourglass formations, we first searched through all acoustic recordings in the vicinity (± 3 n miles) of trawl samples for the bimodal depth distribution characteristic of such formations (see Figs. 2a & 3). From this set of recordings with bimodal distribution we only selected recordings where the acoustic density between the modal peaks did not reach zero, indicating a split between the upper and lower shoal component. To test for differences in maturity stage of herring between the 2 components we only kept recordings with trawl catches taken from either the upper or lower component. All trawl stations with small catches of herring (<100 fish) were discarded, as the low number indicates that the haul missed the targeted acoustic recordings. Importantly, the selection of trawl hauls was done prior to looking at the biological data.

After this final selection, 8 stations were left — 5 from the upper part of the hourglass formation and 3 from the lower part (Fig. 3). These stations originated from 4 different years. A 2-way Rao-Scott likelihood ratio chi-square test design-adjusted to stratified cluster sampling (Rao & Scott 1981) was applied to adjust for the effect of shoal components on the proportion of spawners. Each trawl sample is treated here as a cluster ($n = 8$) and the 2 shoal components (upper and lower) as strata. On one occasion, both the upper and lower components of an hourglass formation were sampled close in time and space (Fig. 2). For a separate comparison between these 2 adjacent samples, all sampled fish were assumed to be independent, and a Fisher-irwin exact test was used to investigate differences between the shoal components with respect to the proportion of spawners. A regular Student's *t*-test was used to test

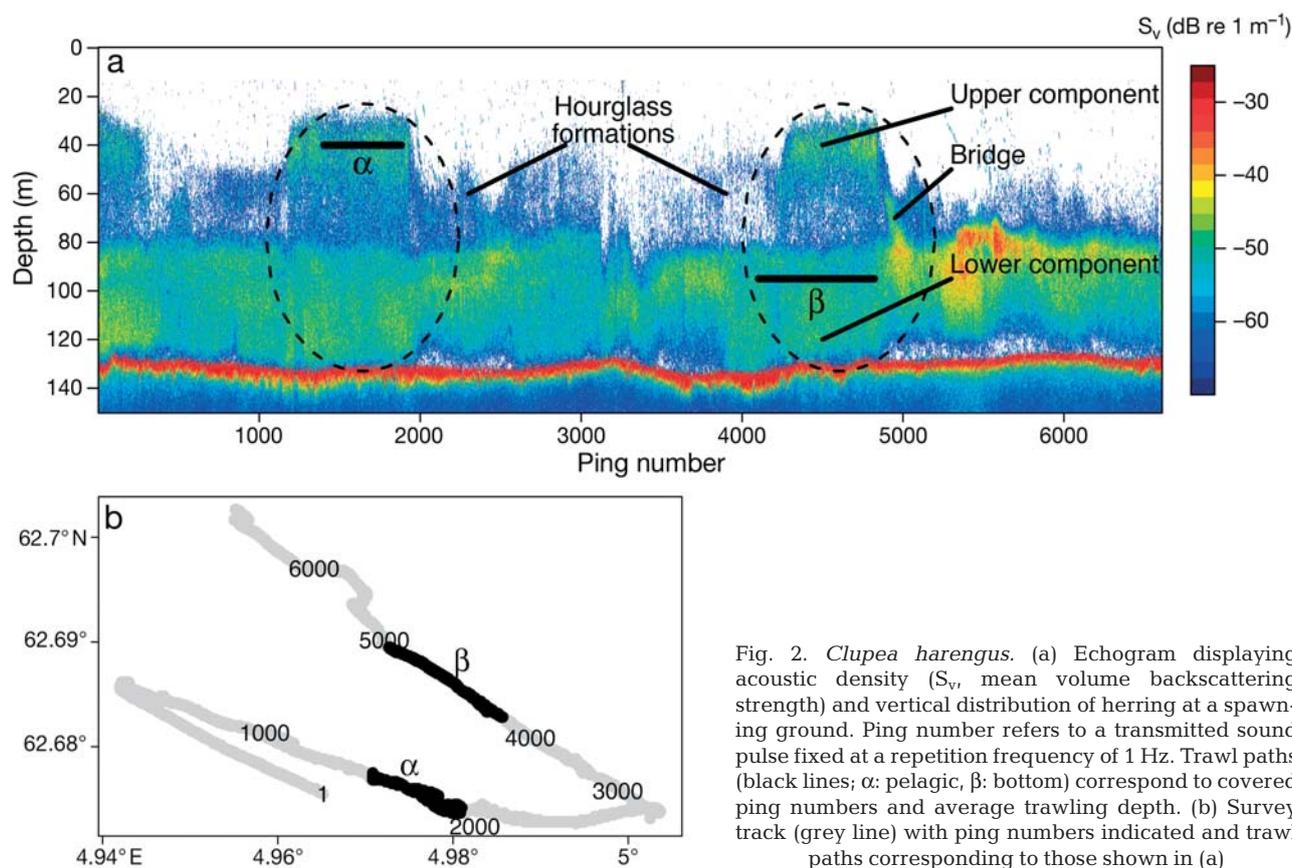


Fig. 2. *Clupea harengus*. (a) Echogram displaying acoustic density (S_v , mean volume backscattering strength) and vertical distribution of herring at a spawning ground. Ping number refers to a transmitted sound pulse fixed at a repetition frequency of 1 Hz. Trawl paths (black lines; α : pelagic, β : bottom) correspond to covered ping numbers and average trawling depth. (b) Survey track (grey line) with ping numbers indicated and trawl paths corresponding to those shown in (a)

for differences in average length between the components.

The predation pressure at the spawning site was investigated at a diel cycle station with a vessel maintaining a stationary position above a main spawning site with herring aggregations. The experiment was carried out in 2001, lasting from 12:48 h UTC March 12 to 02:00 h UTC March 13. The vertical distribution of herring and gadoids was recorded acoustically and gadoids and herring were sampled using gillnets, 2 of them targeting gadoids (mesh-size 90 mm) and 2 of them herring (mesh-size 37 mm) mounted in a chain with each small-meshed followed by a large-meshed gillnet. Stomach samples were obtained from all gadoids caught.

RESULTS

Of the 260 trawl hauls in the data set (Fig. 1), 16 were taken in the vicinity of hourglass formations. In the final selection of 8 trawl catches, there was a significantly higher proportion of spawning herring *Clupea harengus* in the lower than in the upper component of the hourglass formations (Rao-Scott, $p < 0.005$),

demonstrating a depth distribution dependent on maturity stage (Fig. 4). While spawners totally dominated the samples from the lower component, the upper samples revealed a dominance of pre- and post-spawners, and spawners contributed one-third of the total (Fig. 4). Pre-spawners totally dominated 2 of the 5 stations from the upper component, and 1 of the 5 consisted exclusively of post-spawners (Fig. 3). The remaining 2 stations from the upper component consisted of a mixture of pre-spawners and spawners. There were no post-spawners in samples from the lower component.

For the separate comparison between the 2 adjacent stations (Fig. 2), there was a difference in average body length between the upper and lower component ($p = 0.034$). However, the highly significant larger proportion of spawners in the bottom component ($p < 0.001$) supports a vertical positioning dependent on maturity stage.

The vertical distribution of gadoids and herring averaged over all recordings from the diel cycle station showed a bimodal pattern (Fig. 5). However, the depth distribution was different; the gadoids had an upper peak in the recordings around 90 to 95 m and then a lower peak close to the bottom, whereas herring had

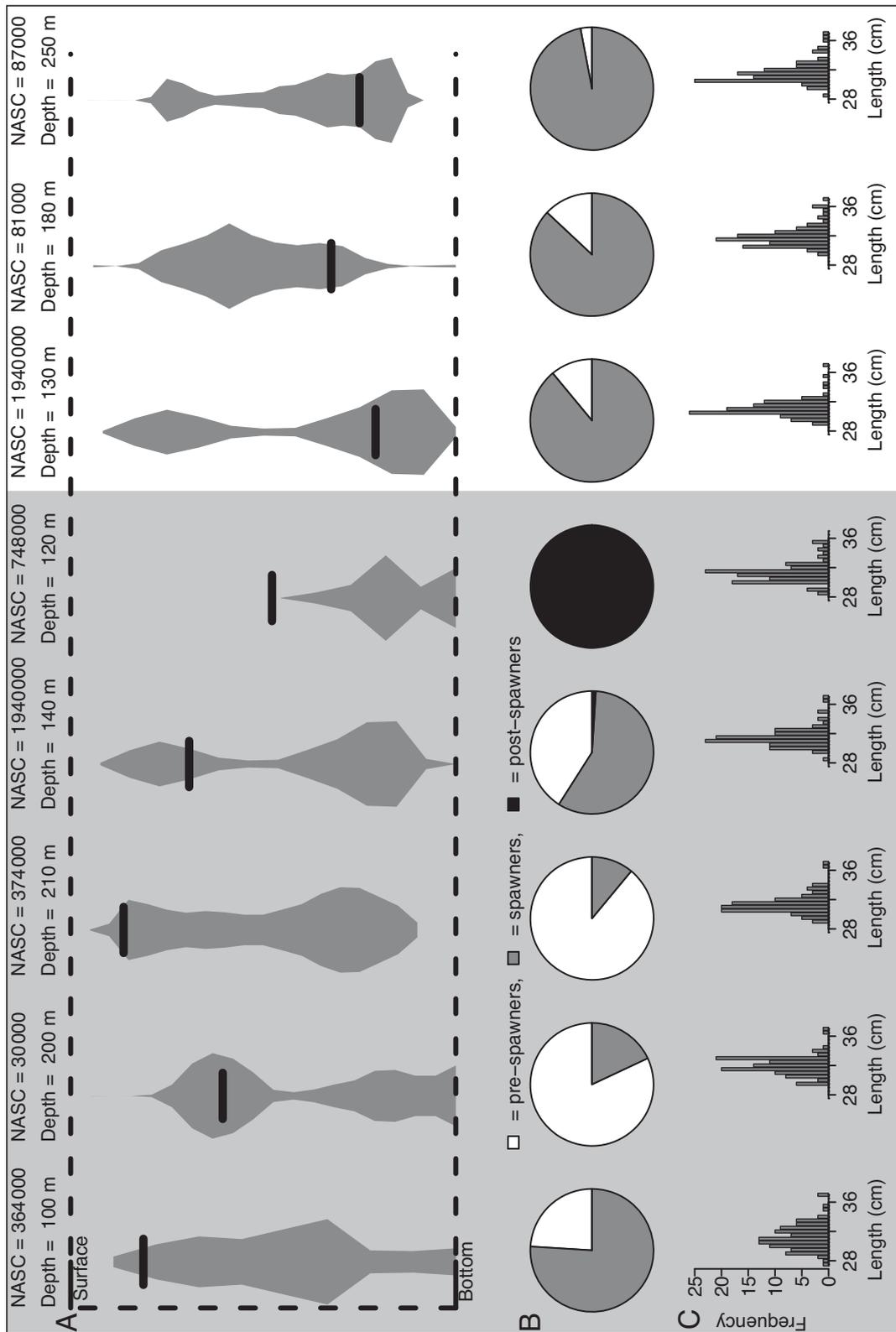


Fig. 3. *Clupea harengus*. Vertical acoustic hourglass formations with appurtenant gonad maturity stages and length distributions in the upper (grey background) and lower (white background) components. (A) Depth and vertical acoustic density (nautical area scattering coefficient, NASC) profiles of herring integrated over a distance of 5 n miles with the starting position of trawling within the third n mile. Black lines indicate average trawling depth relative to the density profiles. (B) Frequencies of the 3 herring maturity stages pre-spawning (white), spawning (grey) and post-spawning (black). (C) Length distributions of herring

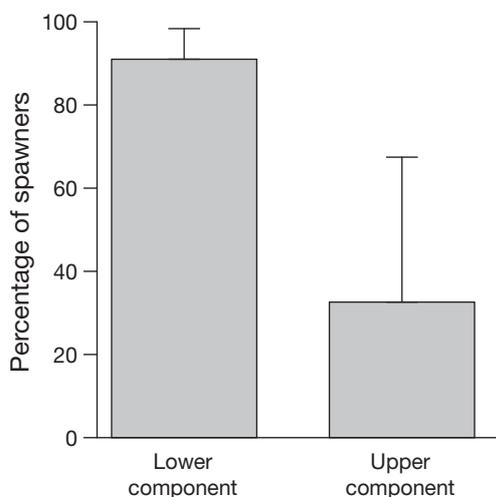


Fig. 4. *Clupea harengus*. Percentage of spawners in upper and lower component of the hourglass formations. 95% confidence bands are based on the design-adjusted Rao-Scott likelihood test applied to stratified cluster sampling where each trawl sample is treated as a cluster ($n = 8$) and the 2 shoal components (upper and lower) as strata

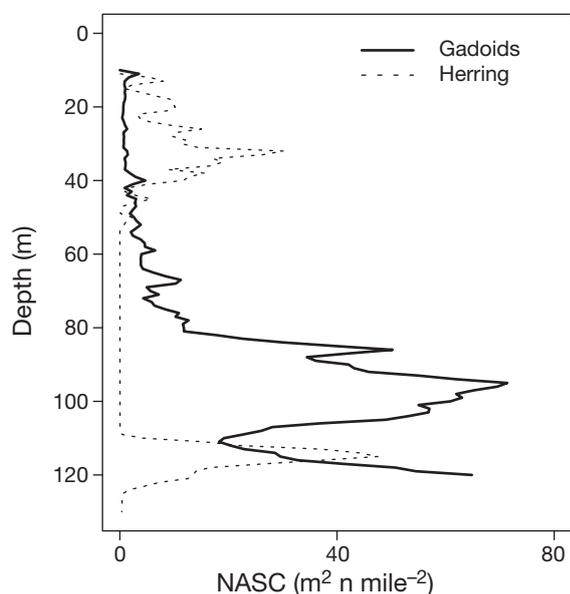


Fig. 5. *Clupea harengus*, *Pollachius virens*, *Gadus morhua*, and *Pollachius pollachius*. Vertical acoustic density profiles for gadoids and herring at a main spawning site of herring from the diel cycle station, 12 to 13 March 2001. NASC: nautical area scattering coefficient

an upper peak at 30 to 35 m and a lower peak at 110 to 115 m. A total of 35 gadoids were caught (saithe *Pollachius virens*, 30; cod *Gadus morhua*, 4; and pollock *Pollachius pollachius*, 1), of which 27 had been feeding on herring with the number of herring in their stomachs ranging from 1 to 5 (2.11 ± 1.42 SD).

DISCUSSION

Our results show that the formation of vertical hour-glasses is a collective behaviour occurring in NSS-herring *Clupea harengus* shoals during the critical spawning period. The frequency of occurrence is hard to quantify, but we show that the behaviour may be maintained over time and that it occurs across years for the main NSS-herring population. We demonstrate that the formations are organised according to maturity stage, with the proportion of spawners being significantly higher in the lower than in the upper components of the hourglass formations. Such a depth preference dependent on maturity state provides empirical support for the hypothesis that the formations are founded in a state-dependent trade-off between reproduction and survival where pre- and post-spawners avoid the bottom zone where density of gadoid predators was found to be highest.

The optimal combination of risk and reward is state-dependent, as has been demonstrated in the compromise in feeding and predator avoidance behaviour of fish with different states of hunger (Milinski 1993). The balance between reproduction and predator avoidance provides a similar compromise if spawning increases predation risk. Axelsen et al. (2000) argued that, even with a uniform vertical distribution of predators, the bottom is a high-risk zone for herring during spawning due to reduced escape possibilities, increased surface-to-area ratio as the school flattens out on the bottom, and reduced polarization of individuals in a school during the spawning act. Our results from the diel cycle station indicate that the predators are not evenly distributed but aggregated close to the bottom during this period. It therefore seems likely that the different depth preferences of individuals reflect a state-dependent compromise between reproduction and avoiding predation. Interesting to note is the relatively high frequency of spawners sampled from the upper components of the hourglass formations, where one would expect to find pre- and post-spawners (Fig. 3). However, spawners can wait for days before depositing the spawn (Hay 1986). In contrast, pre-spawners have to undergo a process of 24 h ovulation before being able to spawn (Gillis et al. 1990) and were only found in low proportions in the lower shoal components.

The motivation of individuals has been shown to organize animal groups on a small scale (<100 ind.), e.g. spider groups arranged according to level of aggression (Rayor & Uetz 1993), whirligig beetles sorted according to how they balance predation risk with hunger level (Romey 1995), and laboratory fish according to hunger level (Krause et al. 1992). Our results provide *in situ* empirical support for the hypo-

thesis of different motivation among individuals as an organising principle in animal aggregations at the scale of large free-ranging fish shoals.

Acknowledgements. We thank D. Tjøstheim, V. Hjellvik and K. Korsbrekke for statistical advice and A. Fernö, A. Johannessen, L. Nøttestad and R. Vabø for comments. The project was supported by grants from the Norwegian Research Council to E.J. and G.S.

LITERATURE CITED

- Axelsen BE, Nøttestad L, Fernö A, Johannessen A, Misund OA (2000) 'Await' in the pelagic: dynamic trade-off between reproduction and survival within a herring school splitting vertically during spawning. *Mar Ecol Prog Ser* 205:259–269
- Blaxter JHS, Hunter JR (1982) The biology of the clupeoid fishes. *Adv Mar Biol* 20:1–224
- Foote KG, Knudsen P, Korneliussen RJ, Nordbø PE, Røang K (1991) Postprocessing system for echo sounder data. *J Acoust Soc Am* 90:37–47
- Gillis DJ, McKeown BA, Hay DE (1990) Physiological and histological aspects of late oocyte provisioning, ovulation, and fertilization in Pacific herring (*Clupea harengus pallasii*). *Can J Fish Aquat Sci* 47:1505–1512
- Hay DE (1986) Effects of delayed spawning on viability of eggs and larvae of Pacific herring. *Trans Am Fish Soc* 115:155–161
- Krause J, Bumann D, Todt D (1992) Relationship between the position preference and nutritional state of individuals in schools of juvenile roach (*Rutilus rutilus*). *Behav Ecol Sociobiol* 30:177–180
- Krause J, Butlin RK, Peuhkuri N, Pritchard VL (2000) The social organization of fish shoals: a test of the predictive power of laboratory experiments for the field. *Biol Rev Camb Philos Soc* 75:477–501
- MacLennan DN, Fernandes PG, Dalen J (2002) A consistent approach to definitions and symbols in fisheries acoustics. *ICES J Mar Sci* 59:365–369
- Milinski M (1993) Predation risk and feeding behaviour. In: Pitcher TJ (ed) *Behaviour of teleost fishes*. Chapman & Hall, London, p 285–305
- Nøttestad L, Aksland M, Beltestad A, Fernö A, Johannessen A, Misund OA (1996) Schooling dynamics of Norwegian spring spawning herring (*Clupea harengus* L.) in a coastal spawning area. *Sarsia* 80:277–284
- Parrish JK, Edelstein-Keshet L (1999) Complexity, pattern, and evolutionary trade-offs in animal aggregation. *Science* 284:99–101
- Pitcher TJ, Misund OA, Fernö A, Totland B, Melle V (1996) Adaptive behaviour of herring schools in the Norwegian Sea as revealed by high-resolution sonar. *ICES J Mar Sci* 53:449–452
- Rao JNK, Scott AJ (1981) The analysis of categorical data from complex sample-surveys: chi-squared tests for goodness of fit and independence in 2-way tables. *J Am Stat Assoc* 76:221–230
- Rayor LS, Uetz GW (1993) Ontogenic shifts within the selfish herd – predation risk and foraging trade-offs change with age in colonial web-building spiders. *Oecologia* 95:1–8
- Romey WL (1995) Position preferences within groups: Do whirligigs select positions which balance feeding opportunities with predator avoidance? *Behav Ecol Sociobiol* 37:195–200
- Stensholt BK, Aglen A, Mehl S, Stensholt E (2002) Vertical density distributions of fish: a balance between environmental and physiological limitation. *ICES J Mar Sci* 59:679–710

Editorial responsibility: Otto Kinne, Oldendorf/Luhe, Germany

Submitted: April 2, 2007; *Accepted:* November 5, 2007
Proofs received from author(s): March 26, 2008