

Collective structures anchor massive schools of lesser sandeel to the seabed, increasing vulnerability to fishery

Espen Johnsen^{1,*}, Guillaume Rieucau^{2,3}, Egil Ona¹, Georg Skaret¹

¹Institute of Marine Research, PO Box 1870, 5817 Bergen, Norway

²Department of Biological Sciences, Florida International University, North Miami, Florida 33181, USA

³Louisiana Universities Marine Consortium, Chauvin, Louisiana 70344, USA

ABSTRACT: Over the last decade, North Sea stocks of lesser sandeel *Ammodytes marinus* have undergone a dramatic decline caused by intensive local fishing pressure. Lesser sandeel is a key species in the North Sea, supporting the largest fishery in this ecoregion. This species has developed the particular ability to burrow in sandy seabeds, while forming large pelagic schools to feed on zooplankton. In this study, we analyzed acoustic data from traditional and multibeam echosounders collected during several annual April–May acoustic surveys in sandeel grounds in the northeastern North Sea. Our results showed that schools in the upper pelagic zone maintain contact with the seabed refuge by forming persistent bridge-like collective structures consisting of several million individuals. Moreover, our simulation approach revealed that all large lesser sandeel schools likely have a seabed connection, and comparisons between conventional and multibeam echosounders showed that conventional echosounders markedly underestimate the occurrence of pelagic schools with a seabed connection. This unique adaptation of forming bridges, which act as natural anchors, likely plays an important role in lesser sandeel ecology, preventing post-settled individuals from being detached from suitable bottom substrate. The resulting limited horizontal migration also increases the vulnerability of lesser sandeel to fishery and other anthropogenic impacts.

KEY WORDS: Lesser sandeel · *Ammodytes marinus* · Collective behavior · North Sea · Acoustics · Anti-predator strategies

— Resale or republication not permitted without written consent of the publisher —

INTRODUCTION

The North Sea is one of the most productive seas in the world. In this area, lesser sandeel *Ammodytes marinus* supports the largest fishery, with historical annual landings exceeding more than 1 million (Furness 1990, Wanless et al. 1999), and is primarily used for the production of fish food, fertilizer and oil (Jennings et al. 2001). This small obligatory gregarious species forms massive pelagic shoals consisting of up to several million individuals that inhabit sandy-bottomed coastal and shallow oceanic waters (Braum 1987). Due to its abundance and fat richness, lesser

sandeel is a key species in the North Sea ecosystem, playing a pivotal role in maintaining the structure of the marine community as a major component of the food web preyed on by a great variety of predator species of marine mammals, piscivorous fish and seabirds (Engelhard et al. 2013).

The importance of sandeel is evident as changes in sandeel abundance are known to induce bottom-up effects on ecosystem processes, e.g. local stock collapses of sandeel caused breeding failure of several seabird species of Shetland and Scotland in the years before 2000 (Frederiksen et al. 2007). Long-lasting local collapses of lesser sandeel have also been

*Corresponding author: espen.johnsen@imr.no

reported in Norwegian waters (ICES 2010). At the beginning of the millennium, lesser sandeel stock in the central North Sea severely dropped due to poor recruitment and high fishing effort, and catches in 2003 and 2004 were ca. 40% of the long-term (1992–2002) average of 870 000 tonnes (ICES 2017).

In contrast to other pelagic species, lesser sandeel hides during large parts of its life by burrowing in sandy seabed where the proportion of fine silt and clay particles is low (Macer 1966, Wright et al. 2000). During the feeding season in spring, adults which have burrowed into the sandy substrate at night emerge at dawn (Winslade 1974), reaching the upper pelagic zone where they form large schools to feed on zooplankton (Freeman et al. 2004). An intense sandeel trawling fishery generally occurs from mid-April to June and coincides with the lesser sandeel's feeding period, and fishing effort is principally limited to a few sandy hotspots covering less than 5 % of the area in the North Sea (Jensen et al. 2011). Despite the fact that they form large schools, post-settled lesser sandeels are remarkably stationary, do not migrate between fishing grounds (Jensen et al. 2011), and only to a small degree within fishing grounds. This non-migratory behavior in combination with a fishing pressure that is highly geographically restricted may result in severe local stock depletion (ICES 2010).

As an adaptation to shallow, sandy-bottomed environments with high predatory pressure, sandeel has evolved 2 distinct anti-predatory strategies: an immobile-buried in the seabed strategy and an extremely dynamic schooling behavior when swimming in the pelagic zone (Pitcher & Wyche 1983) to feed on zooplankton (Macer 1966, Freeman et al. 2004). This strategy of hiding in well-oxygenated sandy substrate (Pitcher & Wyche 1983, Wright et al. 2000, van Deurs et al. 2010) reduces the risk of predation while limiting energetic expenditure (van Deurs et al. 2010). Post-settled lesser sandeel spend most of their time buried in the seabed (Macer 1966, Winslade 1974), and substrate characteristics have high predictive power on their spatial distribution (van der Kooij et al. 2008). While buried, sandeels are in an immobile, non-feeding state. Under fluctuating environmental conditions or predation risk, group-living fish face the constant challenge of fine-tuning their schooling tendency to minimize their vulnerability to predation while maximizing other fitness gains. Common variations in schooling tendency and behavior observed in pelagic fishes are thought to reflect changes in fish fitness tradeoffs (e.g. feeding, survival or reproduction) (Axelsen et

al. 2000, Boswell et al. 2016). The formation of large oceanic schools is commonly understood as an adaptive strategy aimed at reducing the risk of predation (Pitcher & Parrish 1993, Rieucau et al. 2015) through the action of several anti-predatory mechanisms, which include risk dilution (Turner & Pitcher 1986, Pitcher & Parrish 1993), predator detection (Magurran et al. 1985) and confusion (Tosh et al. 2006, Ioannou et al. 2008), or collective responsiveness and coordinated escape maneuvers (Gerlotto et al. 2006, Marras et al. 2012, Rosenthal et al. 2015, Rieucau et al. 2016). Here, we employed the terms large or massive shoals (i.e. a fish aggregation with a level of social cohesion; Pitcher 1983) or large schools (i.e. a shoal where individuals exhibit polarized and synchronous swimming patterns, with inter-fish distances not greater than one body size; Pitcher & Parrish 1993) to refer to aggregations of such a size that any given individual fish is not able to interact directly with all shoal or school mates simultaneously because of cognitive and sensory limitations (see Rieucau et al. 2015). While avoiding predation is the prevailing functional explanation for why many fish aggregate in very large shoals (Rieucau et al. 2015), shoaling also entails other important advantages, such as faster location of resources (Pitcher et al. 1982, Fernö et al. 1998), more efficient migration (Quinn & Fresh 1984, Makris et al. 2009), and energetic and hydrodynamic benefits (Landa 1998, Domenici 2001, 2010, Hemelrijk et al. 2015). Despite security and foraging advantages, the formation of large pelagic shoals can also impose important costs since large groups are more conspicuous and easily detected by predators (Pitcher & Parrish 1993), including fishing fleets. Sandeel lack a swim bladder to control buoyancy, and thus energetic demands to swim towards and remain in the pelagic feeding zone are high.

The shift between 2 different habitats and states entails high risk due to both the danger of ruptured organization in transition phases and the risk of losing contact with the preferred bottom habitat (Hobson 1986). The behavioral adaptations to this challenging life in transit are key to understanding the ecology of lesser sandeel and their vulnerability to heavy fishery pressure and other anthropogenic disturbances; however, they have not been well described, let alone understood. To date, building a better comprehension of sandeels distribution and dynamics remains impaired by the methodological approaches available to study large-scale sandeel schools in natural conditions and linking them with environmental knowledge.

In 2005, the Institute of Marine Research in Norway initiated an acoustic sandeel survey program (Johnsen et al. 2009), and since then, sandeel surveys have been carried out yearly in spring in the north-eastern North Sea on sandeel grounds in Norwegian waters. During surveys carried out from 2009 to 2012, we studied sandeel schooling behavior by observing and quantifying their collective dynamics *in situ* through the use of a suite of hydroacoustic instruments (e.g. traditional and multibeam echosounders) to identify the possible mechanisms explaining how and why post-settled lesser sandeels have limited horizontal movement. Specifically, we examined the occurrence of sandeel schools with seabed connections through vertically extended collective structures (hereafter referred to as 'bridges') by analyzing data from acoustic surveys.

MATERIALS AND METHODS

Acoustic surveys

All data used in this study were collected during the April–May Norwegian acoustic sandeel surveys conducted from 2009 to 2012 on sandeel grounds in the Norwegian zone of the North Sea (Fig. 1). The depths of these grounds are between 45 and 65 m. Pelagic lesser sandeel schools were commonly observed during conventional line transect surveys using hull-mounted downward-looking echosounders. In 2009, the survey was carried out using RV 'G.O. Sars', operating Simrad EK60 18, 38, 70, 120, 200 and 333 kHz echosounders. During a 1 d survey on 25 April 2009, RV 'Simrad Echo' covered a small part of a sandeel distribution area (denoted A in Fig. 1) using its Simrad ME70 multibeam echosounder. The ME70 data were used to resolve schools in 3 spatial dimensions. In 2010 and 2011, surveys were conducted using RV 'Johan Hjort' equipped with Simrad EK60 18, 38, 120 and 200 kHz echosounders. In 2012, a commercial fishing vessel FF 'Brennholm' was rented to carry out the sandeel survey and was running Simrad EK60 18, 38, and 200 kHz echosounders and a Simrad ME70 multibeam echosounder.

Interpretation and visualization of acoustic data

The acoustic recordings from the EK60 were interpreted using the software Large Scale Survey System (LSSS; www.marec.no/english/index.htm) (Korneliuszen et al. 2016), and the identification of sandeel



Fig. 1. Sandeel fishing banks (yellow areas) in the Norwegian Exclusive Economical Zone (indicated by black lines) and study areas A and B (red polygons). Extension of the fishing banks is derived from trawl track information of the Norwegian sandeel fishing vessels for 1996–2008

schools was based on the unique signal characteristics of the schools and the catch composition of the trawl and dredge samples (Johnsen et al. 2009). The ME70 consists of 15 beams, each beam individually interpreted in LSSS using additional information from the EK60 and catch samples. The ME70 recordings identified as sandeel were extracted and used to generate 3D representations of the sandeel schools (Holmin et al. 2012).

From echo energy to number of individuals

The conversion of acoustic energy expressed as nautical area scattering coefficient (NASC; $\text{m}^2 \text{ nautical mile}^{-2}$ [nmil]) to number of sandeel individuals (N) in each school (i) was carried out using standard procedures. To derive the school area (A_i ; nmi^2), we measured the cross-section of some schools, other-

wise we assumed circular school shape. The number of sandeel by length group (l) for each school (i) was calculated as:

$$N_{i,l} = \rho_{i,l} A_i \quad (1)$$

where ρ is the areal density of fish (n per nmi^2) by length group l and calculated as:

$$\rho_{i,l} = \frac{\text{NASC}_{i,l}}{\sigma_l} \quad (2)$$

where $\text{NASC}_{i,l}$ is the nautical area scattering coefficient by school (i) and length group (l) and σ_l is the acoustic backscattering cross-section for a fish of length l . $\text{NASC}_{i,l}$ is calculated as:

$$\text{NASC}_{i,l} = \text{NASC}_i \frac{\sigma_{l,p}}{\sum_l \sigma_{l,p}} \quad (3)$$

where $\sigma_{l,p}$ is the acoustic backscattering cross-section for a fish of length l multiplied by the proportion (p) of a fish of length l in the total length distribution. The acoustic backscattering cross-section (m^2) for a fish of length l is calculated as:

$$\sigma_l = 4\pi 10^{\left(\frac{\text{TS}_l}{10}\right)} \quad (4)$$

where the target strength, TS , for a fish of length l (cm) is calculated as:

$$\text{TS}_l = m \log_{10}(l) + a \quad (5)$$

where m and a are constants in the empirical target strength versus length formula for the species and the frequency. Since we used NASC derived from both 38 and 200 kHz echosounders, we applied 2 separate formulas for estimating TS . For 38 kHz (Simmonds & MacLennan 2005):

$$\text{TS} = 20 \log_{10}(l) - 93 \quad (6)$$

and for 200 kHz (Kubilius & Ona 2012):

$$\text{TS} = 20 \log_{10}(l) - 93.1 \quad (7)$$

These calculations showed that the largest schools observed consisted of at least 100 million individuals.

Simulation of the detection probability of seabed connections

To estimate the detection probability of a school with a bottom connection during a conventional acoustic survey, we simulated the encounter rate based on standard survey settings and school information from all available acoustic recordings. We defined the horizontal cross-section of a school as

an ellipse where the radius of the x direction was sampled from a square root log-distribution (in log scale: mean = $\exp(100)$; SD = 0.45), where the parameters were derived from measurements of detected schools. The radius of the y direction was dependent on the x radius by a proportion randomly sampled from a normal distribution (mean = 1, SD = 0.2). The seabed connection was simulated as an ellipse with the centre randomly positioned along the outskirt of the horizontal school ellipse as described above, and the x and y radii of the seabed connection was given as a random percentage sampled from a log-distribution (in log scale: mean = $\exp(30)$; SD = 0.45) of the x and y radii, respectively, of the pelagic part. For each simulation run ($n = 10\,000$), the vessel sailed along the y axis, using both multibeam and conventional sonars where the beam widths were 4.5 m and 45 m, respectively, at 50 m depth (assumed bottom depth).

RESULTS

During the surveys, bridges were regularly detected in large schools comprised of up to several million individuals (Fig. 2). We tracked zooplankton distribution in the water masses and the interaction with lesser sandeel feeding in the pelagic zone using high-frequency echograms (Figs. 2 & 3). Around sunset, sandeel schools were observed to swim towards the sandy seabed where they burrowed. At the following sunrise, we observed a flow of sandeel emerging from the seabed with a speed of more than 0.3 m s^{-1} to again reach the pelagic zone (Fig. 3).

Based on data collected in 2009 and 2010 at 2 sandeel grounds (Fig. 1) with high abundance of sandeel and high survey coverage, we examined the frequency of occurrence of pelagic sandeel schools with such seabed connections. A school was classified as 'pelagic school' when parts of the school were observed closer to the echosounder transducer depth (10 m) than to the seabed. When a pelagic school extended downwards and some parts were recorded closer than 5 m to the seabed, we defined it as a pelagic school with a seabed connection. The conventional echosounder observations are limited to a 2D display and a narrow echosounder beam.

To overcome this limitation we were able to record with a multibeam echosounder covering a width of about 50 m at 50 m depth (Trenkel et al. 2008), entire school structures could be observed in 3D (Fig. 4, Video S1 in the Supplement at www.int-res.com/articles/suppl/m537p229_supp/). 3D representations

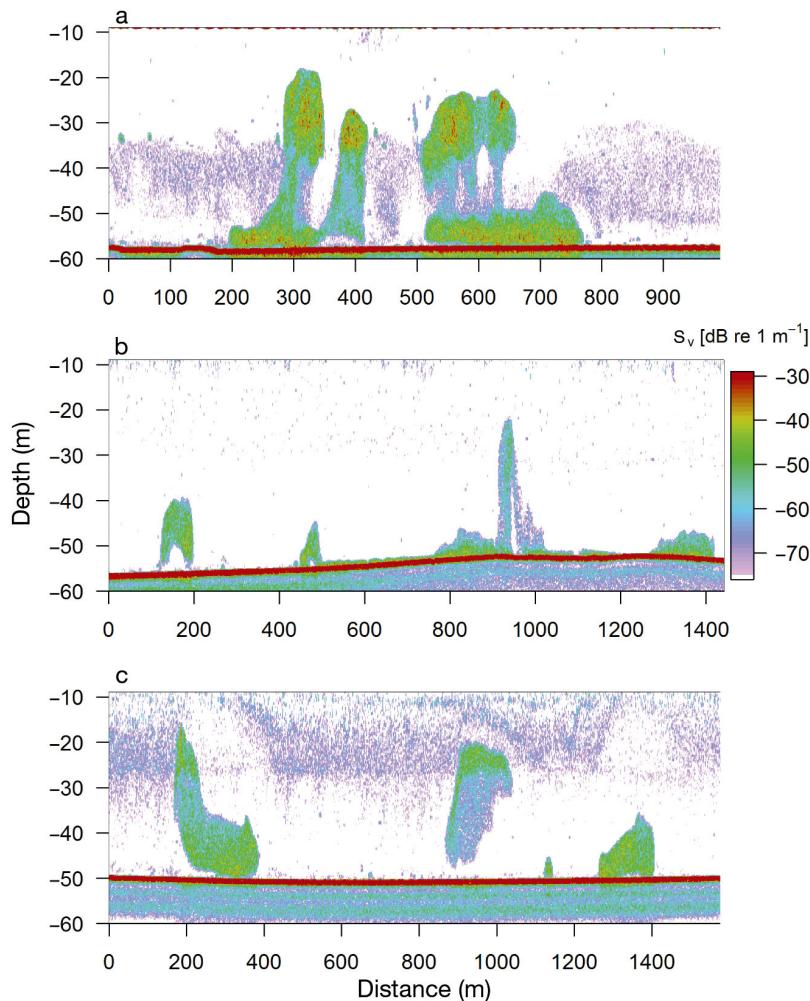


Fig. 2. School structures of lesser sandeel recorded with a Simrad EK60 200 kHz echosounder in (a) area B in 2009 and (b) area A in 2010 and (c) area A in 2012. The estimated number of individuals in the bridge structures are (a) 2.2 million, (b) 0.5 million and (c) 6.7 million. S_v : volume backscattering strength

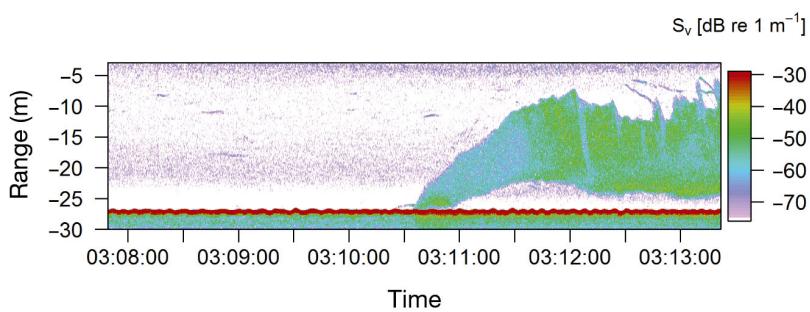


Fig. 3. A school of lesser sandeel emerges from the seabed at sunrise. Recordings were made with an acoustic probe installed with a Simrad EK60 200 kHz echosounder deployed at the exact position in Area B where a sandeel school was observed to burrow into the sandy substrate at sunset the previous day. The probe was lowered to about 27 m above the seabed; sea depth is 59.2 m.

S_v : volume backscattering strength

of schools allowed for detailed examination of the collective structures and swimming dynamics (see Video S1). These recordings revealed that large pelagic sandeel schools apparently swimming freely, as observed with conventional echosounders, were in fact connected to the seabed through a bridge-like collective structure. Comparisons made between the conventional echosounder and the multibeam in our simulations showed that the conventional echosounder markedly underestimated (~50 %) the occurrence of pelagic schools with a seabed connection.

The proportion of schools with a seabed connection increased with school size (Fig. 5) and, without any bias correction for the narrow beam of the conventional echosounder, we found that more than half of all pelagic sandeel schools with a length of more than 75 m were connected to the seabed by a bridge-like collective structure (Fig. 5). Considering the low detection probability of seabed connections when using the conventional narrow beam, this means that nearly all larger sandeel schools (lengths >75 m) may in fact have a seabed connection. As large schools contain more individuals, the majority of sandeels identified acoustically were therefore in schools with a seabed connection. Our observations revealed that sandeel schools can be connected to the seabed through either one bridge or several bridges (Figs. 2 & 3, Video S1).

To examine the persistence of the bridges, as well as the horizontal movement of the schools, one large school structure (Fig. 3) was monitored continuously during 2 5-h periods separated by 4 d (1 May and 5 May 2012). The school was estimated to contain more than 100 million individuals. We found that the school had a permanent seabed connection during both observation periods and showed a very limited horizontal movement ($<0.02 \text{ m s}^{-1}$) towards a weak water current ($0.10\text{--}0.15 \text{ m s}^{-1}$). The centre of this large school moved less than 1 km during the 4 d period.

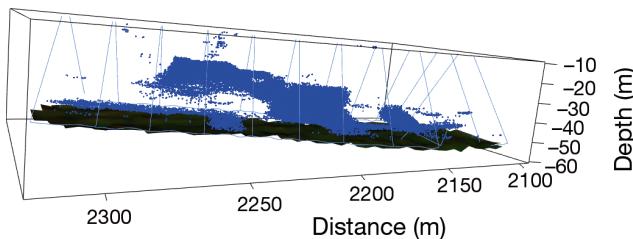


Fig. 4. 3D visualization of a large pelagic school of lesser sandeel connected to the sandy seabed via bridge-like collective structures. Acoustic data were recorded using a multibeam echosounder

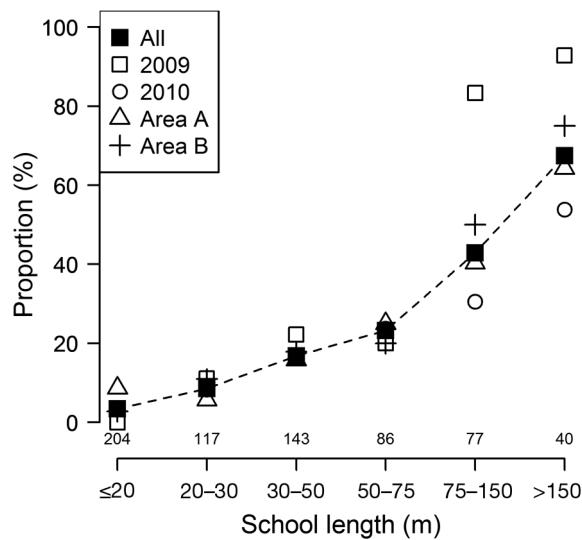


Fig. 5. Percentage of all observed pelagic lesser sandeel schools in the study areas with a seabed connection grouped by different school lengths. The number of observed pelagic schools for all areas by school length interval is indicated above the x-axis

DISCUSSION

By showing that the majority of large pelagic lesser sandeel schools are persistently connected to the seabed through a collective bridge-like structure comprised of several million individuals, combined with the known strong association of settled individuals with sandy-bottomed habitat, our study identifies the possible mechanism responsible for the limited horizontal movements of large sandeel aggregations. As these collective structures were predominantly observed in large schools, our study suggests that a critical number of individuals may be required to form and maintain the collective bridge between the sand-hidden individuals and the feeding-motivated fish that are actively schooling in the pelagic zone. We have also documented that lesser

sandeel emerge synchronously with a high speed from the seabed at dawn to form schools in the upper pelagic zone, indicating a collective decision (Rands et al. 2003, Couzin et al. 2005). The signaling processes eliciting these organized mass movements are currently unknown. However, it is now well understood how large pelagic schools can maintain and grow once established in the open waters as individuals balance upward attraction towards food in the pelagic and downward attraction towards conspecifics and shelter (Rieucau et al. 2015). It has been demonstrated extensively through agent-based models how different aspects of schooling can be understood as leaderless and self-emerging from simple local interactions between individuals (Couzin & Krause 2003, Herbert-Read et al. 2011, Katz et al. 2011, Rieucau et al. 2015, Herbert-Read 2016). In a case analogous to the one studied here, vertical bridges in schools of Atlantic herring *Clupea harengus* emerged from simple rules of local attraction and repulsion, when motivation to go down to the high-risk bottom zone to deposit spawn increased (Axelsen et al. 2000, Johnsen & Skaret 2008, Vabø & Skaret 2008). However, the mechanisms and the collective properties underlying the emergence of these collective bridges in the lesser sandeel still need to be ascertained.

Our approach allows better understanding of the fine-scale movement dynamics of a species with a strong habitat bond. Paradoxically, the particular adaption of sandeel to a life in transit in the water column with the formation of persistent collective bridges connecting the feeding pelagic zone to the refuge seabed also act as natural anchors for large schools, imposing a stationary existence with important survival consequences in the face of sandeel-specialized fishery. The combination of persistent seabed connections restricting migratory tendencies (Gauld 1990, Jensen et al. 2011) with the strong habitat bond of the lesser sandeels makes them exceptionally vulnerable to sediment contamination and high local fishing pressure. It is nevertheless possible that sandeel migratory behavior varies between ecoregions, as differences in the magnitude of horizontal movements have been reported in different studies (Kühlmann & Karst 1967, Hobson 1986, Engelhard et al. 2008). Other large schooling stocks, such as Atlantic herring (Fernö et al. 1998) or mesopelagic fishes that organize in depth-discrete sound-scattering layers (Neilson & Perry 1990, Steinberg et al. 2000, Ariza et al. 2016, Klevjer et al. 2016), perform well-described diel vertical migrations, moving toward shallower waters during night to feed when

the predation risk from visually mediated predators is reduced. In contrast, our study highlights that sandeels reduce the predation risk by burrowing into the seabed at night and are organized in schools that easily can seek protection in the seabed.

Based on the observed behavioral patterns, the local density seems to be of great importance for production and survival of lesser sandeels and should be considered in a sound management of this important prey species of the North Sea and other marine ecosystems. The North Sea sandeel fishery, which is concentrated in late April to June during the sandeel's feeding period, is mostly restricted to a few sandy hotspots (Fig. 1) covering less than 5 % of the North Sea and targets large sandeel schools (Jensen et al. 2011). The fishery effort, therefore, could have important ecological impacts followed by unexpected evolutionary consequences by disrupting anti-predatory adaptations. Whereas most management actions on commercial fisheries of highly aggregative species distributed on restricted patches rely mostly on population dynamic indicators, the sandeel case study pinpoints the critical need for considering fine-scale adaptive behavioral patterns and the underlying collective mechanism to develop efficient conservation and management plans.

Acknowledgements. This work was partly funded by the Research Council of Norway under contract 185065/S40. We thank Kongsberg Simrad for their assistance and data collection with R/V 'Simrad Echo' with ME70. We thank Ronald Pedersen for his excellent work in data collection, and also the crew on board RV 'Johan Hjort', RV 'G.O. Sars' and MV 'Brennholm'.

LITERATURE CITED

- Ariza A, Landeira JM, Escámez A, Wienerroither R and others (2016) Vertical distribution, composition and migratory patterns of acoustic scattering layers in the Canary Islands. *J Mar Syst* 157:82–91
- 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
- Boswell KM, Rieucou G, Vollenweider JJ, Moran JR, Heintz RA, Blackburn JK, Csepp DJ (2016) Are spatial and temporal patterns in Lynn Canal overwintering Pacific herring related to top predator activity? *Can J Fish Aquat Sci* 73:1307–1318
- Braum E (1987) Smith's sea fishes. Edited by M. M. Smith and P. C. Heemstra.—1047 pp. Berlin—Heidelberg—New York: Springer Verlag 1986. ISBN 3-540-16851-6. DM 198,-. *Int Rev Gesamten Hydrobiol* 72:775–776
- Couzin ID, Krause J (2003) Self-organization and collective behavior in vertebrates. *Adv Stud Behav* 32:1–75
- Couzin ID, Krause J, Franks NR, Levin SA (2005) Effective leadership and decision-making in animal groups on the move. *Nature* 433:513–516
- Domenici P (2001) The scaling of locomotor performance in predator-prey encounters: from fish to killer whales. *Comp Biochem Physiol A Mol Integr Physiol* 131:169–182
- Domenici P (2010) Context-dependent variability in the components of fish escape response: integrating locomotor performance and behavior. *J Exp Zool A Ecol Genet Physiol* 313A:59–79
- Engelhard GH, van der Kooij J, Bell ED, Pinneyar JK, Blanchard JL, Mackinson S, Righton DA (2008) Fishing mortality versus natural predation on diurnally migrating sandeels *Ammodytes marinus*. *Mar Ecol Prog Ser* 369:213–227
- Engelhard GH, Blanchard JL, Pinneyar JK, van der Kooij J, Bell ED, Mackinson S, Righton DA (2013) Body condition of predatory fishes linked to the availability of sandeels. *Mar Biol* 160:299–308
- Fernö A, Pitcher TJ, Melle W, Nøttestad L, Mackinson S, Hollingworth C, Misund OA (1998) The challenge of the herring in the Norwegian sea: making optimal collective spatial decisions. *Sarsia* 83:149–167
- Frederiksen M, Furness RW, Wanless S (2007) Regional variation in the role of bottom-up and top-down processes in controlling sandeel abundance in the North Sea. *Mar Ecol Prog Ser* 337:279–286
- Freeman S, Mackinson S, Flatt R (2004) Diel patterns in the habitat utilisation of sandeels revealed using integrated acoustic surveys. *J Exp Mar Biol Ecol* 305:141–154
- Furness RW (1990) A preliminary assessment of the quantities of Shetland sandeels taken by seabirds, seals, predatory fish and the industrial fishery in 1981–83. *Ibis* 132:205–217
- Gauld JA (1990) Movements of lesser sandeels (*Ammodytes marinus* Raitt) tagged in the northwestern North Sea. *ICES J Mar Sci* 46:229–231
- Gerlotto F, Bertrand S, Bez N, Gutierrez M (2006) Waves of agitation inside anchovy schools observed with multi-beam sonar: a way to transmit information in response to predation. *ICES J Mar Sci* 63:1405–1417
- Hemelrijck CK, Reid DAP, Hildenbrandt H, Padding JT (2015) The increased efficiency of fish swimming in a school. *Fish Fish* 16:511–521
- Herbert-Read JE (2016) Understanding how animal groups achieve coordinated movement. *J Exp Biol* 219:2971–2983
- Herbert-Read JE, Perna A, Mann RP, Schaerf TM, Sumpter DJ, Ward AJ (2011) Inferring the rules of interaction of shoaling fish. *Proc Natl Acad Sci USA* 108:18726–18731
- Hobson ES (1986) Predation on the Pacific sand lance, *Ammodytes hexapterus* (Pisces: Ammodytidae), during the transition between day and night in southeastern Alaska. *Copeia* 1986:223–226
- Holmin AJ, Handegard NO, Korneliussen RJ, Tjostheim D (2012) Simulations of multi-beam sonar echos from schooling individual fish in a quiet environment. *J Acoust Soc Am* 132:3720–3734
- ICES (2010) Report of the benchmark workshop on sandeel (WKSAN), 6–10 September 2010, Copenhagen. ICES CM 2010/ACOM:57
- ICES (2017) Report of the benchmark workshop on sandeel (WKSand 2016), 31 October–4 November 2016, Bergen.

- ICES CM 2016/ACOM:33
- Ioannou CC, Tosh CR, Neville L, Krause J (2008) The confusion effect—from neural networks to reduced predation risk. *Behav Ecol* 19:126–130
- Jennings S, Kaiser M, Reynolds JD (2001) Marine fisheries ecology. Wiley-Blackwell, Oxford
- Jensen H, Rindorf A, Wright PJ, Mosegaard H (2011) Inferring the location and scale of mixing between habitat areas of lesser sandeel through information from the fishery. *ICES J Mar Sci* 68:43–51
- Johnsen E, Skaret G (2008) Adaptive mass formations in fish shoals founded in conflicting motivation. *Mar Ecol Prog Ser* 358:295–300
- Johnsen E, Pedersen R, Ona E (2009) Size-dependent frequency response of sandeel schools. *ICES J Mar Sci* 66: 1100–1105
- Katz Y, Tunstrøm K, Ioannou CC, Huepe C, Couzin ID (2011) Inferring the structure and dynamics of interactions in schooling fish. *Proc Natl Acad Sci USA* 108:18720–18725
- Klevjer TA, Irigoien X, Røstad A, Fraile-Nuez E, Benítez-Barrios VM, Kaartvedt S (2016) Large scale patterns in vertical distribution and behaviour of mesopelagic scattering layers. *Sci Rep* 6:19873
- Korneliussen RJ, Heggelundb Y, Macaulay GJ, Patel D, Johnsen E, Eliassen IK (2016) Acoustic identification of marine species using a feature library. *Methods Oceanogr* 17:187–205
- Kubilius R, Ona E (2012) Target strength and tilt-angle distribution of the lesser sandeel (*Ammodytes marinus*). *ICES J Mar Sci* 69:1099–1107
- Kühlmann DHH, Karst H (1967) Freiwasserbeobachtungen zum Verhalten von Tobias-fischschwärmern (*Ammodytidae*) in der westlichen Ostsee. *Z Tierpsychol* 24:282–297
- Landa J (1998) Bioeconomics of schooling fishes: selfish fish, quasi-free riders, and other fishy tales. *Environ Biol Fishes* 53:353–364
- Macer CT (1966) Sand eels (*Ammodytidae*) in the southwestern North Sea: their biology and fishery. *Fishery Investigations Series 2*, Vol. 24, Great Britain Ministry of Agriculture, Fisheries and Food, HMSO, London
- Magurran AE, Oulton WJ, Pitcher TJ (1985) Vigilant behaviour and shoal size in minnows. *Z Tierpsychol* 67: 167–178
- Makris NC, Ratilal P, Jagannathan S, Gong Z and others (2009) Critical population density triggers rapid formation of vast oceanic fish shoals. *Science* 323:1734–1737
- Marras S, Batty RS, Domenici P (2012) Information transfer and antipredator maneuvers in schooling herring. *Adapt Behav* 20:44–56
- Neilson JD, Perry RI (1990) Diel vertical migrations of marine fishes: an obligate or facultative process? *Adv Mar Biol* 26:115–168
- Pitcher TJ (1983) Heuristic definitions of fish shoaling behaviour. *Anim Behav* 31:611–613
- Pitcher TJ, Parrish JK (1993) The functions of shoaling behaviour. In: Pitcher TJ (ed) The behaviour of teleost fishes. Chapman and Hall, London
- Pitcher T, Wyche C (1983) Predator-avoidance behaviours of sand-eel schools: why schools seldom split. In: Noakes DG, Lindquist D, Helfman G, Ward J (eds) Predators and prey in fishes, Book 2. Springer, Dordrecht, p 193–204
- Pitcher TJ, Magurran AE, Winfield IJ (1982) Fish in larger shoals find food faster. *Behav Ecol Sociobiol* 10:149–151
- Quinn TP, Fresh K (1984) Homing and straying in chinook salmon (*Oncorhynchus tshawytscha*) from Cowlitz river hatchery, Washington. *Can J Fish Aquat Sci* 41: 1078–1082
- Rands SA, Cowlishaw G, Pettifor RA, Rowcliffe JM, Johnstone RA (2003) Spontaneous emergence of leaders and followers in foraging pairs. *Nature* 423:432–434
- Rieucau G, Fernö A, Ioannou CC, Handegard NO (2015) Towards a firmer explanation of large shoal formation, maintenance and collective reactions in marine fish. *Rev Fish Biol Fish* 25:21–37
- Rieucau G, Holmin AJ, Castillo JC, Couzin ID, Handegard NO (2016) School level structural and dynamic adjustments to risk promote information transfer and collective evasion in herring. *Anim Behav* 117:69–78
- Rosenthal SB, Twomey CR, Hartnett AT, Wu HS, Couzin ID (2015) Revealing the hidden networks of interaction in mobile animal groups allows prediction of complex behavioral contagion. *Proc Natl Acad Sci USA* 112: 4690–4695
- Simmonds J, MacLennan DN (2005) Fisheries acoustics: theory and practice. Blackwell Science, Oxford
- Steinberg DK, Carlson CA, Bates NR, Goldthwait SA, Madin LP, Michaels AF (2000) Zooplankton vertical migration and the active transport of dissolved organic and inorganic carbon in the Sargasso Sea. *Deep-Sea Res I* 47: 137–158
- Tosh CR, Jackson AL, Ruxton GD (2006) The confusion effect in predatory neural networks. *Am Nat* 167: E52–E65
- Trenkel VM, Mazauric V, Berger L (2008) The new fisheries multibeam echosounder ME70: description and expected contribution to fisheries research. *ICES J Mar Sci* 65: 645–655
- Turner GF, Pitcher TJ (1986) Attack abatement: a model for group protection by combined avoidance and dilution. *Am Nat* 128:228–240
- Vabø R, Skaret G (2008) Emerging school structures and collective dynamics in spawning herring: a simulation study. *Ecol Model* 214:125–140
- van der Kooij J, Scott BE, Mackinson S (2008) The effects of environmental factors on daytime sandeel distribution and abundance on the Dogger Bank. *J Sea Res* 60: 201–209
- van Deurs M, Christensen A, Frisk C, Mosegaard H (2010) Overwintering strategy of sandeel ecotypes from an energy/predation trade-off perspective. *Mar Ecol Prog Ser* 416:201–214
- Wanless S, Finney SK, Harris MP, McCafferty DJ (1999) Effect of the diel light cycle on the diving behaviour of two bottom feeding marine birds: the blue-eyed shag *Phalacrocorax atriceps* and the European shag *P. aristotelis*. *Mar Ecol Prog Ser* 188:219–224
- Winslade P (1974) Behavioural studies on the lesser sandeel *Ammodytes marinus* (Raitt). II. The effect of light intensity on activity. *J Fish Biol* 6:577–586
- Wright PJ, Jensen H, Tuck I (2000) The influence of sediment type on the distribution of the lesser sandeel, *Ammodytes marinus*. *J Sea Res* 44:243–256