Collective behaviour
of herring during spawning

by

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Acknowledgements

Content

Papers 1-5

Summary

The thesis focuses on the collective behaviour of Norwegian spring spawning herring (NSS-herring; *Clupea harengus* L.) in the specific ecological context of reproduction. The major part of the work is based on field research using quantitative echo sounders and sonar in combination with biological sampling. In addition, an individual based schooling model is applied to investigate underlying mechanisms of the collective formations and dynamics. All studies are founded in a classical mechanistic ecological approach interpreting behaviours as optimal evolutionary strategies given an individual's physiological and cognitive constraints, internal state and the specific ecological context.

Two of the works are case-studies from historical spawning grounds of NSS-herring well-known to fishermen and scientists; the shallow (30-40 m) banks off Karmøy (Paper 1) receive a small proportion of the spawning stock, whereas deep (80-250 m) areas off Møre (Paper 2) comprise the main spawning grounds. In both works the areas are covered through repeated acoustic surveys in combination with sampling of herring and predators throughout the 24-h-cycle over several days. Fisheries scientists apply similar acoustic surveying when making abundance estimates of herring that serve as basis for advices of catch quotas. A major challenge during such surveying is the fact that herring tend to avoid the approaching research vessel, rendering them unavailable to detection. How this potential source of error operates during spawning is given the focus in one of the works (Paper 3). In this study we use a simple experimental design where a standard research vessel passes a presumably neutral stationary vessel that records the herring reaction. In the fourth work we apply a rule-based simulation model with high temporal resolution able to recreate life-like collective behaviours (Paper 4). The model is used to explore how collective dynamics and formations are affected when varying the amount of herring present and their degree of motivational synchronisation. In the final work (Paper 5) we investigate 11 years of acoustic data from herring spawning surveys along the Norwegian coast. We frequently find evidence of vertical hourglass formations, and based on knowledge gained from previous studies and the simulation model we formulate and test out a concrete hypothesis; are these formations founded in conflicting individual motivation for spawning?

An overall evaluation of our field results strongly supports that herring behaviour during spawning reflects a compromise between survival and reproduction. We find that herring spawn in highly synchronous waves where individuals aggregate (Paper 2) and move together (Paper 1) in their quest for a successful spawning. This strategy is likely to be advantageous for survival since a synchronous emergence in high numbers will decrease an individual's risk of being targeted by a predator (dilution effect). A similar advantage is gained through spawning in the dark hours when predators are less active. Shoals at night-time were observed to have a stable loose packing density, whereas a variable, but generally high packing density at daytime corresponds well with a presumed higher frequency of predator attacks, since it is known that shoals become more densely packed under attack. At the deep spawning grounds, large proportions of the herring became scattered in pelagic layers at night-time. Interestingly, these layers were positioned according to the thermocline in a way that indicates active use of the

vertical temperature profile to fine-tune maturation rate in the days prior to spawning. The shallow spawning grounds had a different dynamic and such layers were not observed. In these areas, the vast majority of herring were in layers at the bottom at night-time. In this situation, herring did not react to the research vessel (Paper 3), probably because the focus on the spawning activity increases their reaction threshold. At both spawning grounds (Papers 1 and 2), there were substantial vertical dynamics that corresponded well with the results from the schooling model. In the model simulations, shoal height is dependent on the difference in individual motivation for spawning. With strong conflicts in motivation, shoals tend to split in the same way as we observed during spawning in the field (Paper 2), whereas with intermediate conflicts shoals maintain cohesion but become vertically extended like we observed during pre-spawning. A special case of the latter is the vertical hourglass formation that emerges in the model assorted according to maturation state. Similar assortment was observed in the hourglass formations in the wild, where spawners dominated in the lower parts relative to pre- and post-spawners, strongly indicating that motivational conflict is the driving force of the observed formation. Whether such formations are purely emergent from decisions made from local stimuli or implying communication between the two shoal parts is an interesting question open to future investigations.

List of papers

Paper 1:
Georg Skaret, Leif Nøttestad, Anders Fernö, Arne Johannessen, Bjørn Erik Axelsen. Spawning of herring: day or night, today or tomorrow? Aquatic Living Resources 16 (2003) 299–306.

Paper 2:
Georg Skaret and Aril Slotte. Collective behaviour of herring around the spawning peak. Manuscript.

Paper 3:
Georg Skaret, Bjørn Erik Axelsen, Leif Nøttestad, Anders Fernö, Arne Johannessen. The behaviour of spawning herring in relation to a survey vessel. ICES Journal of Marine Science 62 (2005) 1061-1064.

Paper 4:
Rune Vabø and Georg Skaret. Emerging school structures and collective dynamics in spawning herring: a simulation study. Submitted to Ecological Modelling.

Paper 5:
Espen Johnsen and Georg Skaret. Mass formations in giant fish shoals founded in conflicting individual motivation. Manuscript.

Background

A striking feature and genuine characteristic of herring (*Clupea harengus* L.) is the individual's tight link to the collective. Herring is an obligate schooler, swimming in a permanent context of social interaction from late larval stage to fatal end (Blaxter and Hunter 1982). The school is hence the natural entity when investigating herring behaviour. However, underlying mechanisms and functions of schooling like any behavioural phenomenon can only be understood through a classical mechanistic approach with the individual as the unit subject to natural selection (Darwin 1859). Recent advances in individual based modelling have opened new insights into collective behaviour through linking the individual and the collective, and there is now a general acceptance that a fish school must be considered mainly a decentralised system where global patterns emerge from simultaneous local reactions to the neighbours and the immediate surrounding environment (Parrish and Hamner 1997; Camazine et al. 2001; Couzin and Krause 2003). Schooling is an adaptive behaviour seen in more than 4000 pelagic fish (Shaw 1978), and functions can be linked to rapid food finding (Pitcher and Parrish 1993), energy optimisation (Huse and Ona 1996; Herskin and Steffensen 1998) and efficient migration (Huse et al. 2002; Couzin et al. 2005). However, protection against predation is generally considered to be the major function for most schooling species (Godin 1986; Pitcher and Parrish 1993), including herring (Blaxter and Hunter 1982; Axelsen et al. 2000).

There are numerous huge populations of herring worldwide (Hay et al. 2001), and the important ecological role it plays linking apex predators and zooplankton communities in addition to it's economical importance make it one of the most studied fish species in the world. Norwegian spring spawning herring (NSS-herring) is the largest of all herring stocks (Holst et al. 2004), with the combined home range of juveniles and adults extending the entire Barents Sea and Norwegian Sea and even beyond. One of the most striking characteristics of this stock is it's repeated seasonal cycles where the year is divided into defined periods of feeding, wintering and spawning and the behaviour changes accordingly (Fernö et al. 1998). Feeding takes place in late spring and summer involving extensive migrations in the Norwegian Sea, but there are also examples of more local feeding in fjords and coastal areas (Holst et al. 2002; Kvamme et al. 2003). Winter months are spent in extremely large groups aggregating in deep (200-900 m) areas; feeding ceases and movement is restricted to a minimum in what can be seen partly as an analogue to hibernation in mammalian species (Huse and Ona 1996; Slotte 1999). The migration to the spawning areas starts in January-February, and goes to banks along the Norwegian coast ranging from Lofoten to Lista (a distance of approximately 600 nmi). Even though interrupted by decades with absence of herring, an important coastal herring fishery during spawning has been recorded at least back to the 15th century (Vollan 1971). The reasons for this stability are probably linked to the coastal currents as well as the topographic properties of the spawning grounds, because even though a pelagic fish, herring spawn demersally on rocks and coarse gravel (Runnström 1941). Which spawning grounds that attract the most herring has to some extent changed over time (Runnström 1941; Slotte 2001; Beverton et al. 2004), but during the last 20 years spawning herring have been most abundant on the banks off Møre (63°N) (Dragesund et al. 1997; Slotte 2001). When arriving at the spawning grounds most herring are close to ripe, but with individual variation in

state of maturation (Nøttestad et al. 1996; Slotte 1999). Within 1-7 days the spawning of an individual is over (Johannessen 1986; Axelsen et al. 2000). The behaviour and physiology linked to the spawning act has been studied in Pacific herring (*Clupea harengus pallasi*), where spawning was shown to be initiated by a short pheromone-induced period termed ovulation in females and spermiation in males, with the release of milt by a male triggering the act (Stacey and Hourston 1982; Gillis et al. 1990).

There are numerous studies with a large-scale approach to the spawning of NSS-herring. A review of previous work on migration, timing of spawning at the population level and large scale distribution is found in Slotte (1998), and more recently significant works have been done on spawning migration (Slotte and Fiksen 2000), timing of spawning (Slotte 2001) and skipped spawning (Engelhard and Heino 2005). These aspects will not be treated further here. Collective behaviour in relation to spawning has, on the other hand, with a few notable exceptions (Nøttestad et al. 1996; Axelsen et al. 2000), been little studied. The fundamental importance of such studies is at least twofold: understand herring behaviour and decision making in a crucial life history phase, and understand general mechanisms underlying free-ranging marine fish collectives. In addition, behavioural knowledge is a pre-requisite for reliable acoustic abundance estimation during specific life cycle phases.

The short time spent at the spawning grounds, the utmost importance of a successful reproduction and the differences in individual maturation states that should be reflected in differential motivation towards spawning, make the spawning period particularly interesting for studies of collective behaviour. Nøttestad et al. (1996) showed that shoal features like size, packing density, shape and swimming speed changed markedly between pre-spawning, spawning and post-spawning herring. These changes were interpreted to reflect different and changing individual behavioural motivations. At a small local spawning ground, Axelsen et al. (2000) followed a single shoal through the whole spawning process and observed how it split vertically to form two components with periodic contact. They interpreted this formation as a reflection of a precautionary behavioural strategy where pre- and post-spawners minimise the time spent close to the bottom, a zone associated with high predation risk (Høines 1999; Runde 2005). However, whether similar collective behaviour can be found at the main spawning areas with millions of tons of herring is not known. Nor has it been investigated how the time of the day modifies formations and dynamics during spawning, and how hydrographic conditions influence the collective behaviour.

The field within behavioural ecology working on group living animals investigated through theoretical modelling, laboratory studies and field research comprises works from a range of different taxa, including schooling fish (Wilson 1975; Krause and Ruxton 2002). However, works applying this approach to free-ranging marine shoals are scarce (Parrish and Edelstein-Keshet 1999; Krause and Ruxton 2002), and there is a need to supply the knowledge and theory of collective behaviour based on laboratory experiments or small-scale models (10-100 fish), which are often not readily transferable to marine schooling fish in large systems with a complex surrounding environment.

The main objectives of this thesis were to describe collective behaviour in herring during spawning and share light on the underlying mechanisms behind the behaviour as well as its functionality in an evolutionary perspective. As possible influences we take into account differing individual spawning motivation and amount of herring present in the system, predation risk including the threat imposed by a research vessel, light conditions (diel variations), geographical setting (depth, topography) and hydrography.

Summary of papers

Paper 1: Diel variations in schooling patterns and spatial dynamics of herring were studied in a shallow spawning area off south-western Norway using acoustic surveying and school tracking by sonar, diel cycle experiments and biological sampling with gillnet. Herring formed loosely packed spawning layers shortly after darkness that disappeared in the acoustic dead zone near the bottom at night. The following mornings they lifted off and formed dense pelagic shoals during day, but also vertically extended transition schools that were partially located in the bottom channel, partially in the pelagic. We consider night-time spawning to be part of a precautionary strategy towards visual predators, since the bottom is associated with high densities of gadoids. Herring not ready to spawn dominated the bottom samples in 4 out of 5 days, suggesting that pre-spawning herring followed the descent of ripe herring in the evenings. The spawning layers shifted gradually in a south-easterly direction from day to day in diel spawning waves.

Paper 2: Collective behaviour of herring was studied around the peak spawning at the most important spawning ground. Over a period of one month, 17 acoustic surveys (nine at night-time and eight during day) along a pre-defined survey grid covering an area of approximately 450 square nautical miles, were conducted. Estimated herring biomass increased 20-fold during two days to a peak of more than a million tons and decreased to less than the half during the next five days. The synchronised timing of spawning may be attuned through vertical positioning according to the temperature profile, as herring during night were dispersed in layers recorded successively deeper towards the spawning peak corresponding with a gradually rising temperature in deeper waters. The positioning may be a way to adjust the rate of gonad maturation. The spawning was also spatially synchronised through aggregative behaviour, as average shoal size experienced by the individuals increased with increasing biomass. We argue that the aggregation is an anti-predatory strategy through predation swamping decreasing an individual's risk of being targeted by a predator. The largest aggregations were found at the bottom during night-time, indicating that the major spawning happened in darkness. Night-time shoals were characterised by low packing density with little variance contrary to daytime shoals distributed deeply with generally high, but variable packing density. We argue that observed diel variations in packing density are collective responses to the immediate predation pressure that is higher during the day. Throughout the period, there was a successive decrease in shoal height that may reflect a diminishing degree of conflict in behavioural motivation within shoals. This finding supports model results of collective individual's response to reproduction and predation in periods of dynamic motivation. The recorded behaviours in this study resulting in diel variations in acoustic availability and tremendous biomass fluxes have huge implications for acoustic abundance estimates.

Paper 3: Vessel avoidance of spawning herring was investigated on a shallow spawning ground. In eight repeated night-time passages a demersal layer of herring was recorded acoustically by a small stationary reference vessel, while a conventional survey vessel passed at short ranges (8-40 m). No avoidance attributable to the survey vessel was observed. We interpret vessel avoidance as a response to a perceived threat and at the spawning site, the high priority given to

reproductive activities seems to overrule the avoidance responses to a passing survey vessel.

Paper 4: Field observations are only recording resulting patterns of collective behaviour in herring, and not the mechanisms of how individual decisions and interactions lead to the observed formations. In individual based models (IBM) on the other hand, the mechanisms of how low-level individual behaviour influences large-scale behaviour can be investigated. In this study, we use a rule based school model in order to gain understanding of how certain school patterns can emerge during the spawning of NSS-herring. Response to predation and motivation towards spawning are added to the response to nearby fish. Simply by varying population size and how the motivation towards spawning is synchronised between fish with different gonad states, we see different responses in terms of collective dynamics. With high behavioural synchronisation, mainly one integrated school is present in the system, whereas low degree of synchronisation leads to a system with frequent split-offs of small schools. An intermediate degree of synchronisation provides a more complex situation with schools or layers in a dynamic vertical contact and formation of vertical 'hourglasses' or cylindrical shaped schools. This suggests that the degree of motivational synchronisation between individuals in a school will determine whether or to what degree a school splits into different components or remains integrated. Furthermore, distinct and characteristic formations similar to formations observed in the field, may be generated and maintained through mere differences in spawning motivation. We also find that with increasing population size there are new system behaviours emerging, not present with lower population size. Larger populations lead to horisontal extension of the pre-spawning components resulting in two layers connected by vertical bridges. The bridges are formed and maintained by ovulating and spent herring moving across these structures.

Paper 5: Through investigations of acoustic time series data from the spawning ground, we document that vertical hourglass formations are not uncommon at herring spawning grounds. We hence were provided with a basis for testing the hypothesis that such formations are linked to differential individual motivation towards spawning. We find significant differences in maturation state between the upper and lower components of the formations, indicating conflicting individual motivation for spawning as the underlying mechanism of the collective behaviour. We argue that such formations are adaptive with anti-predatory function in periods of inherent natural variation in motivation between individuals, as group cohesion can be maintained through positive feedback across 'fish bridges' despite conflicting motivation for spatial positioning.

Discussion

In the following discussion I will treat five issues that are more or less inter-connected through the assumption that spawning behaviour mainly reflects a compromise between survival and reproduction. First, I discuss predation risk at the spawning ground both considering available information on actual predation pressure and the validity of the assumptions of higher predation risk at the bottom. Next, our behavioural approach to the field of vessel avoidance is discussed, and I ask what might be gained from an understanding of the vessel as a predation threat. Thirdly, I consider whether or to what extent individual motivation and decision-making can be reflected through the shoal descriptors we investigate. Further, the important link between motivational and physiological state is put under the binocular, and I question whether the assumption that physiological state actually reflects motivation is sound, which is a prerequisite for the hypothesis in Paper 5 and the interpretations in Papers 1 and 2. Finally, I discuss to what extent individual based models are able to predict behaviour in the case of the herring and whether the self-emerging properties are sufficient to explain some of the behavioural patterns we observe in nature.

The term 'school' has been subject to debate and numerous definitions (Wilson 1975; Partridge 1982; Pitcher 1983). Pitcher (1983) argues that one distinguishes between 'school' and 'shoal', where 'school' defines fish swimming synchronously and polarised in groups, whereas 'shoal' comprises all social groups of fish (including 'schools'). According to this definition, the correct term to use for all fish groups where levels of synchronisation and polarisation are not known (like for all acoustic data in this thesis), is 'shoal'. However, there is still ambiguity in the literature, perhaps due to an historical comprehension of 'shoal' as a loose aggregation, perhaps due to the lacking distinction between 'school' and 'shoal' in many languages. In Papers 1-5, the terms are applied synonymously like in Blaxter and Hunter (1982), so the 'schools' in Paper 1 are no different from the 'shoals' in Paper 2. However, I adopt the definition of Pitcher (1983) in the following discussion. I also refer to 'systems' when describing collective dynamics, which in this context simply refers to the spawning location (Papers 1, 2, 3 and 5) or the model representation of the spawning location in the case of the simulation model (Paper 4).

Predation risk at the spawning ground

A classic principle in theoretic ecology is that current reproductive success of an organism can only be increased at the expense of future reproduction (Williams 1966; Houston and McNamara 1999). The reason is that reproductive activity lowers probability of survival and/or lowers condition at next spawning attempt. For herring, seasonal investment in reproduction is decided early in the year and then assessed and adjusted during the maturation process through atresia (Oskarsson et al. 2002). Once located at the spawning site however, only two factors are of importance: survival and successful spawning (Lima and Dill 1990; Nøttestad et al. 1996; Axelsen et al. 2000; Papers 1-5).

A bottom line in all works presented here is that herring collective behaviour at the spawning grounds is mainly a reflection of the compromise between reproduction

and survival (Papers 1-5). A pressing question therefore is: what is the real predation pressure at the spawning grounds? It may of course be argued that herring behaviour reflects a precautionary strategy towards predators, not necessarily reflecting immediate predation pressure. However, risk-averse behaviour based on a non-existing risk is not likely to withstand natural selection for long, so a presumed anti-predatory behaviour should be supported by data on the real predation pressure. The by far most comprehensive investigation of predation pressure at the spawning grounds is presented in Høines (1999). He found that adult herring was important prey and constituted a diet shift for cod >50 cm, but concluded that the overall effect of predation on the herring was negligible. However, the main aim of his study was not to evaluate predation pressure on herring, and it suffers from important shortages in this respect, that the author himself points out. Firstly, it is not appropriately scaled to investigate possible predator migration along with the herring as has been documented in other works (Pitcher et al. 1996; Runde 2005). Secondly, and perhaps most importantly, it is based almost entirely on trawl sampling that is known to severely under-sample large fish due to their high swimming capacity and hence easy escape (Wardle 1993). For comparison; in a pinpointed investigation at the main spawning area, fish were sampled using four gillnets linked to each other; two herring gillnets and two large-meshed gillnets for gadoids (own unpublished data). The results are summarised in Table 1. A brief glimpse at the table is enough to add new perspectives to the information from Høines (1999). Consumers comprise several predators, in particular saithe, not only cod as concluded in Høines (1999). The table tells the story of an exceptionally critical period for adult herring. A similar investigation was repeated the year after (Runde 2005), and the predation pressure was then seemingly lower. However, timing and fine-scale positioning of such sampling are likely of utmost importance and inferences should be made with caution.

Table 1. Sampled predators at the herring spawning ground (own unpublished data)

Species	Sample n	No. of herring in stomach ±SD	Predator length ±SD
Pollock (*Pollachius pollachius*)	1	2	66
Cod (*Gadus morhua*)	4	2.67 ± 2.08	73.8 ± 7.3
Saithe (*Pollachius virens*)	30	2.04 ± 1.40	77.7 ± 8.0
Total	35	2.11 ± 1.42	76.9 ± 8.0

Another important aspect when evaluating predation on herring during spawning, is that even if a yearly mortality during spawning of e.g. 1 % seems low *per se*, the cumulative risk of mortality for an individual after the 10th yearly round of spawning (Slotte 1999) has reached almost 10 %. For herring with a reproductive success at population level varying by nearly three orders of magnitude between years and often only one or two successful years during a decade (Sætre et al. 2002), the option of repeated spawning and hence the aspect of cumulative mortality is highly relevant.

There is, in other words, a need of quantifying predation pressure, but it is challenging to design ways of sampling both predators and herring in a representative way. Gillnet sampling like the kind mentioned above may cover both predators and herring, but is highly size-selective (see review in Hamley (1975))

and operational only in the dark. We have yet to come up with a satisfying solution of the sampling problem (Papers 1 and 2), but infer from previous studies that in general the predation pressure at the spawning ground is significant.

There are a few factors in addition to the direct predation pressure that make us infer that the bottom is a sub-optimal zone for survival for herring (Axelsen et al. 2000; Papers 1, 4 and 5). Firstly, manoeuvrability for coordinated avoidance is likely reduced as compared to the free water masses. This postulate seems intuitive, but is certainly not easy to test out. As a criticism one might reason that the bottom also reduces manoeuvrability of the hunting gadoid, but then the hunting predator is unlike herring adapted to a life in this habitat. Secondly, the spawning activity represents *per se* a disadvantage towards predators, since the focus on depositing batches of spawn timely on appropriate substrate necessarily reduces predator vigilance (Paper 3) and also result in non-synchronous swimming (Hourston et al. 1977; Stacey and Hourston 1982; Runde 2005). Also pre-spawning individuals will suffer from the partly disintegration due to spawning activity when present with spawners on the bottom (Papers 1, 2 and 5).

Avoidance reaction towards a research vessel - a potential predator

Although it is known that fish may be attracted to objects acting as 'meeting points' of social aggregations (Freon and Dagorn 2000), a noisy approaching vessel is more likely perceived and evaluated by the fish as a predatory threat, analogous to a wild predator (Vabø et al. 2002; Fernö and Huse 2003; Skaret et al. 2006). In most recorded cases, herring react to a surveying research vessel with avoidance, a behaviour that may introduce severe systematic errors to acoustic abundance estimates (Olsen et al. 1983; Vabø et al. 2002). Adequate correction models to such biases are not only difficult to make, but often problematic to imply. There is a large inherent variation in the reaction *per se;* due to the nature of the sound stimulus, conditions for sound transmission, herring distance to the sound source and the motivation of the fish to avoid the vessel (Olsen et al. 1983; Vabø et al. 2002; Skaret et al. 2006; Paper 3). The representativeness of correction models based on *in situ* studies is therefore difficult to evaluate (Hjellvik et al. 2002; Handegard 2004), and they are hence not straightforward to implement because hidden variability may be added due to false assumptions (Handegard 2004).

It is extremely demanding, perhaps even unrealistic to require reliable quantitative predictions of a correction factor for avoidance from general behavioural knowledge. However, an approach applying optimal behavioural theory to interpret avoidance reactions (Fernö and Huse 2003; Skaret et al. 2006; Paper 3) may give valuable information about the representativeness of *in situ* correction models and allow for inferences about which ecological contexts, areas and groups of the population the model is likely to be valid for. In the case of the spawning we seem to avoid the avoidance problem (Paper 3). We interpret that the reaction threshold of herring to a perceived threat increases during spawning because the trade-off between survival and reproduction at the spawning ground is skewed towards reproduction**.** Our experiments were carried out on herring situated at the bottom presumably engaged in spawning activity, and how representative these results are for herring at the spawning ground in general needs to be verified. Risk-aversion and hence vessel avoidance seems likely during the days prior to spawning, when

still not ready to spawn (Nøttestad et al. 1996; Misund 1997; Skaret et al. 2006), and at the main spawning ground we recorded generally lower herring abundance during daytime than night-time (Paper 2), possibly due to vessel avoidance.

NSS-herring irregularly change migration routes, feeding areas and wintering areas (Fernö et al. 1998). During the last few years, wintering areas have been changing, and the feeding area expanding (Iversen et al. 2006). Hence, it is not easy to establish robust measurement platforms and survey strategies. A previous yearly spawning survey was abandoned some years ago because estimates were considered unreliable (ICES 2004), and there are certainly great challenges connected to the dynamic behaviour influencing acoustic availability (Papers 1 and 2). However, it may be adequate to recommence the surveys if the basis of the estimates can be made reliable. To achieve this, a crucial part is to adjust survey design to our knowledge about the behaviour. Based on the results presented in this thesis, daytime surveys should be avoided (Paper 2), as herring seem less available to detection possibly due to vessel avoidance. At night, avoidance reaction seems to be absent with herring positioned at the bottom (Paper 3), but herring partly disappearing in the bottom dead-zone may be a problem (Paper 1). Perhaps the biggest challenge is linked to the spawning waves that must be timed appropriately. In that regard, stationary acoustics at the main spawning grounds may be a useful complement to regular abundance surveys.

Descriptors of shoaling dynamics

Which shoal parameters are relevant to measure and what can they tell us about the individual decision-making and behavioural motivation in a particular ecological context? Consulting the literature on *in situ* studies of marine shoals, mostly applying acoustic methods, we are presented with a range of different shoal descriptors. Although quantifiable in reliable ways, the ecological interpretation of the descriptors may be vague and the importance and relevance of the descriptor itself hence questioned. A possible reason for this is that the distinction between functional properties and epiphenomenal patterns in fish shoals (as well as other animal groupings) is unclear (Parrish and Edelstein-Keshet 1999). Fumbling in a trial-and-error phase where underlying mechanisms of the observed structure or pattern are unknown, is hence natural. With schooling models a new perspective opened of how one can relate individual behaviour to shoal formation and dynamics and hence evaluate the information and relevance of shoal descriptors in a new way based on the underlying mechanisms (Vabø and Nøttestad 1997; Camazine et al. 2001; Paper 4). I will in the following consider the four shoal descriptors most commonly used in our work: group size, packing density, vertical extension and shape.

Group size is an intuitively important descriptor of social animals, since it defines a group (no less than 2) and rises the question of an optimal group size (Sibly 1983). It is generally acknowledged that group size as a social phenotype should be understood as an evolutionary compromise (Wilson 1975; Pitcher and Parrish 1993; Krause and Ruxton 2002). The reason for this is that even though in theory (but see review in Krause and Ruxton (2002)), the advantage of being in a shoal due to the reduced risk of being targeted is ever-increasing towards an asymptote with increasing number of individuals within a group as $1/N$, the reward will sooner or

later be overruled by the drawbacks due to e.g. competition for mates or access to food (Krause and Ruxton 2002). Interestingly, for herring during large parts of the season, the compromise tips entirely towards large group size and typical activities advantaged by small group size, like foraging cease (Slotte 1999). The giant aggregations indicate that a maximisation of shoal size in such periods is a behavioural strategy. The results from Paper 2 bring evidence that this might be the case also during spawning. If indeed the behaviour reflects aggregation and less congregation at a preferred location (Parrish and Edelstein-Keshet 1999), it raises the question: How are the fish able to evaluate the size of the shoal they are present in? Lone fish are able to evaluate the size of small groups in an aquarium (Reebs and Saulnier 1997). In giant free-ranging marine shoals however, the cues for evaluation must be different, and the amount of penetrating light and decreasing oxygen level have been suggested (Krause and Ruxton 2002). A memory of time elapsed since it last was at the edge of the shoal and even sound stimuli may be suggested as additional cues.

Packing density is a frequently mentioned parameter in acoustic studies of free-ranging marine shoals that may provide detailed information about the internal structure of a shoal (Misund 1993; Gerlotto and Paramo 2003). However, such detailed information about shoal structure is not obtainable from echo sounders that for the most part are applied in our studies (Papers 1, 2, 3 and 5). Inferences based on average values of packing density from whole shoals, on the other hand, are possible to make from echo sounder data. Packing densities of whole shoals are largely influenced by predation pressure (Major 1978; Allan and Pitcher 1986; Magurran and Pitcher 1987; Morgan 1988), in extreme cases reducing inter-individual distance to zero (Axelsen et al. 2001). We interpret the packing density during spawning largely as reflectors of immediate predation pressure, and show that the diel variation is consistent and hence seems predictable for the spawning situation (Papers 1 and 2). Dispersed herring layers observed at night-time in Paper 2 had a very low packing density and whether they can still be defined as shoals is an open question, but it is interesting to what degree neighbour contact persists in such loose layers. Laboratory studies have shown that schooling ceases when light intensity drops below 0.5 to 0.003 mc (Blaxter and Parrish 1965), and dispersion in darkness may be viewed as a passive process resulting from random swimming patterns (Freon et al. 1996; Nilsson et al. 2003). However, entirely random swimming resulting in lost contact with neighbours may be costly, and we argue that contact is maintained and swimming therefore not entirely random (Paper 2). This postulate is left largely unproven since we infer from rather rough estimates of nearest neighbour distance. However, this should be possible to investigate through acoustic tracking of individuals and their swimming relative to neighbours (Handegard et al. 2005; Onsrud et al. 2005). The dispersed layers represent an extreme end of the spectre of observed packing densities (Papers 1 and 2), with pelagic shoals at daytime representing the other extreme.

An important inference from Paper 4 used in the interpretation of the results in Paper 2 is that the level of motivational synchronisation between individuals may explain vertical dynamics within a system. This explanation seems both intuitive and plausible, and may, in retrospective, explain the high vertical extension of the 'transition schools' in Paper 1. The sampled herring there had various states of gonad maturation, likely to result in conflicting motivation for vertical positioning

within the shoal. An interesting feature about the vertical extension is that it is independent of group size, given group size is large enough to cover the range of preferred vertical positions of individuals within the shoal (Paper 4).

With the simulation model we show that whereas the shape descriptor was very helpful with a limited number of individuals, a high number provided us with a range of different shapes with the exact same model setting and degree of motivational synchronisation. The formations, in addition to being dependent upon motivation, are thus dependent upon the amount of herring present in the system. A system with intermediate motivational conflicts will typically start out displaying cylindrical shaped hourglass formations (Axelsen et al. 2000; Papers 2, 4 and 5). With increasing population size, the upper and lower components increase until they become two interconnected flakes, before, with large population size (N=8000), ending up with amorphous morphologies unified at several points. This important insight tells us that the shape is not necessarily the most informative parameter unless there is detailed knowledge of the mechanisms behind the formation (Papers 4 and 5). The same inference was done by Gerlotto, et al.(2004) showing that internal shoal structure remained stable whereas external morphology changed with prevailing conditions and size.

A particular shape given much attention in this thesis is the vertical hourglass (Papers 2, 4 and 5). The reason is that we view it as an adaptive formation rather than an epiphenomenal shape or pattern. The important distinction between epiphenomenal patters and adaptive formations is pinpointed in Parrish and Edelstein-Keshet (1999), but is indeed not easy to make out in the field. Some of the classical patterns of short duration observed in schooling fish under predator attack (Pitcher and Parrish 1993) may well be epiphenomena in the sense that individuals make the same decisions and react in the same manner but patterns differ according to e.g. school size or the movement of the predator (Vabø and Nøttestad 1997; Parrish and Edelstein-Keshet 1999; Axelsen et al. 2001). So even if the coordinated reaction is adaptive, it can be questioned whether each pattern deserves to be called a specific 'strategy', when they may be better explained as compromises between the need to keep in contact with conspecifics and the need to keep a distance to the predator (Parrish and Edelstein-Keshet 1999). So what distinguishes the vertical hourglass formations from mere epiphenomenal patterns? Given such formations have some stability over time, like seen in our model, individuals may reach preferred depth according to behavioural motivation without leaving the shoal. Individuals polarising with and following others to avoid being alone when crossing from one component to the other, establish and maintain 'bridges' through a positive feedback loop (Deneubourg et al. 1989). Stability of the hourglass formations is also indicated in Paper 5 where the formation seemed to be persistent for more than half an hour. Similar bridges persistent for hours in large shoal formations were observed by Makris et al. (2006). Even though the fish in this case crossed in the horizontal dimension, the underlying mechanism may be the same, a pathway where individuals exchange positions according to motivation between locations with different properties. However, the question remains whether the natural vertical hourglass behaviour is an emergent pattern, entirely based on local stimuli as shown to occur in the model (Paper 4), or if there is a decision-making involved requiring mutual attraction through communication between the two components. Indeed, the latter is no prerequisite for it being adaptive, given

that individuals present in shoals large enough to create the formations gain a slight evolutionary advantage.

Does maturation state reflect motivation for spawning?

Although often intuitive to the observer, the motivation of an individual fish is hard to measure *in situ*. A herring sampled with empty stomach does not necessarily imply that it had a high motivation for feeding. Wintering herring are good examples of this (Slotte et al. 2000). And even more extreme, a ripe herring might still have motivation for postponing (Paper 5), or even skip the spawning and follow the emigrating majority of fish out of the area (Axelsen et al. 2000; Papers 2 and 5). Such observations underline that inferences about motivation can not be done *a priori* from knowledge about individual physiological state and ecological context. In models, however, individual motivation can be carefully controlled, and set to e.g. follow the state of gonadal maturation (Paper 4).

What then about motivation *in situ*? Is it not a paradox to postulate that motivational state not necessarily follows from physiological state and then in Paper 5 test the hypothesis of motivational conflict by investigating maturity state? The answer is no. There is a fundamental difference between sampling a ripe herring and postulate that it had high spawning motivation and sampling a herring that you hypothesise has got high motivation for spawning based on a behavioural criterion and find that it is ripe.

In Paper 1, there is an interesting difference in behaviour related to the maturity state from what we observed in Paper 5. Whereas pre-spawners were almost absent from the bottom component of the vertical hourglass formations in Paper 5, they were present with the spawners, and even dominating in the bottom samples in Paper 1. In the simulation model (Paper 4), such integrated systems where cohesion persists despite differences in maturity state are observed when motivational synchronisation is high. However, in a risk averse system where the number of surrounding neighbours decides the degree to which an individual responds to it's own motivation towards spawning, integration is also likely to be high despite motivational differences towards spawning. This was demonstrated in the simulation model when applying density dependence (Paper 4). Shoals in such systems do not split or partly split before two large aggregates of individuals with highly conflicting motivations polarise at opposing ends of the group. Density dependence can be viewed as an analogue to the dynamic risk aversion with group size in Magurran et al. (1985). In this study, a predator was approaching a group of fish and the time elapsed before foraging ceased in the group was shown to increase with increasing group size. The effect at the spawning site would be that a shoal of individuals with conflicting motivations does not split below a certain threshold group size. This could explain why we only see splits with pre-spawning and post-spawning herring above spawning fish with large amounts of fish (Paper 5) and not off Karmøy (Paper 1). The effect of numbers is obviously hard to test out experimentally in a stringent way, but it finds some support in the observations by Nøttestad et al. (1996) where pelagic shoals were observed above spawning layers at Karmøy indicating vertical hourglass formations similar to what we observed in Paper 5 at these shallow spawning grounds when more fish are present. It is conceivable that in integrated systems, highly motivated individuals determine

positioning, even though they are in minority (Reebs 2000; Huse et al. 2002; Couzin et al. 2005). Ripe individuals with high motivation towards spawning could hence pull the rest towards the bottom (Paper 1). There are two additional reasons why integration should be enhanced in Paper 1 relative to Paper 5. With few individuals present, a permanent contact with the group to take advantage of pheromone exchange may be advantageous. In addition, predation protection in itself is a trade-off between staying in the pelagic to avoid the high-risk zone and aggregate to take maximum advantage of the dilution effect towards predators (Paper 2). This trade-off is obviously influenced by the number of individuals present in the group. However, there is a puzzling contradiction to our observations in the study by Axelsen, et al. (2000), where a small number of individuals indeed split vertically. Why this paradox is not clear, but difference in actual predation pressure may be lanced as a speculation. However, the partial split may also be based on more than local cues, which will be further discussed in the last section.

What can you expect from a herring? - Behavioural models facing the real world

For the fisheries scientist entrapped on a large rigid research vessel sailing the seven seas along strictly defined survey lines and observing the herring as coloured pixels on a computer screen, it is indeed easy to become instrumental in his reflections upon the fish. We are just starting to understand the herring behaviour; in terms of its behavioural strategies, its cognitive and communicative abilities, and how it samples and evaluates its three-dimensional environment including the shoal of which it makes up a part.

The recent progress from rule-based models of fish shoals has brought forward the important insight that internal shoal structure, large-scale morphology and complex collective behavioural dynamics can emerge through self-organisation based solely on local information (Parrish and Hamner 1997; Camazine et al. 2001; Couzin and Krause 2003; Paper 4). However, the fact that simple rules may generate life-like behaviour in simulations is no guarantee that living systems follow simple rules (Parrish and Edelstein-Keshet 1999). Parts of the herring behaviour can be explained from decision-making based on mere local stimuli and parts involve further-reaching cognitive abilities. To disentangle the two is a major challenge. In the following two sections I will debate two of the main results and inferences from Paper 4; self-emerging assortment and vertical hourglass formation, and compare them with other works, ecological reasoning and own observations.

Assortment in fish shoals after phenotypic traits such as body length, colour and species, but also parasite load is commonly observed (Krause et al. 2000). An interesting question in that concern is whether the sorting is passive or active (Couzin and Krause 2003). Passive assortment has been demonstrated to emerge in schooling models due to slight differences in size of repulsion zone to schooling neighbours (Couzin et al. 2002) or individual motivation (Paper 4). In both cases sorting emerges on the basis of small *behavioural* differences. It is an appealing thought that such passive assortment accounts for the segregation we observe in animal groups. As suggested by Couzin and Krause (2003) specific behaviour leading to assortment may be tailored through natural selection in contexts where sorting is advantageous, and cognitive abilities such as recognition and decision-

making regarding sorting is not a necessary prerequisite for the behaviour. However, at least for herring, the theory of passive assortment does not fit entirely with realities. In a mixed-species shoal of foraging herring and small (20-25 cm) saithe (*Pollachius virens*) subject to attacks from a large predator, herring surrounded by other herring ceased feeding and polarised with their neighbours to rapidly segregate into a separate herring group (Wolf 1985; Allan and Pitcher 1986). However, lone herring surrounded by saithe polarised with the saithe in an initial slack phase of the attack. When the attack intensified, the lone herring joined the segregated herring group that had separated during the escape. The interesting observation was the swimming trajectory of single herrings when joining the group, as it was totally unsynchronised with other fish, in many cases perpendicular to the polarised escape direction of saithe (pers. obs.). The observation demonstrates that herring are indeed capable of recognising and make the active decision to join conspecifics in an initially mixed-species constellation. The short-term benefits of such species-separation has been questioned (Couzin and Krause 2003) since a large group size should be beneficial towards predator attacks and the negative effect of phenotypic disruption or 'oddity' seems to disappear with larger group sizes (Landeau and Terborgh 1986). However, the long-term negative effect of permanently lost contact with conspecifics for single or small groups of herring is presumably strong, and may alone explain the behaviour. Whether recognition of individuals or groups can happen based on more subtle cues than species-specific traits, like maturation state is not known, but this opens up the debate about the behavioural basis of the vertical hourglass formations (Paper 2,4,5).

To embark on that subject it may be appropriate to discuss the term *await* in the pelagic (Axelsen et al. 2000) that was challengingly lanced as a fourth option of herring adding to the classic *stay*, *join* or *leave* (Pitcher and Parrish 1993) as behavioural alternatives for an individual within a shoal. During large parts of their life herring will be located in the interior of a large shoal (Huse and Ona 1996) in reality left with only one option: to *stay* (within the shoal). However, in periods like during foraging, individuals continuously make decisions whether to *leave* the group, if only for a second, to capture a prey or to *join* a group within visible range for instance during intensive predation attacks. If the strategy *await* is to be seen as a fourth option adding to the existing three, it seems a reasonable requirement that an individual actually makes an active decision to await. In other words, if the vertical hourglass formation is emergent like we demonstrate in the simulation model (Paper 4), then individuals are in reality only *staying* within the shoal and the formation is truly emergent from the combination of internal motivation and external environment (although an artificial 'preferable location' is generated in the model as I will come back to). Even though *await* is the ultimate result also in this case, the requirement of an active decision is not fulfilled and the term *await* seems somewhat synthetic besides the other three. It may of course still be defended based on the argument that individuals (for instance spent) could have chosen to leave for a more favourable location, but then the term to *stay* is left with little content since the compromise between being in a favourable environment (to fulfil immediate needs) and continued connection with the group will be ever-present in an obligate schooler like herring. It is important to recognise that in the model (Paper 4) we create an artificially stable situation with little horizontal movement through only implementing attraction and repulsion forces. Adding alignment to neighbours as a decisional rule would lead to a more realistic swimming pattern, but not necessarily

a more realistic ecological situation since there may be little horizontal movement, but due to other factors like profitable environmental conditions, or indeed an active 'await' strategy.

If 'await' is an active decision made by the herring, some cognitive abilities must be in place. Firstly, herring must be able to evaluate the size of the shoal it is part of. Secondly, it must infer the size sub-optimal given the ecological context. Thirdly, it must have information about a neighbouring shoal or shoal component. The first point of size evaluation is discussed in a previous section, where some possible cues were mentioned. The second point is likely to be fulfilled given an ecological context where aggregation is profitable such as wintering (Huse and Ona 1996), migration (Fernö et al. 1998) or spawning (Paper 2). An attraction towards the other shoal either through an await strategy to increase safety or an active approach, is then likely to occur similar to an attraction towards some food (Reebs 2000) or the spawning substrate (Paper 4). The third point however, is the challenging one. How are the shoals aware of each other? Although the two shoal components in our case might well be within visual range, this will only be the case for individuals at the edge close to the other component. Audible stimuli however, may be available information to all individuals within a shoal, and herring have well-developed hearing abilities (Blaxter and Hunter 1982) and extensive sound production suggested to have social mediation (Wilson et al. 2004). An interesting, though anecdotal support of an active 'await' strategy is the fact that we record a pure catch of spent individuals in the upper component of the vertical hourglass formations in Paper 5. Spent individuals are likely to have strong motivation for foraging (Nøttestad et al. 1996), and this activity is not done best in giant shoals (Pitcher and Parrish 1993). Hence, if there is not a serious sampling bias in this case, it is a possible example that individuals actually 'await' in the pelagic.

It seems intuitive that behavioural studies of NSS-herring should be done in open sea areas where the main population is found during major parts of the year. In this work, however, we see examples that ideas and hypotheses generated from pinpointed studies on small, local herring populations, are relevant for the vast NSS-population. An important example is the vertical hourglass formation that was described and interpreted in Axelsen et al. (2000) for a local herring population in a narrow fjord, but shown in Papers 4 and 5 to be relevant for NSS-herring. Furthermore, the active tuning of maturation rate that we describe in Paper 2 was first suggested in Langård et al. (2006) based on studies of local herring in a small basin. In such small-scale studies the conditions for field experiments, in terms of weather, waves and vessel traffic are often largely superior to the open seas and allowing for sophisticated technology. In addition, the dynamics happen on scales where the entire chain from individual behaviour to overall ecosystem dynamics can be monitored on fine time-scale within the frames of a reasonable scientific effort. For future investigations on herring behaviour, when moving more towards testing of concrete hypotheses, local herring at sheltered locations may turn out to be keystones in the combination with large-scale studies.

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