

Herring (*Clupea harengus*) in Lindåspollene before and during spawning: spatial decisions and school dynamics

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Abstract

This study reports on the school dynamics of a self-sustained local population of Atlantic herring (*Clupea harengus*) in Lindåspollene, south-western Norway, during pre-spawning and spawning, observed over a period of four years (2007-2010) by means of hydroacoustics.

The school depth, horizontal and vertical extents and acoustic backscattering density were determined and used for estimation of school packing densities. The biological state of the herring and its gadoid predators were investigated by gillnet and tangling net samples, while the hydrographical conditions were recorded by means of CTD profiling.

In all four years the adult herring were predominantly confined to a single school within a small geographical area (7000 m²), indicating strong site fidelity during the spawning process. The pre-spawning site, which was characterized by a 25-40 m deep trench connecting directly to the deepest part a basin, was located close to historical spawning grounds. During the pre-spawning period the herring remained in the pelagic environment while maturing, increasing the distance to the bottom in the presence of gadoid predators.

The school occupied deeper waters near the bottom as spawning commenced and stayed there for a period of at least 9 and 48 days in 2009 and 2010. This suggests that the overall predation pressure from demersal fish was relatively low and that the duration of spawning was long compared to that of Norwegian spring spawning herring, which was supported by biological samples of herring.

In 2009 a group of herring remained in the pelagic for at least 6 days as the main school moved to the bottom, indicating conflicting motivations between early pre-spawners and ripening individuals. The school packing density increased as spawning commenced, which could reflect increased vigilance while staying at the bottom, the home range of demersal predators such as cod. The school dynamic turbulence was lowest in the early pre-spawning period, highest in the late pre-spawning and early spawning period, before decreasing again in the late spawning period. These dynamic features could reflect conflicting interests of ripe individuals attracted to the bottom and pre-spawners preferring to remain in the pelagic prior to spawning. Similar conflicts could appear between individuals with a motivation to migrate to the spawning grounds and individuals that prefer to stay near the shelter of the deeper basin.

The herring school dynamics in the pre-spawning and spawning periods persisted over the four study years even though some aspects of the behaviour changed markedly in 2010. The spawning processes

within the small system in Lindåspollene closely resemble those of the highly migratory Norwegian Spring spawning herring stock, although the processes take place within a very small area and in 'slow motion', demonstrating that small ecosystems like Lindåspollene may be a representative and a cost effective way of studying marine ecosystem processes.

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1 Introduction

Herring (*Clupea harengus*) is widely distributed throughout the Atlantic, Baltic, Pacific and the White Sea, and is, due to its ecological, economical and cultural importance, one of the most studied fish species in the world (Blaxter, 1985; Whitehead, 1985; Klinkhardt, 1996). Despite this several major herring stocks have at some point in the last few decades collapsed or been severely depleted (see for example Jacobsson, 1985; Stephenson, 1997). One contributing factor to the collapses, in addition to high fishing pressure, have been the large, unpredictable fluctuations in stock sizes, which seems to be affected by the ocean environment or long term climate changes, although the mechanisms are not fully understood (Hay et al., 2001).

After having metamorphosed (at 2.5 months of age and 30 mm length), herring spend the majority of their life schooling (Blaxter and Hunter; Fuiman, 1989; Axelsen et al., 2001). A school is defined as fish swimming synchronously and polarized in a group (Pitcher, 1983), and school dynamics are a good example of self-organized group-behaviour, where collective dynamics is a result of the simultaneous movements of numerous individuals responding to the behaviour of the neighbouring fish and their environment (Parrish et al., 2002). Size, density and shape of fish schools can vary substantially (Misund, 1993), and are affected by physical factors such as topography, currents, depth, salinity, oxygen, temperature and illumination, biotic factors such as food availability and predator pressure, as well as the internal state and motivation of the fish. These features can vary both spatially and temporally, between seasons as well as between day and night.

The main function of schooling is protection against predators (Pitcher and Parrish, 1993): there is less chance of being eaten for an individual fish in a group consisting of numerous individuals than on its own (Major, 1978; Morgan and Colgan, 1987), due to dilution and confusion effects and evolved attack mitigations – and evasion strategies (Pitcher and Parrish, 1993). Moreover, a larger group of fish is capable of finding food faster and schooling may thus increase feeding efficiency (Pitcher et al., 1982). Although individuals in a group may collaborate, they are at the same time competing for limited food resources (Nøttestad et al., 2004). Hence, larger schools will have stronger competition for food between the individuals, and protection against predators may conflict with foraging efficiency. However, anti-predator behaviour will normally take precedence over foraging behaviour, since it is fundamentally more important to stay alive than to forage (Ryer and Olla, 1998). The outcome of this trade-off between foraging and staying alive will, however, depend on the risk an individual is willing to take. Laboratory studies have shown that starving fish was more risk prone than satiated fish (Croy and Hughes, 1991),

and that school density decreased for fish with increasing food deprivation (Robinson and Pitcher, 1989). Other functions of schooling can be linked to energy optimisation (Huse and Ona, 1996; Herskin and Steffensen, 1998) and efficient migration (Huse et al., 2002; Couzin et al., 2005).

Adult herring follow repeated annual cycles divided into defined seasonal periods of feeding, overwintering and spawning. In order to take maximum advantage of their surroundings, herring may carry out extensive migrations between feeding – and overwintering areas and spawning grounds, but the extent of such migrations varies according to population size, environment and food availability. The Norwegian spring spawning (NSS) herring populations are among the largest and most studied in the world (Holst et al., 2004), and their annual cycle will be used as an example for the behavioural changes of herring through different seasons.

During the feeding season between April and September the NSS herring are distributed over large areas (300 000-500 000 km²) in the Norwegian Sea (Nøttestad et al., 2004). Their horizontal and vertical distribution are predominantly determined by the distribution of zooplankton, their main prey (Misund et al., 1997; Dalpadado et al., 1998; Kvamme et al., 2003), but may also be modified by competitive interaction with other pelagic planktivores and the predation pressure (Mackinson et al., 1999). Herring tend to descend at dusk to avoid predators and ascend at dawn to forage, thus being more dynamic during the night than at daytime (Mackinson et al., 1999). During the feeding season the herring have to accumulate energy reserves for maturation of the gonads, overwintering, and next year's spawning migration and spawning (Misund et al., 1998), and thus while the distribution area is large, school sizes tend to be relatively small in order to reduce food competition (Mackinson et al., 1999).

Food abundance drops and prey become increasingly more inaccessible as winter approaches (Melle et al., 2004) and the gain of foraging no longer outweighs the costs and risks associated with it, gradually leading the herring to adopt to a more risk-averse strategy as they migrate to the overwintering areas (Fernö et al., 1998; Kvamme et al., 2003). The herring are normally not foraging in a period of several months prior to spawning (October – March) (Nøttestad et al., 1996; Slotte, 1999a), and the winter spent in extremely large groups with restricted movement can be looked upon as a period of predator avoidance and energy conservation (Huse and Ona, 1996 ; Slotte, 1999a).

The large aggregations of herring during overwintering may attract visual predators, such as saithe and killer whales, which forces the herring to stay deep during daytime (Nøttestad et al., 2002). Herring

ascend at night to refill their swim bladder to avoid becoming negatively buoyant (Huse and Ona, 1996) and to avoid oxygen depletion (Dommasnes et al., 1994).

The spawning migration commences in January or February (Holst et al., 2004) and the herring then swim deep and fast presumably to avoid predators (Nøttestad et al., 1996). Although a pelagic fish species, the herring spawn demersally. The Pacific herring (*Clupea harengus pallasii*) and Baltic herring (*Clupea harengus membras*) prefer to spawn on bottom vegetation (Haegele et al., 1981; Aneer, 1989), while the Atlantic herring, including the NSS herring, prefer to spawn on gravel and rocks (Runnström, 1941). The demersal zone is assumed to be a high risk habitat for herring, as it is the home range of gadoid predators, and because of reduced manoeuvrability and escape possibilities (Pitcher and Parrish, 1993; Axelsen et al., 2000; Runde, 2005). The predation pressure can be very high at herring spawning grounds (Høines and Bergstad, 1999; Runde, 2005).

Herring seem to be able to adapt to high predation pressure on spawning grounds. For example, they often spawn during the night in order to be less susceptible to visual predators (Kjørsvik et al., 1990; Runde, 2005; Skaret and Slotte, 2007) that are less active at low light levels (Løkkeborg and Fernö, 1999). Herring have also been reported to take advantage of topographical features at the spawning grounds. Runde (2005) and Skaret and Slotte (2007) observed herring hide in deep trenches during daylight, in order to stay out of reach and out of sight from predators.

The situation for herring changes drastically before, during and after spawning (Nøttestad et al., 1996). Before spawning their focus should be on completing spawning successfully, hence avoiding predators. During spawning the herring seem to concentrate on the spawning act itself (Johannessen, 1986), while after spawning they become motivated to feed. Nøttestad et al. (1996) found distinctive differences in school characteristics such as size, packing density, shape, and swimming speed between pre-spawning, spawning and post-spawning schools.

The rapid motivational changes may lead to motivational conflicts among individuals within a school, for example between ripe and pre-spawning herring (Axelsen et al., 2000). If there are several schools in the area individuals have the option to split and join another school of individuals with more similar motivation and state. For example, if a post-spawner is schooling with pre-spawners, it should rather join or form a feeding school (Pitcher, 1995). If there are no nearby schools, motivational conflicts within a school can emerge as complex school shapes and structures (Axelsen et al., 2000). Axelsen et al. (2000)

observed a single herring school on a local spawning ground. When spawning commenced the school split into one pelagic and one demersal component, probably reflecting motivational conflicts between ripe herring searching towards bottom and pre-spawners searching towards the pelagic, away from the home range of gadoids. In a later study Johnsen and Skaret (2008) confirmed that in similar structures on a large spawning ground pre and post-spawners dominated the pelagic component, while ripe herring dominated the demersal component.

The spawning period is presumably the most crucial time of the year for herring, and the motivation of individuals change markedly before, during and after spawning, which makes the spawning period ideal for studying behaviour and school dynamics.

Challenges with studying herring biology such as the complexity of biological and ecological processes governing the population dynamics, were addressed at a herring committee meeting in the International Council for the Exploration of the Sea (ICES) as early as in 1961. The scientists recognized the need for performing intensive and comprehensive studies on small, self-contained, easily accessible herring populations. This led researchers to a local herring population at the west coast of Norway (Dahl et al., 1973). The self-sustained population in Lindåspollene was chosen due to the small size of this semi-enclosed marine ecosystem, and the low growth rate of the resident herring that made it possible to distinguish it from other populations. There is also a component of herring that most likely is originating from adjacent coastal and/or oceanic populations present in Lindåspollene. Johannessen et al. (2009) found strong indications for that the two components were interbreeding, and therefore the herring in Lindåspollene could be defined as a metapopulation (Levins, 1969; Levins, 1970).

The herring population in Lindåspollene follows an annual micro-scale migration pattern within the ecosystem. They feed during the summer in small epi-pelagic schools. During winter they stay somewhat deeper in larger schools in the two largest basins (Lie et al., 1978; Langård et al., 2006). In January the herring has been reported to aggregate to a single, large school at the entrance of one of the basins and remain there until spawning commences (Lie et al., 1978; Aksland, 1983; Langård et al., 2006; Johannessen et al., 2009).

In the present study we observed by means of hydroacoustics the herring population in Lindåspollene before and during spawning in four consecutive years (2007-2010). Herring, predator and environmental data were obtained from gillnet and tangling net samples, and CTD casts, respectively.

The objective of the present study was to analyse the herring school dynamics before and during spawning, and subsequently relate it to external (environment, predators) and internal (maturity) factors.

2 Materials and methods

2.1 Study area

The study area, Lindåspollene, is a small semi-enclosed marine ecosystem in south-western Norway, located approximately 40 km north of Bergen (**Figure 2.1**). Lindåspollene extends over approximately 7 km² and consists of three separate basins. The outermost basin, Straumsosen, is about 65 m deep and is connected to Lurefjorden through three narrow channels, each with strong tidal currents. The second and deepest basin (89 m depth), Spjeldnesosen, is connected with Straumsosen through a four meter deep threshold. The innermost basin, Fjellangervågen, is anoxic from a depth of ~20 m to the bottom. A detailed description of the Lindåspollene ecosystem can be found in Dahl et al. (1973), while a description of the local herring population are available in Lie et al. (1978).

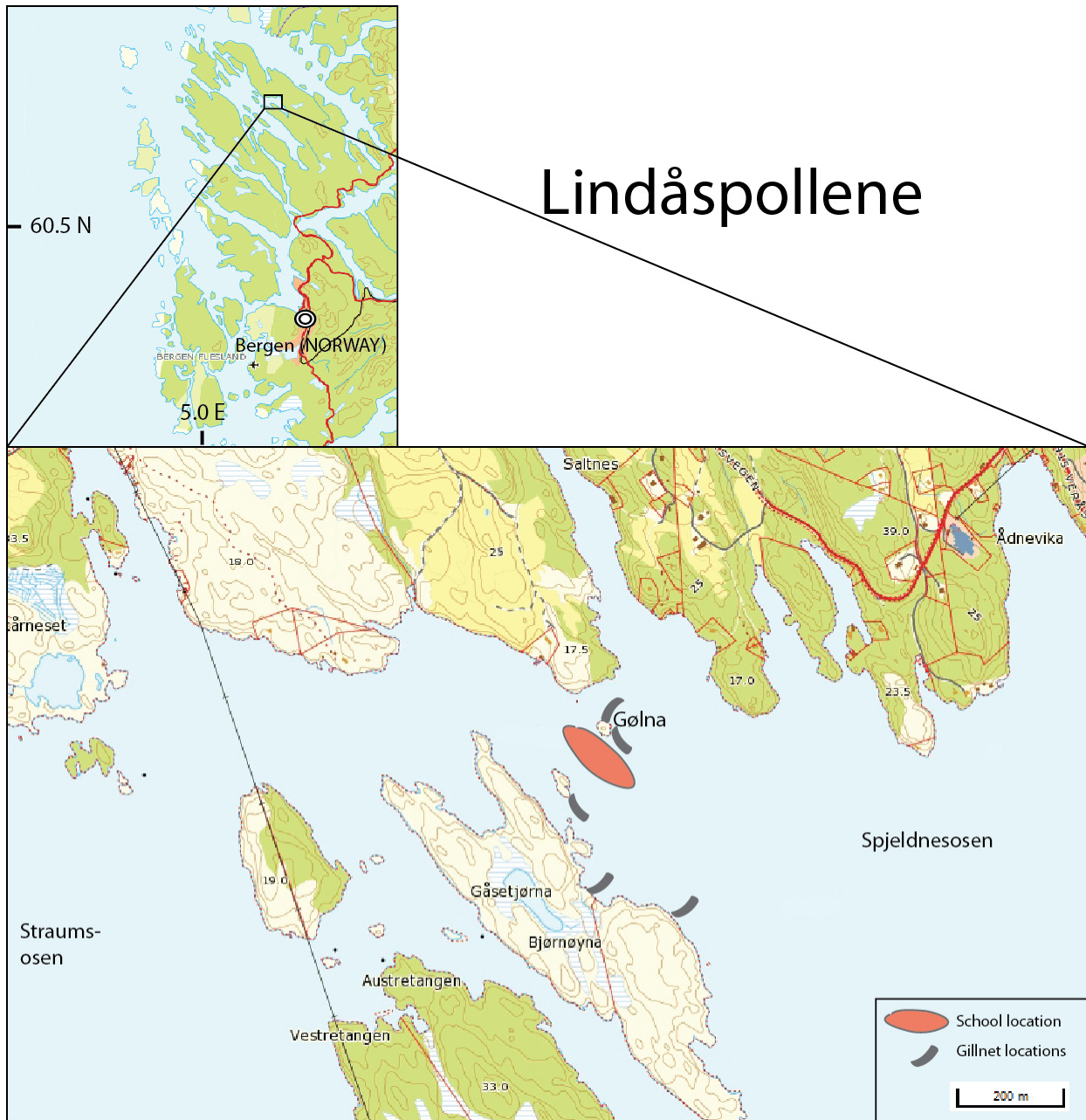


Figure 2.1: Map over Lindåspollene showing the location of the school and herring gillnets, and parts of two of the larger basins, Straumsosen and Spjeldnesosen.

2.2 Study design

The results presented in this thesis are based on hydroacoustic surveys of the herring population in Lindåspollene before and during spawning (February-April) in 2007-2010 (See **Table 2.2**). The acoustic data were supplemented by herring gillnet samples obtained in order to estimate the mean length, weight and age structure of the herring population, and to follow the progression of the maturation process throughout the spawning period. Predator entangling nets were set in order to identify potential herring predators, and to verify whether they preyed on herring. Environmental conditions (oxygen, temperature and salinity) in the study area were also monitored.

2.3 Acoustic data collection

At the start of an acoustic survey, the vessel followed a pre-set track of courselines (modified according to ice cover) to locate herring schools. One main herring school was found in the same area in all years, and this school was subsequently monitored by acoustic methods (sonar and echosounder). Biological fish samples were collected by gillnets and entangling nets, while environmental factors were monitored by CTD casts.

R/V Hans Brattström (24 m LOA, 6.5 m width, 79 GRT), the main surveying vessel used during the study, was equipped with a Simrad EK60 (38 kHz) echosounder transducer used to record the herring school, predatory fish and for bottom detection. A 15 ft Pioner (small boat) with a 15 HP outboard engine was utilized in order to conduct manual acoustic surveys in between the main surveys with the R/V Brattström in 2010. A Simrad EK60 echosounder with a 120 kHz transducer was mounted at the side of the boat, and submerged about 0.25 m below the water surface during operations. In 2008 the same echosounder system was also bottom-mounted on an 'upwards pinging lander' at the position of the school. In 2009 and 2010 it was mounted on an aluminium rod attached to the rocks at Gølna pinging in the upper pelagic with an angle of 15° towards the surface from 2 m below. Stationary recordings were conducted in order to monitor the school without vessel interference, and to investigate the diel school dynamic pattern.

The data were analyzed using the software Echoview (R) v. 4.90, thus obtaining centre school depth, vertical and horizontal school extent, bottom depth (excluding recordings from the horizontally mounted transducer), coordinates (latitude/longitude in decimal degrees), school volume density s_v (dB re 1 m²), Nautical Area Scattering Coefficient (s_A , m²/nmi²), and horizontal/vertical roughness (dB re 1 m²/m³). Altogether 347 school observations were analysed. The minimum s_v -threshold applied was -70 db, to

ensure that fish echoes were included while any plankton detections below this level were left out from the analysis.

2.3.1 Calibration

The echosounders were calibrated by the standard reference target procedure (Foote et al., 1987). The transducer settings and instrumentation on the R/V Brattsröm changed over the four study years, and an overview is given in **Table 2.1**, including the settings for the stationary 120 kHz transducer.

Table 2.1: Transducer settings.

	2007	2008	2009		2010		
	13/02	13/02	16/02	24/02	08/02	22/02	09/04
Absorption coefficient (dB/m)	0.0099695	0.0097853	0.0093762	0.0093762	0.0093762	0.0374403	0.0093762
Transmitted power (W)	2000	2000	1000	1000	1000	500	1000
Two-way beam angle (dB re 1 Steradian)	-15.5	-20.6	-15.5	-15.5	-15.5	-21	-15.5
Transducer gain (dB)	19.44	26.5	19	20.66	20.66	27	20.51
Sa correction (dB)	-0.39	0	0	-0.54	-0.54	0	-0.57
Transmitted pulse length (ms)	1.024	1.024	0.256	1.024	1.024	0.256	1.024
Frequency (kHz)	38	38	38	38	38	120	38
Minor-axis 3 dB beam angle	11.5	7.1	12.16	12.16	12.16	7	11.9
Major-axis 3 dB beam angle	11.71	7.1	12.1	12.1	12.1	7	12.42

2.3.2 Calculation of school packing density

The packing density (n/m^3) of the herring school observations was calculated by first finding the mean target strength (TS) of the herring according to (Ona, 2003):

$$TS = 20 \times \text{LOG}_{10}(L + 0.25) - 2.3 \times \text{LOG}_{10}\left(1 + \frac{D_{sch}}{10}\right) - 66.1 \quad (1)$$

Where L is the mean total length of herring assembled from gillnet samples, rounded down to the nearest 0.5 cm. The added 0.25 compensate for the length lost by rounding down the length value. -66.1 dB is the b_{20} value, as found by Ona et al. (2001) at 38 kHz for herring in February, i.e. the same period as in the present study. The corresponding b_{20} constant at 120 kHz was -68.3 dB. The mean backscattering cross-section of an individual herring (σ) was calculated from the TS values from equation 1 according to (Maclennan et al., 2002):

$$\sigma = 4\pi \times 10^{\frac{TS}{10}} \quad (2)$$

while the packing density (ρ) of herring schools (n/m^3) was defined by (Anon., 1999):

$$\rho = \frac{S_A}{1852^2 \times \sigma \times z} \quad (3)$$

Where s_A is the nautical area scattering coefficient (m^2/nmi^2) and z is the vertical extent of the school (m).

2.3.3 School dynamic turbulence index

The school observations were categorized as 'stable', 'intermediate' or 'turbulent' according to the horizontal and vertical roughness coefficients, the vertical cross-sectional area and perimeter. Overall school roughness was found by

1. Merging horizontal (HR) and vertical roughness (VR) to according to:

$$R = \sqrt{HR \times VR} \quad (4)$$

2. Calculate circularity (C) from school perimeter (P) and area (A):

$$C = 10000 \left(\frac{50 \times P \sqrt{A}}{A \sqrt{\pi}} \right)^{-1} \quad (5)$$

3. Calculate the school dynamic turbulence parameter, S_{dyn} , which expresses the roughness and circularity of the school. High values indicate high roughness and low circularity.

$$S_{dyn} = 1000 \times \sqrt{\frac{R}{C}} - 1 \quad (6)$$

4. Normalize the school dynamic values to values between 0 – 1:

$$S_{dyn_{norm}} = \frac{S_{dyn_x} - S_{dyn_{min}}}{S_{dyn_{max}} - S_{dyn_{min}}} \quad (7)$$

5. The normalized school dynamic values were categorized as 'stable' for $S_{dyn_{norm}} < 0.2$, as 'intermediate' when $S_{dyn_{norm}}$ was 0.2 – 0.5 and as 'turbulent' when $S_{dyn_{norm}} > 0.5$.

2.3.4 School biomass

The school biomass (B_{school}) was calculated according to

$$B_{school} = \rho \times L^2 \times z \times W_{fish} \quad (8)$$

where L^2 is the observed length of the school. Since there was only information from one dimension the width was assumed to equal the length, therefore the observed length (L) is squared. W_{fish} is the mean herring weight attained from gillnet samples.

2.3.5 School categories

The herring school observations were divided into three categories: (1) Pelagic (no bottom contact, mean vertical extent >7 m), (2) Demersal (Contact with bottom) and (3) Sub – pelagic (mean vertical extent of school \leq 7 m and no bottom contact).

2.3.6 Predatory fish

Single target tracks on echosounder recordings were identified as gadoids based on the entangling net samples.

2.4 Environmental data

2.4.1 CTD data

A CTD (STD/CTD, model SD204, SAIV) was used to measure the temperature, oxygen level and salinity. CTD – samples were conducted at fixed locations throughout Lindåspollene, but overall most of the samples were obtained from the exact location of the school or in close proximity of the school. The CTD samples used in this thesis were all obtained within 400 m from the school location. The closest CTD stations in time and space were used to calculate the mean bottom layer (from bottom to 2 meters above bottom), top (1 – 5 m water depth) and school vertical extent values for temperature, oxygen and salinity and link it directly to the acoustic school observations. In addition the temperature, oxygen and salinity from 15 m depth were recorded.

2.5 Fish biology

2.5.1 Herring gillnet samples

Herring gillnets were set from the surface within 400 m from the pre-spawning area (**Figure 2.1**). Monofilament gillnets with a length of 25 m, depth of 4 m and mesh sizes of 24-26 mm were used along with nylon gillnets with a length of 28 m, depth of 4 m and mesh sizes from 28-34. Total lengths (to the nearest 0.5 cm below) and wet weights (to the nearest g below) were measured, while sex and maturity stage were determined from the gonad maturity index GI (1-8), stages 1-2 immature, stages 3-5 maturing, stage 6 running, stage 7 spent and stage 8 resting. Scales and otolith samples were collected for age determination and vertebrae counted for determination of population. The stomach contents of the herring were only recorded in 2008. These analysis were made in accordance with the Institute of Marine Research (IMR) sampling manual (Manger et al., 2010).

2.5.2 Predator entangling net samples

Entangling nets were set to identify potential herring predators such as large gadoids (> 50 cm in length), and to compare the predation pressure between years. The predation pressure was calculated as catch per unit effort (CPUE):

$$CPUE = \frac{n \text{ fish}}{n \text{ entangling nets}} \quad (9)$$

Of which the type of entangling nets, net location and soaking time were standardized. However, in 2010 the entangling nets were set directly on the herring spawning ground, which could have led to higher CPUE as predatory fish probably are attracted to the spawning ground.

2.6 Time of spawning and spawning grounds

The estimated day of peak spawning was decided based on herring maturity data. It was set as the day when 50 % of the population had reached maturity stage 6 (running).

Detection of spawning grounds was facilitated by large aggregations of common eider ducks (*Somateria mollissima*) in 2008-2010, which are potential herring egg foragers in Lindåspollene. The spawning location was verified based on direct observations of herring egg deposits on the bottom, and stomach content analysis of gadoid fish (cod and pollock). The spawning ground was not located in 2007.

2.7 Definition of periods in relation to peak spawning

The periods were defined based on the estimated day of peak spawning. The late-spawning/post-spawning period (SII) was defined to be from the day after the day of proposed peak spawning and onwards. In three of the four years of this study, spawning commenced within ten days prior to the day of proposed peak spawning. This formed the basis of the definition of the early-spawning/spawning period (SI), which is defined as ten days before and until peak spawning. The long pre-spawning period was divided in two, an early and a late pre-spawning period. The February surveys went under the early pre-spawning period (PI), while the surveys in early March went under the late pre-spawning period (PII). **Table 2.2** displays the four periods based on days relative to day of spawning. The days relative to spawning are also converted into day of year (Julian day) and date for each year.

Table 2.2: The four observation periods (PI, PII, SI and SII) in relation to the estimated day of peak spawning and Julian day (Year day). The grey areas show the days within the periods that acoustic recordings were conducted.

Period	PI																															
Day (peak spawning = 0)	-55	-54	-53	-52	-51	-50	-49	-48	-47	-46	-45	-44	-43	-42	-41	-40	-39	-38	-37	-36	-35	-34	-33	-32	-31	-30	-29	-28	-27	-26	-25	
Julian day 2007	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	
Julian day 2008	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	
Julian day 2009	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	
Julian day 2010	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	
Period	PII											SI							SII													
Day (peak spawning = 0)	-24	-23	-22	-21	-20	-19	-18	-17	-16	-15	-14	-13	-12	-11	-10	-9	-8	-7	-6	-5	-4	-3	-2	-1	0	1	2	3	4	5	6	7
Julian day 2007	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85
Julian day 2008	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94
Julian day 2009	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90
Julian day 2010	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101

2.8 Data treatment and statistical analysis

All data were organized in Microsoft Office Excel 7, as well as preparations of tables and some figures. Statistical analysis and most of the figures were prepared in the statistical software R 2.11.1 (<http://www.r-project.org/>).

The data were non-normal distributed and heteroscedatic and therefore non-parametric statistics were employed. The applied statistical tests used are given in the results chapter.

3 Results

The main herring school was observed within the same limited area both before and during spawning in all years (2007-2010), except for five single observations in 2010. The main school initially stayed in the pelagic in the pre-spawning period, but when spawning commenced it moved down to the bottom and stayed there for a minimum of 9 days in 2009 and 48 days in 2010. In these years acoustic observations were also conducted during spawning. The vertical school extent, packing density and school dynamic turbulence changed over time.

3.1 Habitat and environment

3.1.1 Weather conditions

The weather was generally good during the study period with predominantly overcast conditions, but during the surveys in the early pre-spawning period (PI) in 2010 it was sunny and cold (down to -15°C). In period PI (16th to 20th of February) in 2007 there was a 2-3 cm thick ice layer covering the herring pre-spawning area. In 2008 there was an ice layer located about 500 m south of the pre-spawning area from the 13th to the 14th of February (PI). Although the winter in 2010 was very cold, there was almost no ice on Lindåspollene due to the high salinity level at the surface, probably a result of little precipitation and run-off from rivers this year.

3.1.2 Hydrographical conditions

The sea water temperature in Lindåspollene was stable within years but was getting progressively colder for each year within the study period, from an average of 6.3°C at 15 m depth in 2007 to 5.7°C in 2008, 5.1°C in 2009 and 3.2°C in 2010 (**Figure 3.1 a**). In 2010, the last study year in the period, the temperature at 15 m depth was markedly lower, almost 3°C below the average for the preceding years. The surface temperature was low during winter and increased towards spring, when spawning took place. In 2007 it increased from 6.0 to 7.0°C , in 2008 from 4.9 to 5.8°C in 2009 it increased from 4.6 to 5.4°C , while in 2010 it increased from 2.2 to 5.6°C . In 2007 a distinct thermocline was present at ~ 18 m depth that was not present in the following years (**Figure 3.2**).

The water column was generally well oxygenated throughout the study period (>4 mg/L shallower than 40 m depth). An oxycline was present at ~ 18 m depth in 2007 and 2008 and at ~ 40 m depth in 2009, while in 2010 the oxygen level was relatively homogenous throughout the water column (**Figure 3.2**). The oxygen level at 15 m depth was between 6.0 - 8.5 mg/L throughout the study period in 2007. In 2008 the oxygen level was relatively stable around 7.5 - 8.5 mg/L. In 2009 the oxygen level increased from 6.3 - 7.3 mg/L during the study period, while it increased from 5.3 to 8.5 mg/L in 2010.

The salinity was stable at about 30-32 PSU (practical salinity units) below 20 m depth, while it decreased at shallower depths in all years, down to 22 PSU, except for in 2010 where the salinity was homogenous throughout the water column (**figure 3.2**).

The hydrographical conditions were similar in 2007-2009, while in 2010 the water masses were well mixed with homogenous conditions throughout the water column, and the temperature was markedly lower.

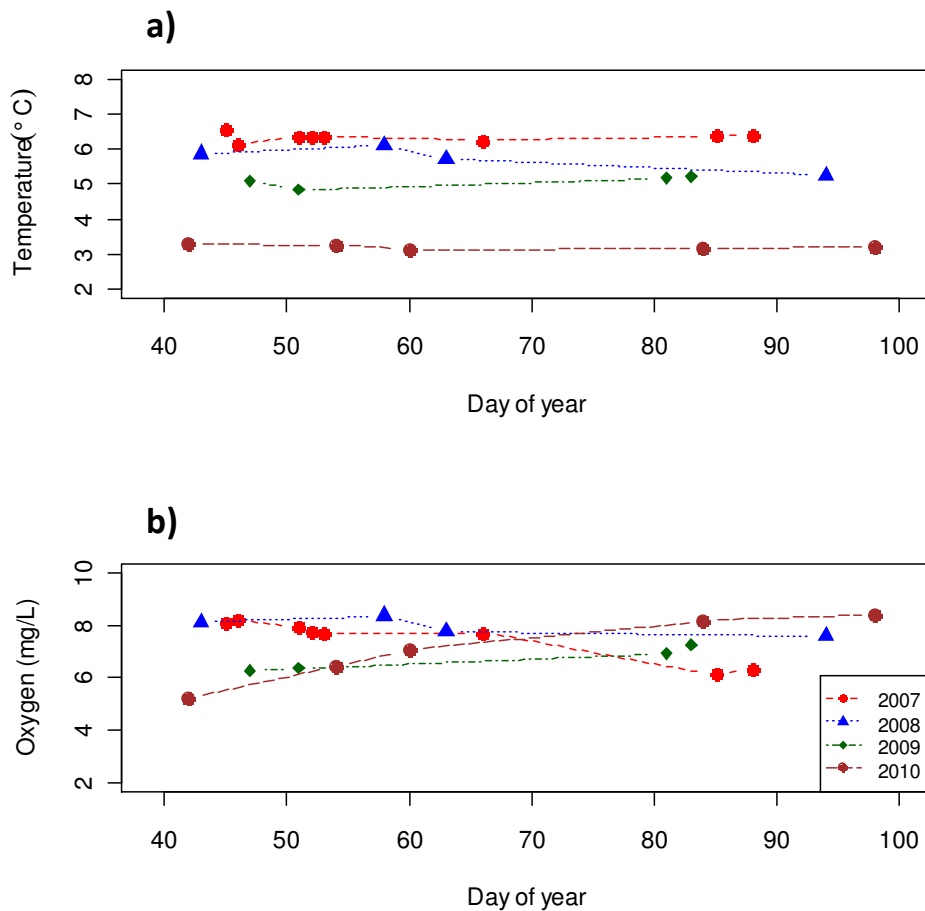


Figure 3.1: The **a)** temperature (°C) and **b)** oxygen content (mg/L) at 15 m depth in 2007-2010. All CTD casts were conducted within ~400 m of the pre-spawning area of the herring school.

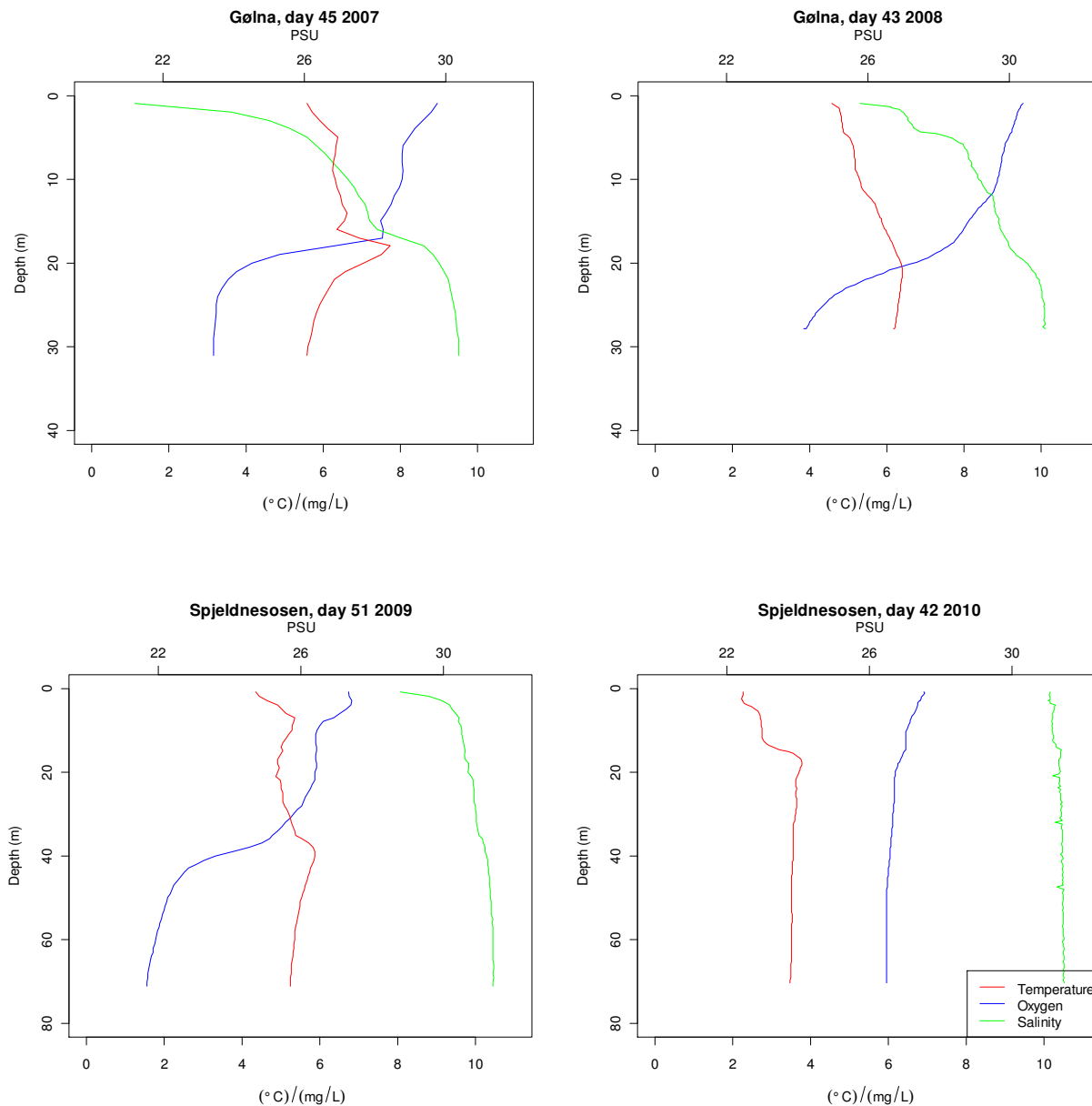


Figure 3.2: The temperature (°C), oxygen level (mg/L) and salinity (PSU) in period PI at the pre-spawning area (Gølna) in 2007 and 2008, and ~400 m further southwest in Spjeldnesosen in 2009 and 2010.

3.1.3 Predation

Cod (*Gadus morhua*), pollock (*Pollachius pollachius*), saithe (*Pollachius virens*) and haddock (*Melanogrammus aeglefinus*) were sampled by means of entangling nets nearby the location of the school. All these species are known predators of herring and herring eggs (Høines and Bergstad, 1999; Runde, 2005), although haddock preferably forage on herring eggs (Tøresen, 1991; Høines and Bergstad,

1999). Cod was the most abundant of the fish predators caught, and the only predator that had ingested adult herring (Table 3.1).

The abundance of cod in Lindåspollene was highest in the last study year (2010) with a CPUE of 3.9, while the CPUE in 2007 and 2008 were 1.6 and 1.7, respectively. In 2009 only one individual cod was caught (Table 3.1). The percentage of cod >50 cm that had preyed on herring was 21.4 in 2007 and 31.6 in 2008. Other potential predators in the entangling net samples were scarce, and none had preyed upon herring prior to the sampling. However, in 2008 a single large pollock (88.0 cm) was caught in a herring gillnet with 4 adult herring in its stomach.

Stomach fullness was recorded for all gadoids in all years, while stomach content had only been obtained in 2007 and 2008. The only fish over 50 cm caught in 2009 had stomach fullness level of 5 (completely full stomachs). In 2010 20 % of the fish had a stomach fullness level of 5. Gadoids >50 cm in Lindåspollene with full stomachs in January-March strongly indicates that herring were their main prey in this period (A. Johannessen, pers. comm.).

Table 3.1: Entangling net catches of potential herring predators >50 cm in length in the winter and spring of 2007-2010. '-' denotes no data available.

Year	Gillnets	Predator fish	n	CPUE (n fish/gillnet)	n fish with ingested herring	% fish with ingested herring	Mean length (cm)	Length SD (cm)
2007	9	Cod	14	1.6	3	21.4	59.4	9.8
		Pollock	3	0.3	0	0.0	56.3	5.7
		Saithe	2	0.2	0	0.0	76.0	1.4
		Total	19	2.1	3	15.8		
2008	22	Cod	38	1.7	12	31.6	70.0	18.9
		Pollock	3	0.1	0	0.0	61.7	6.4
		Saithe	1	0.0	0	0.0	83.0	0.0
		Total	42	1.9	12	28.6		
2009	5	Cod	1	0.2	-	-	70	0.0
		Pollock	0	0	-	-		
		Saithe	0	0	-	-		
		Total	1	0.2	-	-		
2010	11	Cod	43	3.9	-	-	56.3	10.5
		Pollock	1	0.1	-	-	81.0	0.0
		Saithe	1	0.1	-	-	74.0	0.0
		Total	45	4.1	-	-		

Harbour seals (*Phoca vitulina*) were observed on several occasions in 2009 and 2010. On the 19th of February 2009 two harbour seals were observed only about 150 m away from the herring pre-spawning area, and on the 20th of February about 1000 m further north. In the end of March 2010 two seals were

observed 1000 m south of the pre-spawning location, and observations from locals suggest that the harbour seals stayed year round in the area (E. Marås, pers. comm.) Herring is the most common prey for harbour seals (Haug, 1998). There was also several occupied sea otter (*Enhydra lutris*) nests in Lindåspollene in the study period, and in 2007 a sea otter was caught in a pot trap (R. Bergfjord, pers. comm.). Also this species is a known predator on adult herring (Lee et al., 2009).

Great cormorants (*Phalacrocorax carbo*) were commonly observed in Lindåspollene during the study period in all years. This species is known to be an opportunistic forager (Steven, 1933), and can easily dive below ten meters of water depth, which makes it a potential herring predator (I. Byrkjedal, pers. comm.). In 2010 a great cormorant was caught in a herring gillnet, and several scavenged herring with beak marks were caught in the gillnet samples.

3.1.4 Spawning grounds

The main spawning ground was in 2008-2010 located at the shallow threshold area separating Straumsosen and Spjeldnesosen, although in 2008 the spawning ground did not seem to be as extensive as in 2009-2010 (**Figure 3.3**). In 2007 no spawning ground was located. In 2009 herring eggs were found attached to a pot trap line in the pre-spawning area, indicating that some herring had spawned outside of the main spawning area.

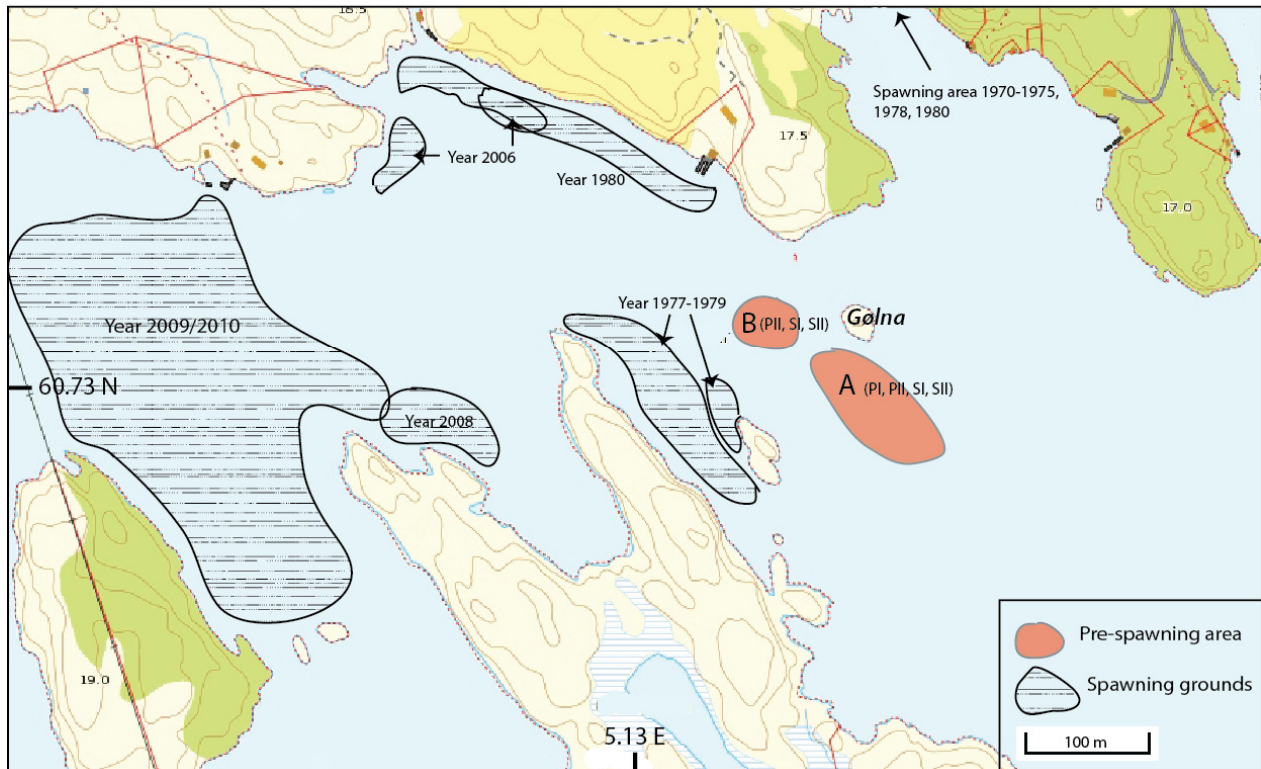


Figure 3.3: An overview of the pre-spawning area of the herring school and known spawning grounds. The spawning ground in 2008-2010 was about 600 m away from the islet Gølna, which is close to pre spawning area A and B. Spawning grounds found in earlier studies were included for comparison (Lie and Dahl, 1978; Johannessen, 1986).

3.2 Herring biology

3.2.1 Size, age and maturity stage

The average length, weight and age of the herring all differed significantly between the years (Table 3.2) (Kruskal-Wallis test (KW), χ^2 (3)=268.5, $p < 0.001$), but the difference in fish length was minimal. The weight and age were, however, higher in 2009 compared to the three other years.

Table 3.2: Sample size (n), total length (cm), total wet weight (g) and age (years) of herring sampled with gillnets within 400 m of the school location.

Year	n	Length mean (cm)	Length SD (cm)	Weight mean (g)	Weight SD (g)	Age mean	Age SD
2007	234	29.9	2.1	237.6	53.3	7.5	3.3
2008	293	31.3	2.1	251.7	58.2	8.8	3.6
2009	538	32.4	1.5	302.6	50.1	11.3	3.5
2010	364	31.7	2.3	251.0	52.5	9.2	5.1

The majority of the herring were running (gonad maturity stage 6) from the 80th Julian day and onwards in all years (**Figure 3.4**). Based on the maturity development the proposed day of peak spawning was calculated to Julian day 78 in 2007, Julian day 87 in 2008, Julian day 83 in 2009 and Julian day 94 in 2010. **Figure 3.5** shows the proportions of pre-spawning, running and spent herring by period and year. In 2007 and 2009 running herring were only found in the late pre-spawning periods (SI, SII), while in 2008 and 2010 running herring were seen already in the late pre-spawning period (PII), 11-20 days before estimated peak spawning.

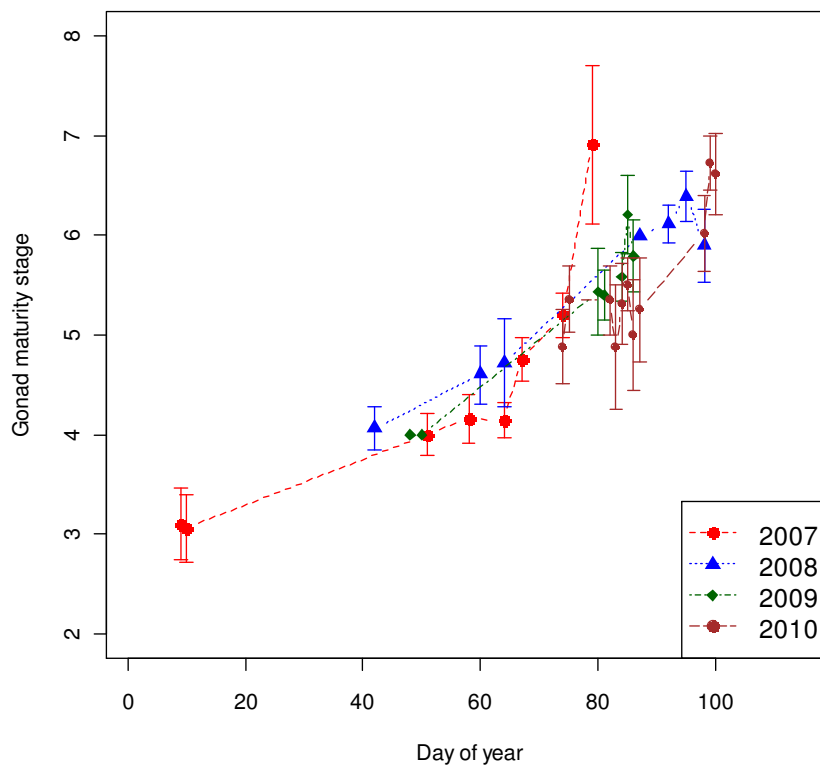


Figure 3.4: Gonad maturity stage of herring with standard deviation bars during the pre-spawning and spawning periods for all years. Maturity stages 2-5 are defined as maturing, 6 as mature, 7 as spent and 8 as resting.

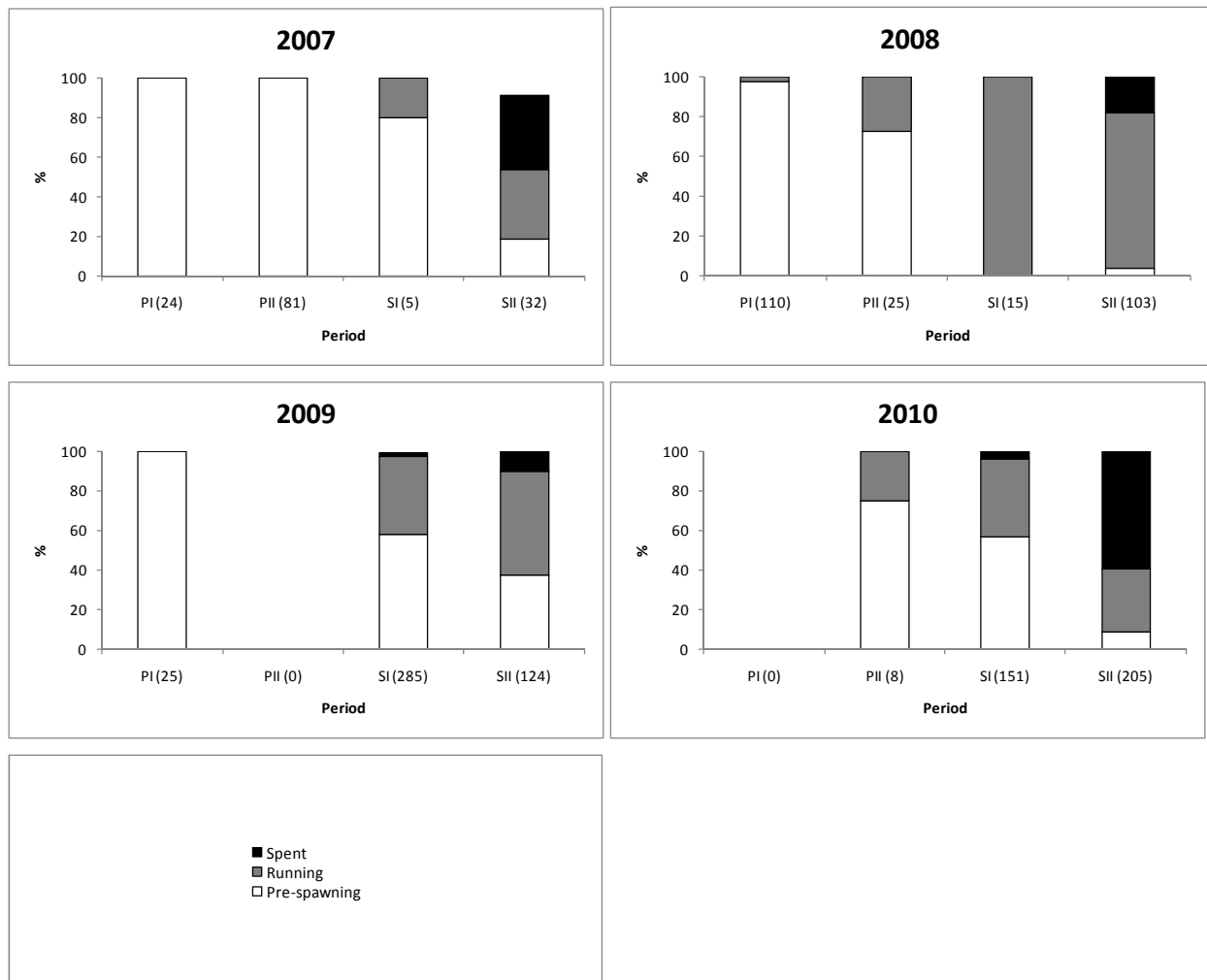


Figure 3.5: The percentage of pre-spawning, running and spent herring in 2007, 2008, 2009 and 2010 per period. The number of fish samples is given in the parentheses after the period. Maturity stage 8 is included as 'Spent'.

The stomach content of the herring recorded in 2008 showed that there was no feeding until the late spawning period (SII) in which 6 % (n=118) of the sampled fish had been feeding. Half of these herring were running and the other half was spent.

3.2.2 Estimated school size

The herring school was estimated to be largest in 2007 (8.1 ± 3.0 tons), followed by 2009 (4.2 ± 1.2 tons), and 2010 (1.5 ± 0.1 tons). School size could not be estimated in 2008 as position data were not available this year. The estimates are somewhat rough and are based on the assumption that the school widths equal the recorded school lengths. In 2009 there were only data from the spawning periods (SI, SII), and the school size was likely somewhat underestimated due to smaller groups splitting from the main school and difficulties of separate echoes originating from the school and from bottom echoes. In 2010

the school was avoiding the vessel, which also could have led to an underestimation of abundance this year.

3.3 Herring school dynamics

In 2010 the behaviour of the herring prior to and during spawning differed from the corresponding periods in 2007-2009. Despite frequent surveying, the number of school observations was low, as it was difficult to locate the school, presumably due to strong reactions to the research vessel. In an attempt to quantify this behavioural change, the mean time lag of acoustic recordings between school observations was calculated for the different periods and years (**Table 3.3**). These results should, however be interpreted with caution as differences in time lags could also be explained by other factors such as acoustic availability and the presence of ice cover, like in 2007. However, the mean time lag between observations was markedly higher in 2010 from the other years, suggesting that the herring reacted stronger to the vessel this year. It also seems like the herring were harder to detect during the late pre-spawning (PII) and spawning periods (SI, SII) compared to the early pre-spawning period (PI).

Table 3.3: Survey time (in minutes), number of school observations and time lag between observations. Periods with no acoustic surveys are marked with ‘-’.

Year	2007				2008				2009				2010			
Period	PI	PII	SI	SII	PI	PII	SI	SII	PI	PII	SI	SII	PI	PII	SI	SII
Survey time (min)	2280	235	-	-	300	-	-	-	1655	-	530	340	550	365	230	145
School obs.	61	18	-	-	12	-	-	-	156	-	16	6	14	3	4	2
Min/school obs.	37.4	13.1	-	-	25.0	-	-	-	10.6	-	33.1	56.7	39.3	121.7	57.5	72.5

3.3.1 Spatial dynamics

The school was stationary and stayed within the same limited area of ~7000 m² during the pre-spawning and spawning periods in 2007-2010 (**Figure 3.3**), except for five observations made in 2010. The survey in period PI in 2008 and 2009 did not have a GPS connected to the echosounder and the coordinates could thus not be recorded, but based on stationary echo recordings and reports from cruise members, the school was present at the same location also during those surveys. In the early pre-spawning period (PI) the school stayed in a trench close to a wall by the islet Gølna (Pre-spawning area A, **Figure 3.3 and 3.6**). The trench leads to Spjeldnesosen, the deepest basin in Lindåspollene (~90 m depth). As spawning was approaching (PII in 2007, SI, SII in 2009-2010) the school was in addition to pre-spawning area A observed closer to the spawning ground in shallower waters (~25m depth, pre-spawning area B). In the late pre-spawning period (PII) the variation in horizontal distribution was significantly higher (Fligner-Killeen (FK), $\chi^2(1)=23$, $p < 0.001$). In 2010 the variation in spatial distribution was not different between

periods (FK, χ^2 (3)=2.41, $p<0.48$). In 2008 and 2009 there were coordinates available from one period only.

During the spawning periods (SI, SII) in 2009 the school seemed to split in two parts: the main school settled demersally while a sub-school remained in the pelagic (**Table 3.4**). The pelagic sub-school was only observed in pre-spawning area A, similar to the main school during the early pre-spawning period (PI). The observations of the main school that stayed on the bottom were evenly distributed in pre-spawning area A and B (**Figure 3.6**), and the variation in spatial distribution was significantly larger than the pelagic sub-school (PK, χ^2 (1)=3.9, $p=0.048$). Some observations of the demersal school were closer to the spawning ground than any of the sub-pelagic school observations, but others were further away, hence the average distance to the spawning ground was ~ 600 m for both schools.

It is noteworthy that about 50 % of the observations in the spawning periods (SI, SII) were made in close contact or within 10 m to a submerged water pipeline (**Figure 3.7**).

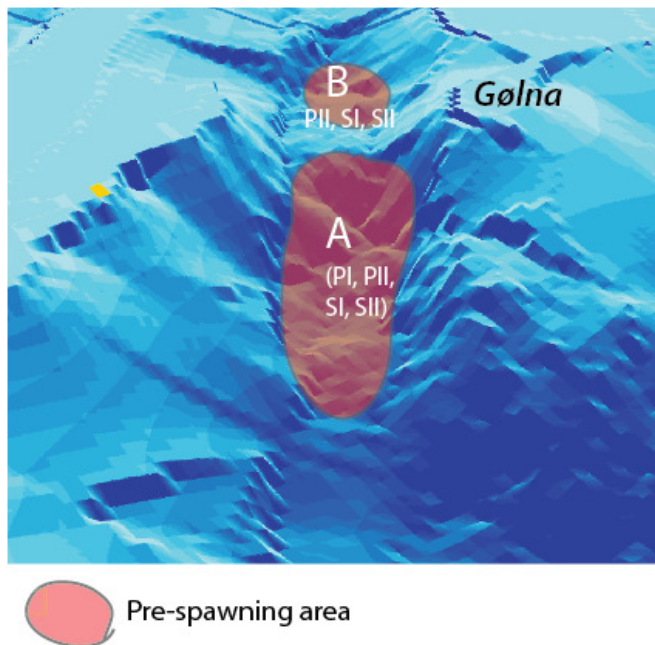


Figure 3.6: The topography in the pre-spawning area and the position of the school in different periods. The school was observed in a trench, close to the steep ‘wall’ at pre-spawning area A . In the periods PII, SI and SII the school was also observed in the shallower pre-spawning area B.

Period PI was in all years dominated by pelagic school observations (~ 88 %), while SI and SII were dominated by demersal school observations (~ 71 %) (KW, χ^2 (3) =268.5, $p<<0.001$) (**Table 3.4**). The school

appeared to split in two approximately equally big parts in Period PII in 2007, resulting in more pelagic sub-school observations than observations of a pelagic main school. In 2009 a small group remained in the pelagic when the main school moved to the bottom. The corresponding period in 2010 only demersal school observations were made. Pelagic sub-school observations in PI and PII may partly represent recordings where only the edge of the main school was covered. In 2009, however, a pelagic sub-school was observed in periods SI and SII as the main school settled on the bottom. Examples of typical school shapes are shown in **Figure 3.7**.

Table 3.4: Different types of school observations in different periods in 2007-2010.

Year	2007				2008				2009				2010			
Period	PI	PII	SI	SII	PI	PII	SI	SII	PI	PII	SI	SII	PI	PII	SI	SII
Pelagic school obs.	47	8	-	-	10	-	-	-	151	-	2	1	7	0	0	0
Demersal School obs.	0	0	-	-	0	-	-	-	1	-	10	3	3	3	4	2
Pelagic sub-school obs.	13	10	-	-	2	-	-	-	4	-	4	2	4	0	0	0

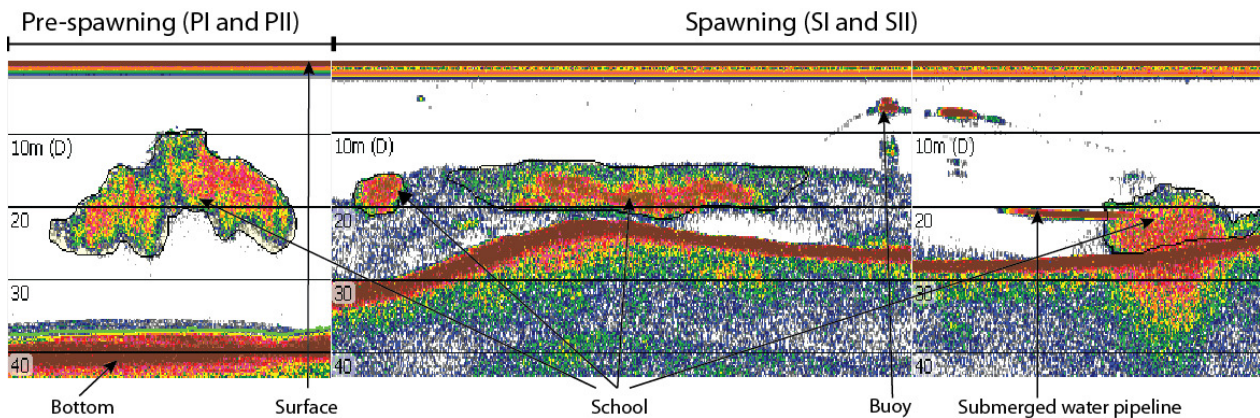


Figure 3.7: Typical examples of the shape of the herring school observations in the pre-spawning and spawning periods.

There were differences in school depth between years during the early pre-spawning period (PI), where the school with few exceptions stayed in the pelagic (**Table 3.4**). In 2010, when the school seemed to avoid the surveying vessel, the school stayed significantly deeper than in the previous years (WRST, $W=1836$, $p < 0.001$). The school was also staying deeper in 2009 than in 2007-2008 (**Figure 3.8**) (WRST, $W=1836$, $p < 0.001$). The distance between the school and the bottom was usually more than 5 m, except for the last year (2010) when it was significantly shorter compared to the preceding years (**Appendix B, Figure B-1**) (KW, $\chi^2(3)=16.7$, $p < 0.001$). The school generally kept a distance of ~ 8 m to the surface in all years (**Appendix B, Figure B-2**).

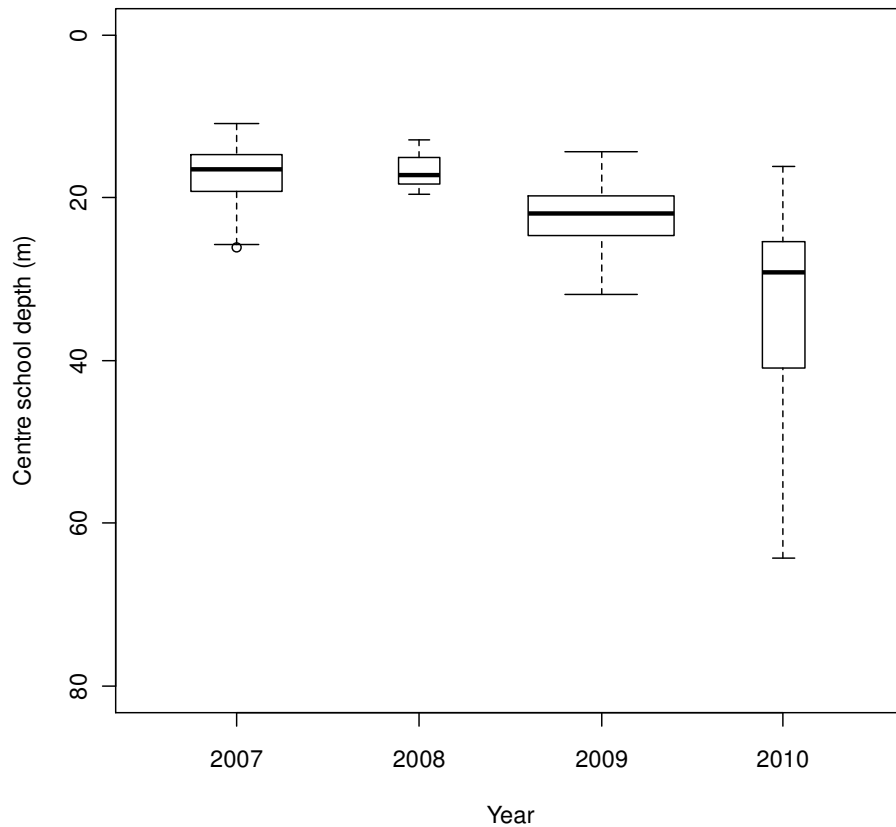


Figure 3.8: The centre school depth in period PI in 2007 – 2010. Thick lines represent the medians, boxes the upper and lower quartiles and whiskers the minimum or maximum values. Dots represent outliers. The width of the boxes shows the number of observations for each year.

The school was generally swimming to shallower waters when it moved towards the bottom (**Figure 3.9**). This pattern was clearest in 2009 (WRST, $W=580$, $p=0.0017$). In 2010 the school stayed in shallower waters in PII compared to in PI (WRST, $W=33$, $p=0.005$), whereas the differences between PI and SI were near significant at the 5% level (WRST, $W=37$, $p=0.056$) and the difference between PI and SII was not significant (WRST, $W=18$, $p=0.23$). In 2007 and 2008 there were no observations of the school during spawning.

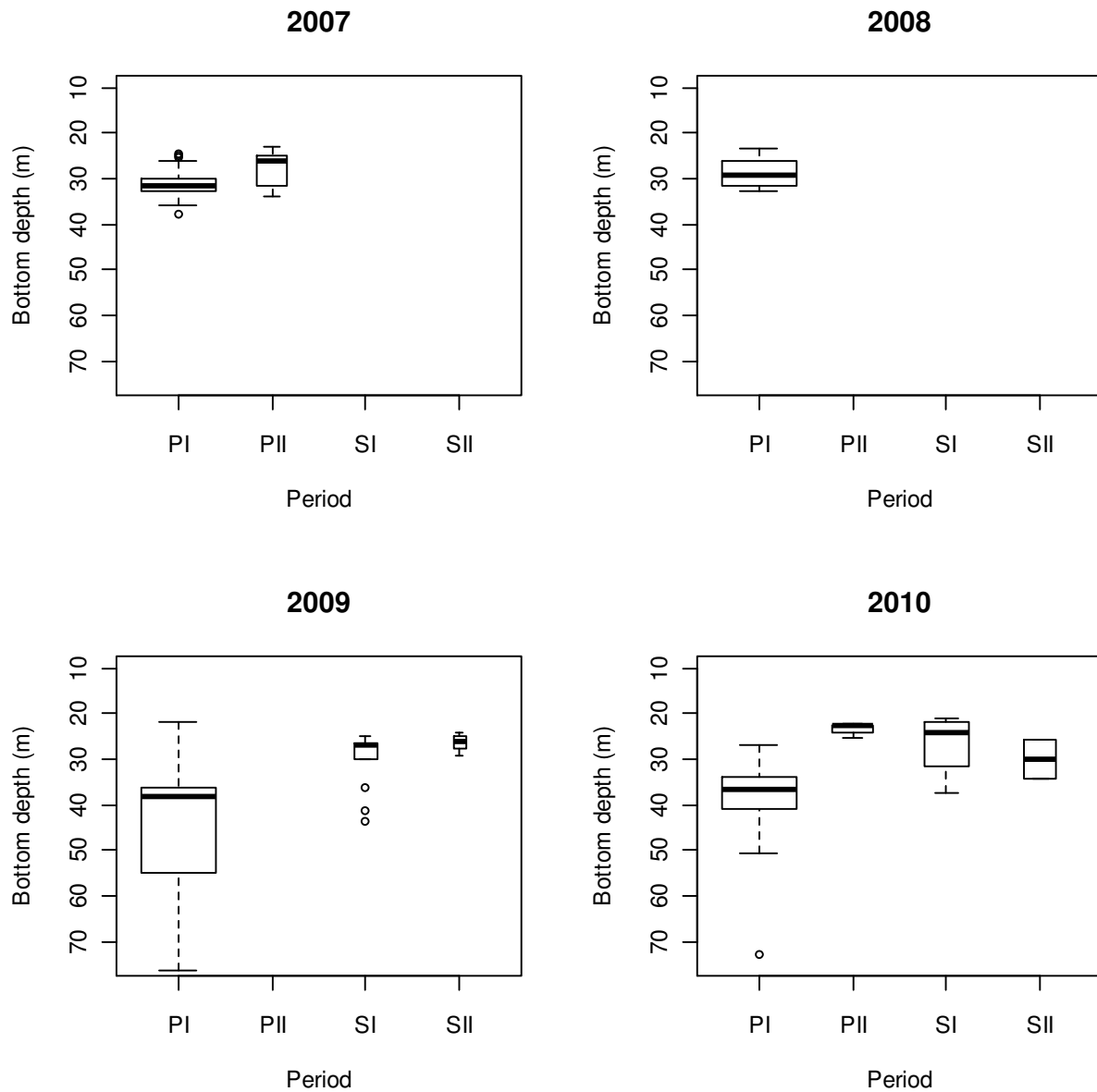


Figure 3.9: The bottom depth at the location of the school in different periods in all years. Dots represent outliers. The width of the boxes shows the number of observations for each year.

The presence of predators influenced how near the bottom the school stayed. The school response towards bottom dwelling gadoids was generally increased distance to the bottom when one or more gadoids were present in the vicinity of the school (WRST, $W=6731$, $p < 0.001$). (**Figur 3.10**).

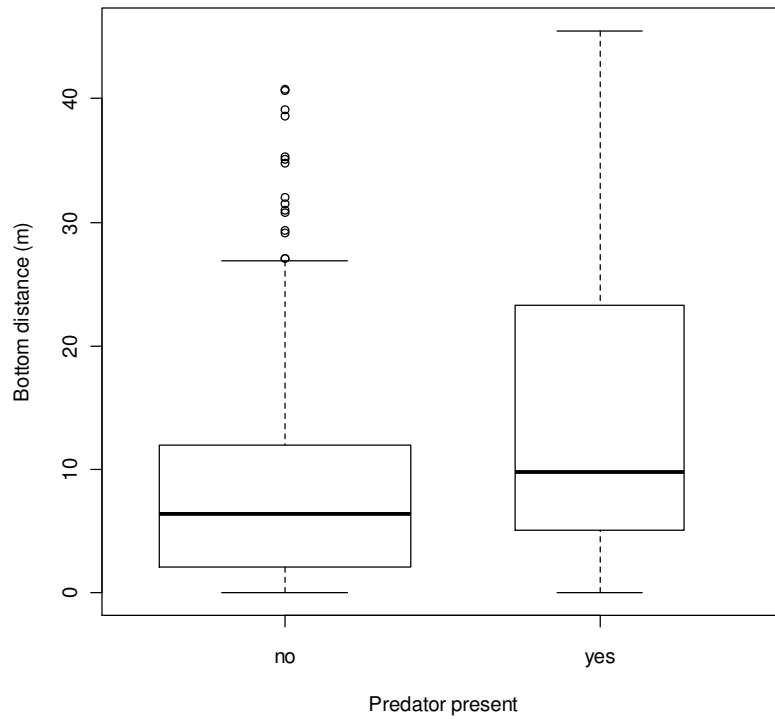


Figure 3.10: The distance between the school and the bottom in the absence/presence of gadoid predators as seen on the echogram recordings. Data pooled for all years (2007-2010). Dots represent outliers. The width of the boxes shows the number of observations for each year.

The centre school depth in relation to the temperature and oxygen profiles is shown in **Figure 3.11**. The centre school depth appears to correlate with the oxycline and thermocline in 2007, and is just above the oxycline in 2008. The oxycline was deeper in 2009 than in 2007 and 2008 and the mean center school depth followed the same pattern. In 2010 the temperature and oxygen levels were homogenous throughout the water column indicating a high degree of mixing, and this year the school stayed the deepest and its depth varied the most compared to the other years (FK, $\chi^2(3)=48.3$, $p < 0.001$).

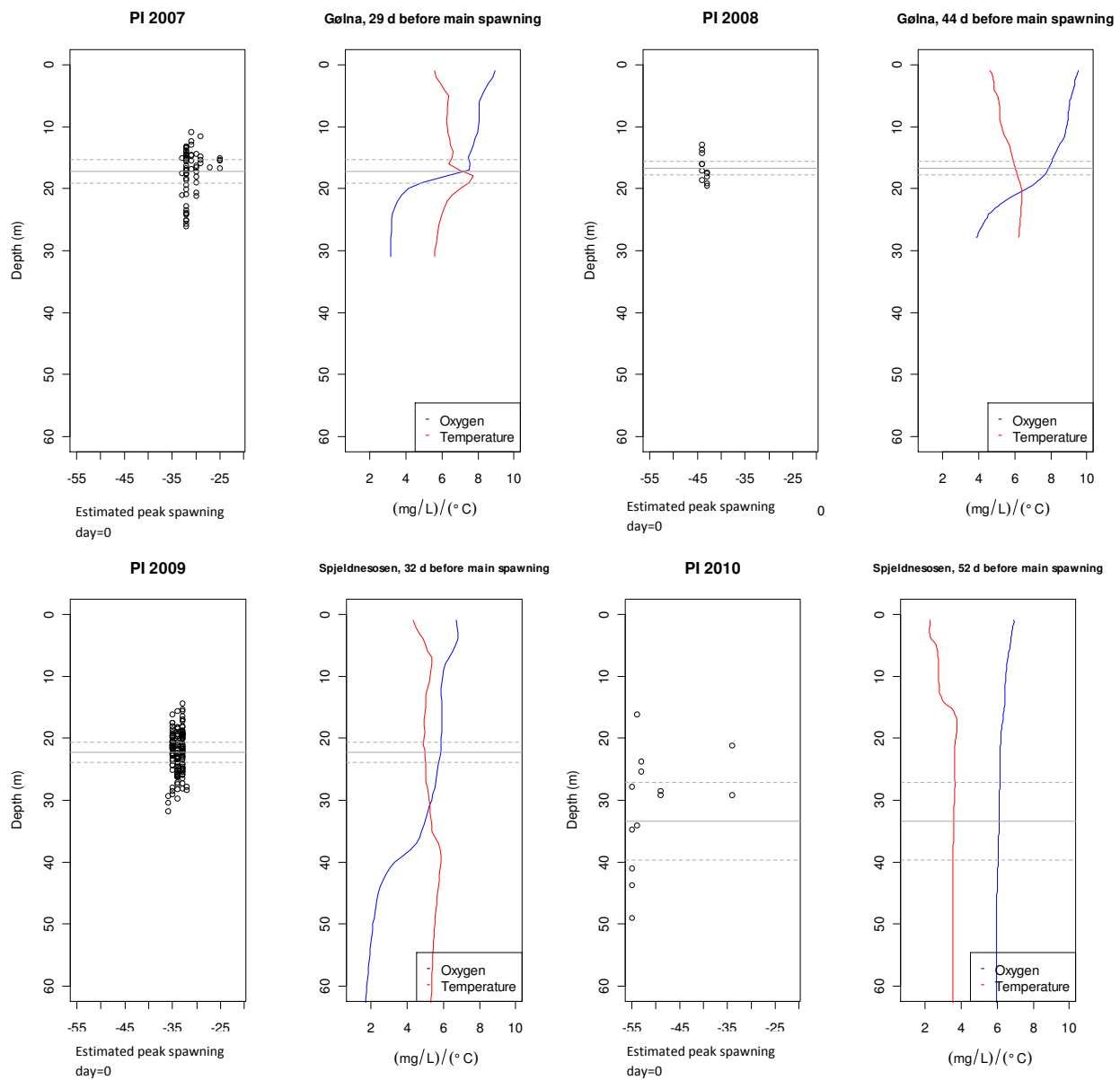


Figure 3.11: Centre school depth (dots) in period PI in relation to temperature ($^{\circ}\text{C}$) and oxygen (mg/L) level. The grey line gives the mean centre school depth and the dotted lines the standard deviation.

3.3.2 Vertical school extent

The vertical extent of the school was generally highest in the early pre-spawning period (PI). In 2007 the mean school was higher in period PI than in PII (**Figure 3.12**, WRST, $W=278$, $p=0.03$), and in 2009 the vertical extent was higher in PI than in the spawning periods (SI, SII) (WRST, $W=569$, $p<0.005$). In 2010 no difference in the vertical extent of schools between periods was noted (KW, $\chi^2(3)=2.2$, $p=0.53$), but also here the observation with highest vertical extent was made in period PI, and the observation with the lowest vertical school extent was noted in SII. In 2008 acoustic surveys were only made within period PI.

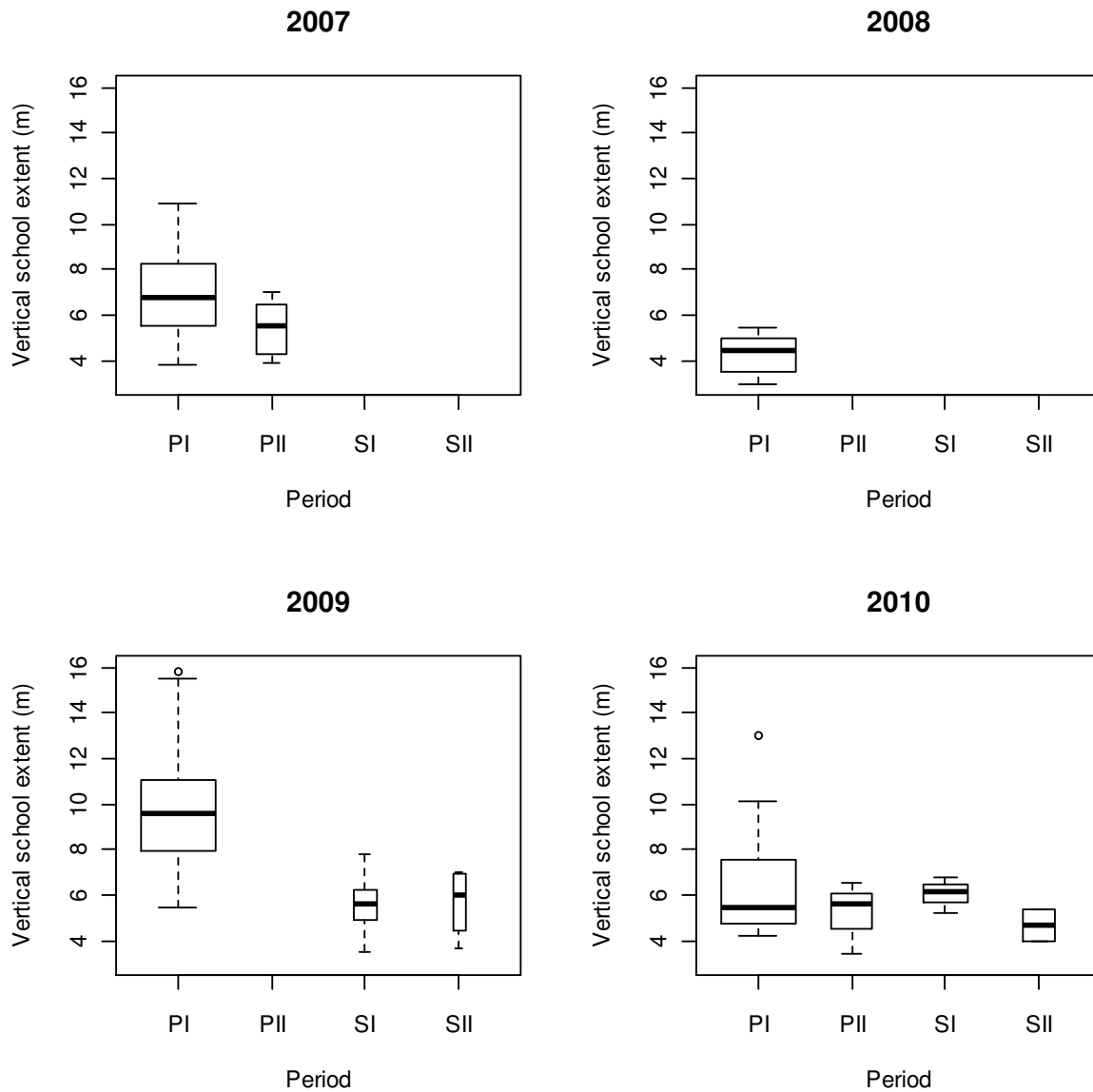


Figure 3.12: The mean vertical school extent (m) of the main school in the different periods in 2007-2010. Dots represent outliers. The width of the boxes shows the number of observations for each year.

3.3.3 School packing density

The herring was generally staying closer together during spawning than during pre-spawning (**Figure 3.13**). In 2007 the mean packing density of the school was significantly higher in the late pre-spawning (PII) period than in the early pre-spawning period (PI) (WRST, $W=101$, $p=0.04$), and the variance was higher (FK, $\chi^2(1)=5.4$, $p=0.02$). Also in 2009 the mean density was higher in the SI and SII periods than in period PI (WRST, $p<0.005$, $W=32$), and the variance was also significantly different between periods within this year (FK, $\chi^2(1)=5.4$, $p<<0.001$). In 2010 the packing density in SI was significantly higher than in the other periods (WRST, $p<0.025$, $W=7$), but the variation between observations were not significantly different (FK, $p<0.15$, $\chi^2(3)=5.3$).

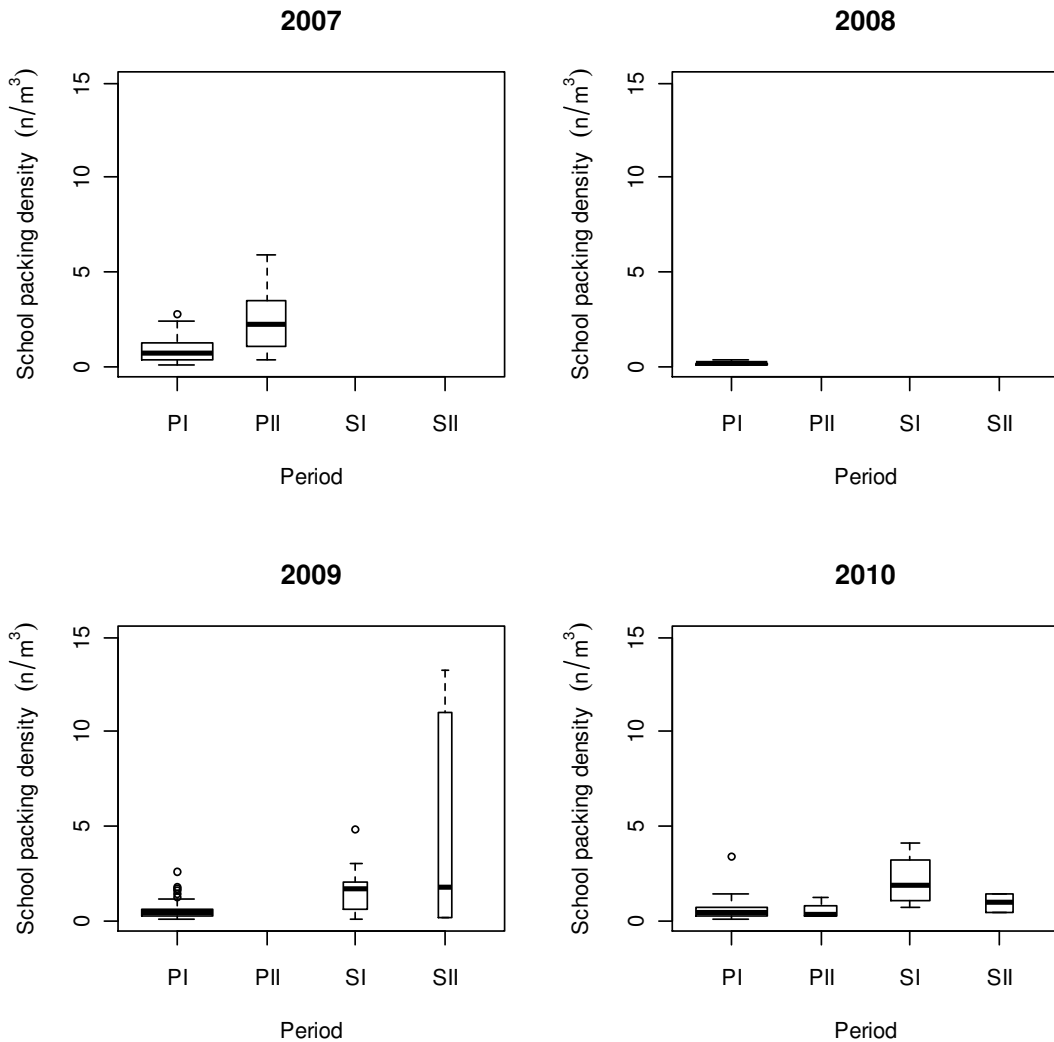


Figure 3.13: The packing density of the main school in the different periods in 2007-2010. Dots represent outliers. The width of the boxes shows the number of observations for each year.

In 2007 the school packing density was significantly higher for the observations where fish predators were observed acoustically near the school than in observations without adjacent predators (**Appendix D**, WRST, $W = 99$, $p = 0.048$), but no differences were found for the other years

3.3.4 School dynamic turbulence

The school dynamic turbulence index (STDI) indicated that the school was less dynamic in period PI than in PII, SI and SII, lowest in PI, highest in PII and SI, and somewhat decreasing from SI to SII. The STDI was significantly higher in PII than in PI (WRST, $W=276$, $p<<0.001$).

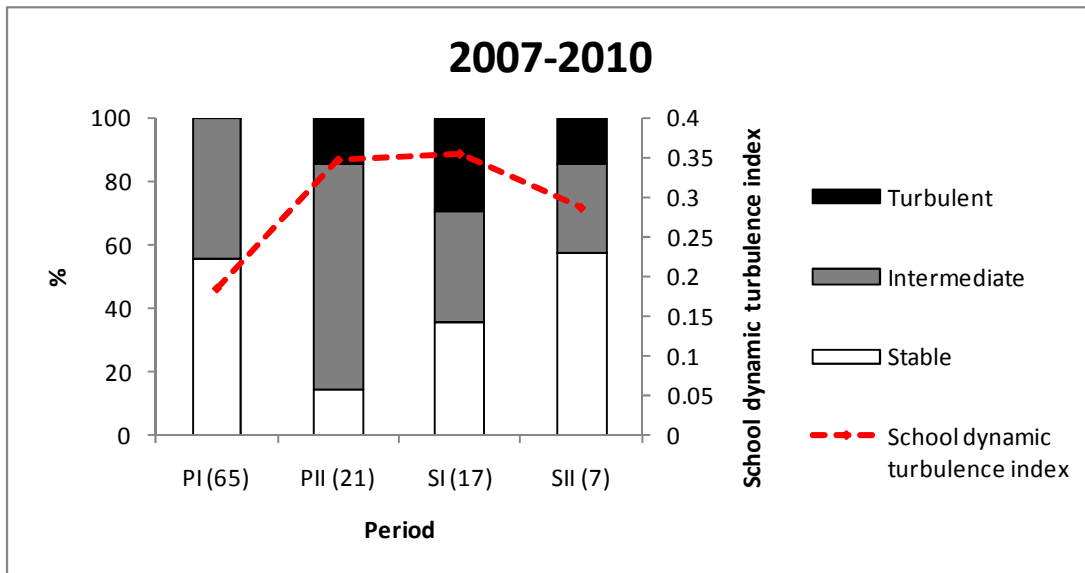


Figure 3.14: Prevalence (%) of the school dynamic turbulence index observations categorized as 'stable', 'intermediate' or 'turbulent' by period for all years merged together. The number of school observations is indicated on the x-axis.

4 Discussion

This is the first study analysing the pre-spawning and spawning behaviour of herring at a school level over several succeeding years. The herring showed high fidelity towards the same, small area in all study years. From this area the herring were close to present and historical spawning grounds, and had direct access to the deepest basin in the system. The herring was aggregated into a single stationary pelagic school in the early pre-spawning period (February), which could be explained by predator avoidance and energy conservation. The school avoided the surface (0-8 m depth), probably to be less vulnerable towards visually mediated predators, perhaps particularly seabirds, and the distance to the bottom was influenced by the presence of bottom-dwelling gadoid predators. As spawning commenced (March) the school settled on the bottom and stayed there for a period of at least 9 days in 2009 and 48 days in 2010. The school dynamic turbulence was higher close to and during spawning than in the early pre-spawning period, likely indicating conflicting motivations between ripe and pre-spawning herring within the school. In the last study year the behaviour of the herring changed to some extent markedly and they seemed to avoid the research vessel, staying deeper and closer to the bottom than in the preceding years.

4.1 Methods and data quality

The data material was pre-assembled, except for the last year (2010) where I participated in surveys, thus I had no control over the experimental setup and sampling in those years. The studies in Lindåspollene had multiple purposes and were thus not designed for the present study alone. The field work could not be conducted at precisely the same time each year, but was always carried out within the spawning and pre-spawning periods. However, the school dynamics reported in this thesis are not related to the time of year as such, but rather to the time of peak spawning, which varied only slightly between the years of study.

During the survey in 2008 and the first survey in 2009, the GPS was not available, and it only worked properly for part of the work carried out in 2010, and thus the geographical coordinates of some school observations were missing. However, the cruise members noted school positions manually, confirming that the school stayed within the same area. The school size and school dynamic turbulence index could, however, not be calculated for these observations.

The surveys were only conducted during daytime between 8 am to 6 pm local time, and this thesis therefore focuses on the daytime aspects of the herring schooling dynamics. To reveal a diurnal behavioural pattern a stationary transducer was placed on a lander within the pre-spawning area. From these recording the school appeared to dissolve at dusk, before re-aggregating at dawn, a pattern that is

in agreement with earlier studies on diurnal dynamics in herring and other pelagic fish (Blaxter, 1985; Skaret and Slotte, 2007).

Limited resources led to the need to prioritize some activities over others, such as biomass estimation and stomach content analysis. The abundance of herring prey was not regarded as crucial since earlier studies both from Lindåspollene (Langård et al., 2006) and elsewhere (Nøttestad et al., 1996) have found that herring normally do not feed prior to spawning. This was confirmed by analysis of stomach contents obtained in 2008 in the present study.

Many pelagic fish initiate avoidance reactions in response to vessel influence (Olsen et al., 1983). This could be regarded as anti-predator behaviour (Freon et al., 1993; Vabø et al., 2002), which is state-dependent. Strong vessel avoidance reactions have been reported prior to spawning (Mohr, 1973; Olsen et al., 1983; Vabø et al., 2002), while during the spawning period the herring does not seem to respond (Johannessen, 1986; Skaret et al., 2005). The research vessel could therefore have different effects on the observed behaviour during pre-spawning and spawning for parameters such as vertical position of school, packing density and biomass estimates. The primary reaction of fish schools to vessels in shallow water is a vertical escape (Olsen et al. 1983, Misund & Aglen 1992). However, during the present study the herring did not seem to react towards the research vessel, except for in 2010.

4.2 Challenges for the herring population in Lindåspollene before and during spawning

Herring faces challenges before and during spawning that may vary between populations and environments. Here I will present the challenges for the herring in Lindåspollene before and during spawning.

In the pre-spawning period it is crucial for herring to minimize the predation risk to increase the probability of completing spawning, especially since they at this point have invested considerable resources into reproduction. There were several real and potential herring predators in Lindåspollene like gadoids, harbour seals, sea otters and sea birds (great cormorants). The main anti-predator strategy for herring is schooling. Individuals are safer in a large than in a small school (Pitcher and Parrish, 1993). The herring population in Lindåspollene is relatively small and minimizing predation risk may explain why only one single school was observed prior to spawning in the present study. The herring is expected to maximise the reproductive output and should not expend unnecessary energy, such as excessive avoidance reactions to predators or other disturbances (Johannessen, 1986; Skaret et al., 2006). Herring in Lindåspollene do not feed in the time prior to spawning (Langård et al., 2006) thus it is crucial to

allocate resources wisely. The resulting behaviour of herring in the pre-spawning period should therefore reflect the balance between predation pressure and conservation of energy.

Herring spawn on the bottom which should make them more vulnerable to predation due to bottom dwelling gadoids (Axelsen et al., 2000). The herring in Lindåspollene prefer to spawn on hard substrates (rocks and boulders) from high tide water level down to a depth of 10 m (Johannessen, 1986). Spawning in shallow water may reduce the manoeuvrability and escape possibilities, in addition the herring would be more vulnerable to sea birds, marine mammals and gadoids. Therefore they should not stay on the spawning ground for a prolonged time.

4.3 Behavioural variations between years in relation to environmental factors

The herring behaviour seemed to be relatively similar from 2007 to 2009. In 2010, however, the behaviour differed from the preceding years. That year the school seemed to avoid the surveying vessel, a reaction not observed in the preceding years. In addition the only five observations of the school outside of the pre-spawning area were recorded in 2010, and the school was generally staying deeper and closer to the bottom during the pre-spawning period.

The behavioural change in 2010 could be explained by increased predation pressure, for example the presence of a new predator. Two harbour seals were observed during the spawning period in both 2009 and 2010, and herring is the most common prey of harbour seals (Haug, 1998). The harbour seals could have been responsible for increased vigilance in 2010. However, one would expect similar behaviour in 2009. That was not the case and the effect of the harbour seals is therefore uncertain.

In 2010 the catch per unit effort (CPUE) of cod was twice than in the other years, and such an increase could have led to increased vigilance. However, the entangling nets were placed closer to the spawning ground in 2010. The spawning ground probably attracts gadoids, and this could have resulted in higher CPUE of cod. Moreover, low temperatures reduces the metabolic rate in fish (Claireaux and Lagardère, 1999), and slower digestion could have resulted in that cod were not able to eat as much herring in 2010 as in the previous years, because of the low temperature.

Based on the biomass estimates the school seemed to be considerably smaller in 2010 than the preceding years. Laboratory experiments have shown that a small school would react stronger to a predator than a large (Maguarran et al., 1985). This may explain the change into a more vigilant behaviour. However, the biomass estimates could have been underestimated as it was difficult to detect the school.

Why the herring school stayed deeper and closer to the bottom in 2010 could be a result of increased vigilance, i.e. that the surveying vessel scared the school, which could also explain why the only school observations made outside of the pre-spawning area was this year.

The most notable environmental difference between 2010 and the preceding years was the cold and sunny weather (air temperature down to -15°C), leading to on average 2-3 $^{\circ}\text{C}$ lower water temperature than in 2007-2009. Temperature is known to have an effect on escape latency in animals (Webb, 1978; Preuss and Faber, 2003). Preuss and Faber (2003) found that cooling had contrasting effects on escape behaviour in goldfish, with negative effects on locomotor performance, latency and directionality, but with increased responsiveness, that was suggested to in part compensate for the reduced ability to escape. If the temperature has similar effects on herring, this factor may partly explain the avoidance reactions in 2010.

The fact that the school was observed in deeper water and closer to the bottom in the early pre-spawning period in 2010 could also be caused by the sunny weather leading to higher light levels in the water column. Herring are known to have a light-preferendum in order to avoid predators (Blaxter, 1985), and the sunny weather may explain why the school stayed so deep and might also have explain why the herring appeared to be more vigilant, as higher visibility would make them more vulnerable to visual predators. The school stayed closest to surface in 2007 and 2008, which could also be related to that there was ice covering the system during the surveys these years. An ice cover would have mitigated aerial attacks from sea birds (great cormorants) and air-breathing harbour seals and sea otters that were observed during the study and would also have led lower light levels.

The oxygen level in Lindåspollene was decreasing with increasing depth in 2007-2009, and below 60 m the level sunk to under 2 mg/L. In 2010 the oxygen level was more homogenous throughout the water column and over 5 mg/L even at the bottom of the deepest basin, Spjeldnesosen. This indicates that the bottom water had been exchanged with denser water from the outside fjord, brought in by the tidal currents and wind forces. An exchange of bottom water often takes place during cold winters in Lindåspollene (Lie and Dahl, 1981). The high oxygen level in deep waters could have allowed the school to stay deeper in 2010 than in the preceding years. In fact, the school most often seemed to stay above the oxycline the preceding years, which led the school to stay at shallower depths in 2007 and 2008, when the oxycline was at a relatively shallow depth. In 2009 the oxycline was deeper and the school also stayed a little deeper than in 2007 and 2008. This could indicate that the herring preferred to stay where the oxygen level was high.

It is at present not possible to determine which factor or factors that resulted in the deviating behaviour in 2010. Since the school seemed to behave more vigilant it seems likely that it is connected to predation pressure and school size.

4.4 Fidelity to the pre-spawning area

The herring school stayed within the same limited area of 7000 m² (155 m x 45 m) during the pre-spawning and spawning stages in all four years, except for five observations in 2010. This area was close to present and historical spawning grounds. Aggregations of herring in the same area and period have been observed before, all the way back to the seventies (Lie et al., 1978; Aksland, 1983; Langård et al., 2006), hence the herring appear to have a high fidelity to this area that may have persisted for a long time. The school have been reported to stay in the area 2-3 months prior to spawning (Lie et al., 1978; Langård et al., 2006). A number of herring stocks aggregate close to the spawning area for some time before actually moving on to the grounds to spawn. There has been a pre-spawning congregation of Norwegian spring spawning (NSS) herring just offshore lasting about a month before the fish move the final few kilometres into the coast to spawn (Baker, 1978; Aasen, 1982).

In the present study the school remained in the area for at least 22 days in 2007, 2 days in 2008 (only one survey), 1.5 months in 2009 and two months in 2010, both prior to and during spawning, the most crucial period of the year for herring. The pre-spawning area should therefore be expected to provide advantages related to spawning, predator protection and energy conservation.

The pre-spawning area is surrounded by historically known spawning grounds, as well as being close to the detected spawning grounds in the present study (~600 m). The proximity to suitable spawning substrate is thus presumably an important factor in deciding where to stay in the period prior to spawning. However, the long time spent in the pre-spawning area before and during spawning, could suggest that the choice of spawning ground in Lindåspollene is dependent on the location of the pre-spawning area and not the other way around. This is supported by historic spawning grounds that, although the locations varied, always were close to the pre-spawning area.

The choice of pre-spawning site could reflect properties that allow precautionary anti-predator behaviour. The pre-spawning area consists of a trench (~35 m deep) that leads directly to the depths of the largest basin, Spjeldnesosen (~90 m). This basin may function as an 'emergency exit' for herring in case they face a predator attack. Gadoids, harbour seals, sea otters and great cormorants are all potential herring predators in Lindåspollene. Herring have been reported to hide in deep trenches close

to the spawning ground during daytime to avoid visual predators (Runde, 2005; Skaret and Slotte, 2007), which shows that herring can adapt to topographic features and use them to their own advantage. Moreover, massive aggregations of overwintering herring in northern Norway stay deep during the day to avoid killer whales that pose an imminent threat (Nøttestad et al., 2002).

However, due to swimbladder compression at high pressure in deep waters that leads to loss of buoyancy, the herring should expend increasing amounts of energy with increasing depth, hence they should not stay deeper than necessary. Although difficult to measure and compare, the predation pressure is likely lower in Lindåspollene than at coastal spawning grounds of the NSS herring (Toresen, 1991; Høines and Bergstad, 1999; Runde, 2005). Thus they appear to take a precautionary approach by staying in a place where they have direct access to the deepest basin, that could function as an escape route rather than a 'hiding place' as seen in other studies (Nøttestad et al. 2002; Runde, 2005; Skaret and Slotte, 2007).

The relative stationary and restricted of school swimming within a limited area means that the herring spent little energy, thus having more to allocate to reproduction. Langård et al. (2006) observed overwintering herring in Lindåspollene that swam with extended pectoral and pelvic fins, permitting gliding behaviour and thus slower descent. Overwintering herring and sprat (*Sprattus sprattus*) have been observed to perform a 'rise and glide' type of behaviour, presumably to avoid sinking in an energetically efficient manner (Huse and Ona, 1996; Kaartvedt et al., 2009).

After spawning had commenced and the school had moved down to the bottom, the school was 50 % of the time observed in close contact or within 10 m of a submerged water pipeline. Pelagic fish are known to associate with objects or topographic structures in the ocean (Fréon and Dagorn, 2000; Castro et al., 2001), and so-called fish aggregating devices (FADs) have been widely deployed to attract and concentrate tropical pelagic fish for the purpose of catching them (Fonteneau et al., 2000). The reason why fish are attracted to FADs are not completely understood (Castro et al., 2001; Girard et al., 2007). The three main hypotheses are 1) FADs protects against predators, 2) FADs serves as reference points and 3) FADs serves as meeting points (Castro et al., 2001). It seems unlikely that the herring school was hiding from predators by staying close to the water pipeline. The location of the pipeline was in the direction of the spawning ground, and it might have been used as a reference point during spawning, to guide horizontal migrations of herring to the spawning ground and back.

The meeting point hypothesis suggests that fish use FADs to increase the encounter rate with other fish to form schools (Fréon and Dagorn, 2000). This hypothesis is supported by observations of larger tuna schools in the vicinity of FADs than elsewhere (Fonteneu, 1992). Moreover, Soria et al. (2009) observed that bigeye scat (*Selar crumenophthalmus*) left FADs in larger groups than those that they had arrived in, the FADs thus enhancing the schooling behaviour. In the same manner as the pipeline, the topographic features of the pre-spawning area (the steep trench sidewall) could in fact function as such a meeting point. Stationary echogram recordings obtained by the lander revealed that the school dispersed during the night, and tagging experiments conducted during the same surveys as the present study (Langård et al., unpublished) showed that individuals, possibly in small groups, split from and rejoined with the main school, possibly to assess the surroundings for suitable spawning areas.

Herring is suggested to be a conservative species (Fernö et al., 1998) that appears to develop references for spawning and wintering grounds, and return for a number of years even if the environment gradually changes. This could imply that the current pre-spawning area in Lindåspollene was a choice made for many years ago, based on past environmental conditions, and the reason for returning could thus be based on tradition. Recruits can in principal make new choices, but in practice they will follow older herring to traditional spawning and overwintering grounds (McQuinn, 1997). The only time recruits break the tradition is when there is scarcity of older individuals, if a large proportion of recruits dominates the population, or if the distribution of the recruits are abnormal, and thereby spatially separated from the older herring (Corten, 2001; Huse et al., 2002; Huse et al., 2010). This could mean that traditions play a role in why the herring population in Lindåspollene return to the same pre-spawning area every year.

The term 'homing' among fishes is often limited to describe the return of spawning adults to the place where they were hatched (Stott et al., 1963). A more general definition of homing was proposed by Gerking (1959): 'the choice that a fish makes between returning to a place formerly occupied instead of going to other equally probable places.'

The herring school in the present study was observed at the same location in the pre-spawning and spawning period all four years within an area of only 0.005 km², which fits with the definition proposed by Gerking (1959). Although we cannot directly prove that the same individuals were returning to the pre-spawning area in the study years, it is extremely unlikely that no herring were returning, meaning that none of the herring that was present in the pre-spawning area in 2008 were present in 2009. Therefore I feel confident that the returning of Lindås herring to the same location prior to spawning

every year is a form of homing behaviour based on learning. Previous studies in Lindåspollene all the way back to the 1970s also reports that the herring was staying in the same area in this period (Lie et al., 1978; Aksland, 1983; Langård et al., 2006), which could mean that this homing pattern has prevailed in over three decades. It is also widely accepted that herring tend to spawn on the same spawning grounds in subsequent years (homing). Both Pacific herring (Hourston, 1982) and Atlantic herring (Wheeler and Winters, 1984) have high homing rates.

4.5 School dynamic patterns in the pre-spawning and spawning periods

4.5.1 Horizontal and vertical dynamics

In the early pre-spawning period, the herring was generally aggregated in a single school within pre-spawning area A (**Figure 3.5**). Here the school stayed, with few exceptions, in the pelagic, most often keeping a distance of at least 8 m to the surface. This may reflect avoidance from diving seabirds (great cormorants) (Blaxter et al., 1985), as well as an avoidance of the light surface where the herring is more vulnerable to visual predators like gadoids, harbour seals and sea otters. The school predominantly kept an average distance of 8 m also to the bottom, but it was also observed quite close to it. About 70 % of the gadoids adjacent to the school as seen on echogram recordings were staying below the school.

The school's distance to the bottom was on average significantly higher when gadoid predators were close to the school. The demersal zone has generally been assumed to a high risk habitat due to bottom dwelling gadoids (Axelsen et al., 2000; Runde, 2005; Skaret and Slotte, 2007; Johnsen and Skaret, 2008). The present study provides the first empirical support for this assumption as the herring was adjusting their bottom distance in relation to the presence or absence of predators.

Just prior to and during spawning the school also stayed in pre-spawning area B, an area somewhat shallower (~25 m deep) than pre-spawning area A, and closer to the main spawning ground of 2008-2010 (~600 m). However, the school was also observed in the opposite end of pre-spawning area A, thus it seems that the school became spatially more active just before and during spawning. This might indicate conflicts among ripe herring seeking towards the spawning ground and pre-spawners preferring to stay closer to pre-spawning area A that probably is a safer place closer to large depths.

In 2009 a small group of herring remained in the pelagic environment within pre-spawning area A, when the majority of fish moved to the bottom. This indicates conflicting motivations between pre-spawning individuals preferring to stay in the pelagic environment and ripening herring attracted to the more unsafe bottom. Similar processes have been observed in earlier studies (Axelsen et al., 2000; Johnsen

and Skaret, 2008). During the present study we were not able to take samples of the two components, and neither did Axelsen et al. (2000). However, Johnsen and Skaret (2008) found significantly more pre and post-spawners in the upper part of the school. This part was connected to the lower part, probably by descending ripening herring and ascending post-spawners.

The main school stayed at the bottom a minimum of 9 days in 2009 and 48 days in 2010, ~600 m from the main spawning ground, and this long period indicates that pre-spawners were staying the bottom together with ripe individuals. Previous studies from spawning areas have suggested that the herring, although they must spawn at the bottom, minimize its time spent there, mainly due to a high abundance of predators (Axelsen et al., 2000; Johnsen and Skaret, 2008). In Lindåspollene, however, the predation pressure is likely lower than at coastal spawning grounds, where it has been found to be high (Toresen, 1991; Høines and Bergstad, 1999; Runde, 2005). Hence staying on the bottom, even for an extended period of time, may not be that critical. The predation pressure is, however, difficult to measure, especially in the sea, and a quantitative comparison between spawning grounds is thus not possible.

Another possible reason for individuals to stay at the bottom for such a long time could be related to school size, thus explaining that only one main school was observed during this study. In a school model developed by Vabø and Skaret (2008), they underlined that the number of individuals is in itself an important factor in determining the behaviour of a school. The present study might provide a good example of this effect during spawning: although the estimates were rough, the school was most probably larger in 2009 than in 2010, due to either recruitment or immigration of foreign herring. This could be the reason why the school split and one part remained in the pelagic in 2009, while in 2010 all the fish seemed to be contained within the same demersal school. The herring was, however, hard to detect in 2010, which could have affected both the biomass estimates and that we did not locate a pelagic school component this year.

But why would a large group of pre-spawners generally follow ripe herring, as indicated by the long duration of spawning? Pre-spawning herring could have followed in order not to break up the school. Keeping together in a school at the bottom could be better for individual herring than staying in a smaller separate pelagic school. The smaller group of herring remaining in the pelagic in 2009 may have consisted of less ripe herring than the herring within the main school at the bottom.

4.5.2 Vertical school extent, packing density and school dynamic turbulence

The vertical extent of the main school seemed to decrease as spawning approached in 2007 and during spawning in 2009 and 2010, compared to the early pre-spawning period. This could have been caused by a reduction of the number of fish, as some individuals might leave the school to feed in smaller groups after having spawned. The stomach samples from 2008 indicated that some herring (6 %) started feeding after spawning commenced, and half of them had spawned. In 2009 a smaller group of herring remained in the pelagic when the main school moved to the bottom and this should also reduce the vertical extent.

Earlier studies have suggested that the vertical extent and shape could reflect motivational differences between individuals within the school. Fish schools are normally horizontally elongated (Wrzesinski, 1972; Misund, 1993; Nøttestad et al., 1996), but vertical extended shapes have been observed on the spawning ground. In a study by Axelsen et al. (2000) on a herring spawning ground, a cylindrical school shape that was stretched out in the vertical plane dominated the observations, and was interpreted to represent a motivational conflict within the school between ripening fish attracted towards the bottom, and early maturing fish preferring to remain in the pelagic. The fact that the vertical of the main school decreased towards spawning, and that the shape remained elongated in the horizontal dimension increasing the contact surface with the bottom, suggests that the attraction towards bottom was mutual between individuals within the school. Since pre-spawners most certainly were present within the school as indicated by the long stay at the bottom, this might imply that the attraction towards bottom is initiated some time before an individual is ripe.

(Skaret et al., 2003) found that pre-spawners followed ripe herring to the bottom and actually dominated the demersal gillnet samples. They suggested that determined behaviour of ripe herring moving to the bottom may influence the pre-spawning individuals to follow in connection with the collective behaviour of the school (see also Fernö et al., 1998; Axelsen et al., 2000; Huse et al., 2002). Skaret et al. (2003) also suggested that the ripening process could be accelerated by staying in close contact with ripening individuals, due to active release of pheromones.

The packing density generally seemed to be higher during spawning than pre-spawning. This could represent precautionary behaviour in a riskier habitat (bottom) (Skaret and Slotte, 2007), since adhering more closely to conspecifics enables the herring to take better advantage of cooperative escape tactics (Pitcher and Parrish, 1993). The packing density also increased in the late pre-spawning period in 2007,

when the school seemed to have split in two sub-schools staying next to each other. This could be to compensate for the increased predation risk caused by the school splitting (Nøttestad et al., 2002).

The school dynamic turbulence index was quantified through a normalized function merging the circularity and roughness (dispersion of acoustic energy) of the school. To my knowledge, this is the first study where the turbulence index has been investigated acoustically before and during spawning. In the pre-spawning period the turbulence index was low, while it increased in the late pre-spawning and early spawning period, before decreasing in the late spawning period.

It is reasonable to assume that a school with low conflict level among the individuals shows low dynamic turbulence and vice versa. The fact that the vertical extent of the school did not increase when spawning commenced, but rather decreased, indicates that the school dynamic turbulence index did not reflect conflicts between pre-spawning/post-spawning individuals searching for the safer pelagic and ripe individuals searching towards the bottom. However, the increase in school dynamic turbulence could reflect conflicts between ripe individuals searching horizontally towards the spawning ground, and pre and post-spawners wanting to remain close to the depths of the 'emergency exit' Spjeldnesosen.

The presence of predators did not affect the turbulence index. Predator interference could either stabilize the school or cause turbulence. For instance, if the school is approached by a predator individuals could react by swimming closer together and get more polarized, which would decrease the school dynamic turbulence. However, if a predator attacks, the dynamic level should increase, due to the fact that individual herring closest to attacking predator(s) would actively avoid it, thereby influencing and disturbing the school dynamic turbulence.

4.6 Spawning duration

Biological samples of herring and acoustic observations indicated that herring spawning in Lindåspollene extends over a period of 1-4 weeks, which is substantially longer than previously been found at school level (one day to several days) (Axelsen et al., 2000; Nøttestad et al, 1996). Even though this study followed herring on school level, it was at the same time followed on a population level, since the whole adult population seemed to aggregate into only one school as a result of a small population size. The fish had then no opportunity to join other school with conspecifics of similar size and maturity stage. Large and old fish usually spawn earlier than smaller fish (Slotte, 1999b), and fish organize themselves in schools with conspecifics of similar size (Pitcher and Parrish, 1993) if possible. The spawning duration in

Lindåspollene is therefore more comparable to that reported on the population level (Johannessen et al., 1995) than to that at the school level (Nøttestad et al., 1996; Axelsen et al., 2000).

The school stayed on the bottom for at least 9 and 48 days during spawning in 2009 and 2010, respectively. The predation pressure in Lindåspollene is probably lower than at the coastal spawning grounds of the NSS herring due to the concentration of several predator types along the coast during the herring pre-spawning and spawning period (Høines and Bergstad, 1999; Runde, 2005). Hence, individuals organizing in schools with conspecifics of similar gonad maturation stages could be crucial on the coastal spawning grounds in order to minimize the time spent on the bottom, whereas such time constraints may be much weaker for the herring in Lindåspollene.

4.7 Concluding remarks

- 1.** The local herring in Lindåspollene seem to have adapted to a relatively small resident population size and the prevailing predation pressure by aggregating into only one school just prior to and during spawning, which indicate a risk-averse spawning strategy.
- 2.** Although the herring seemed to be more vigilant in 2010, the school dynamic patterns before and during spawning were similar in all four study years.
- 3.** The school stayed in the same, small area during pre-spawning and spawning, indicating strong site fidelity. This area is close to present and historical spawning grounds and adjacent to the deepest basin in the system that may function as an 'emergency exit', emphasising the precautionary approach adapted by the herring.
- 4.** The school adjusted the distance to the bottom according to the presence or absence of demersal predators (gadoids).
- 5.** As spawning commenced the school moved down to the bottom and stayed there for a minimum of 9 days in 2009 and 48 days in 2010. The spawning processes in Lindåspollene thus take place at a much lower pace than in oceanic waters, and the predation pressure in Lindåspollene is likely comparatively low compared to the coastal spawning grounds, where it can be rather high (Toresen, 1991; Høines and Bergstad, 1999; Runde, 2005).

6. In 2009 a small group of herring remained in the pelagic when the school settled on the bottom, which may reflect motivational differences between ripe individuals searching towards the bottom and pre-spawners preferring the pelagic environment.

7. The extended time spent on the bottom and for spawning indicates that pre-spawners followed ripe herring down. The vertical school extent decreased as it settled on the bottom, which could mean that also pre-spawners were attracted to the bottom.

8. The school packing density increased towards the time of spawning as the school settled on the bottom. This could be another precautionary action when moving into a more hazardous habitat than the pelagic.

9. The school dynamic turbulence index was highest as spawning commenced. This might reflect conflicting motivations between pre-spawning and ripe herring. Ripe herring may have been attracted to the adjacent shallow spawning ground, while pre-spawners preferred to stay close to the 'emergency exit'.

The spawning strategy of the herring population in Lindåspollene seems to have been shaped primarily by the small population size, the low predation pressure and the collective processes crucial to successful reproduction and survival.

The herring spawned in very shallow waters, where the manoeuvrability and escape possibilities are reduced, and where they are more vulnerable to predation. Hence they should not stay directly on the spawning ground for a prolonged period of time. That could also attract more predators to the spawning area that might forage on the eggs. The pre-spawning area may therefore best be understood as a 'base camp', as it is close to the shallow spawning ground, but at the same time adjacent to the deepest basin of the system. I suggest that herring in Lindåspollene spawn in waves, i.e. in a 'split-off system' where small groups split off like droplets from the main school in order to spawn (Vabø and Skaret, 2008). In Lindåspollene this would mean that they leave the school and migrate to the spawning grounds that in 2008-2010 was ~600 m away, before returning to the 'base camp' after spawning.

To aggregate into a single main school is probably a well-functioning anti-predator tactic. However, humans can exploit this aggregative behaviour of fish, and the Lindås herring may thus be highly vulnerable to fishing in the pre-spawning period, a factor that should be taken into account in the management of small, local herring populations.

The school dynamic patterns of the Lindås herring before and during spawning resemble herring in large marine ecosystems, such as the Norwegian spring spawning herring. Small-scale studies performed under controllable conditions such as in Lindåspollene, can provide crucial knowledge about how spatial preferences and dynamics of schooling fish are influenced by environmental factors, predation pressure and their internal states, and it is far more cost-efficient than research on any oceanic populations.

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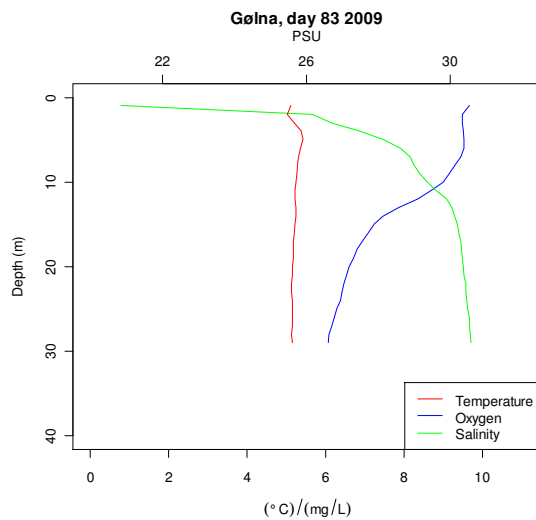
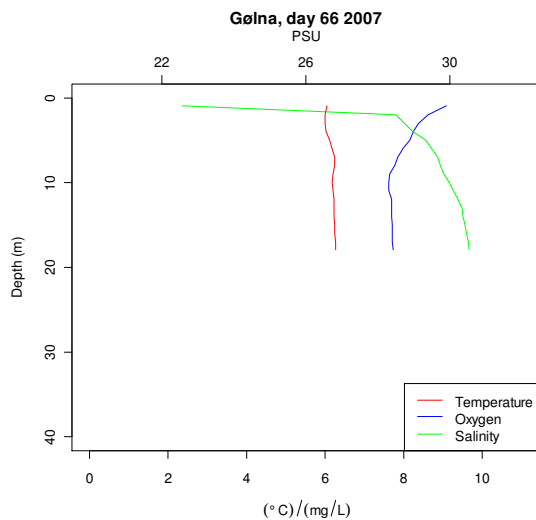
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Appendix

Appendix A

Table A-1: Temperature (°C), oxygen level (mg/L) and salinity (PSU) over the vertical school extent, at the bottom and at the surface in the different periods in all years.

Year	Period	Temperature						Oxygen						Salinity					
		School		surface		Bottom		School		surface		Bottom		School		surface		Bottom	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
2007	PI	6.70	0.29	6.01	0.19	5.64	0.05	5.66	1.35	8.31	0.08	3.22	0.05	30.24	0.79	27.60	0.74	31.20	0.23
	PII	6.39	0.05	6.05	0.01	5.11	0.29	7.22	0.22	8.30	0.02	1.21	1.67	30.54	0.08	29.01	0.05	31.29	0.20
	SI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	SII	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2008	PI	5.85	0.27	4.85	0.24	6.20	0.23	7.97	0.59	9.30	0.20	3.93	0.61	29.76	0.35	27.15	0.37	31.01	0.06
	PII	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	SI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	SII	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2009	PI	5.02	0.11	4.62	0.25	5.18	0.16	5.93	0.37	6.67	0.09	4.04	2.36	30.77	0.08	29.99	0.17	31.11	0.27
	PII	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	SI	5.20	0.12	5.39	0.17	5.18	0.04	6.22	0.81	9.49	0.00	3.35	2.98	30.64	0.27	27.69	0.73	30.95	0.42
	SII	5.16	0.02	5.40	0.18	5.18	0.04	6.70	0.34	9.49	0.01	3.18	3.17	30.57	0.25	27.73	0.77	30.98	0.45
2010	PI	3.33	0.23	2.24	0.14	3.26	0.23	6.06	0.55	6.53	0.81	6.11	0.42	29.96	2.37	29.11	3.23	30.08	2.23
	PII	3.82	1.15	3.57	1.22	3.08	0.06	7.23	0.65	8.50	1.00	7.20	0.38	31.19	0.67	28.45	1.09	30.48	1.98
	SI	3.31	0.29	4.40	0.25	3.29	0.35	7.83	0.19	9.16	0.15	7.48	0.10	31.70	0.27	28.60	0.95	31.75	0.26
	SII	3.11	0.03	5.55	0.47	3.10	0.01	7.62	0.86	9.40	1.09	8.54	1.86	31.64	0.03	29.01	0.05	31.68	0.01



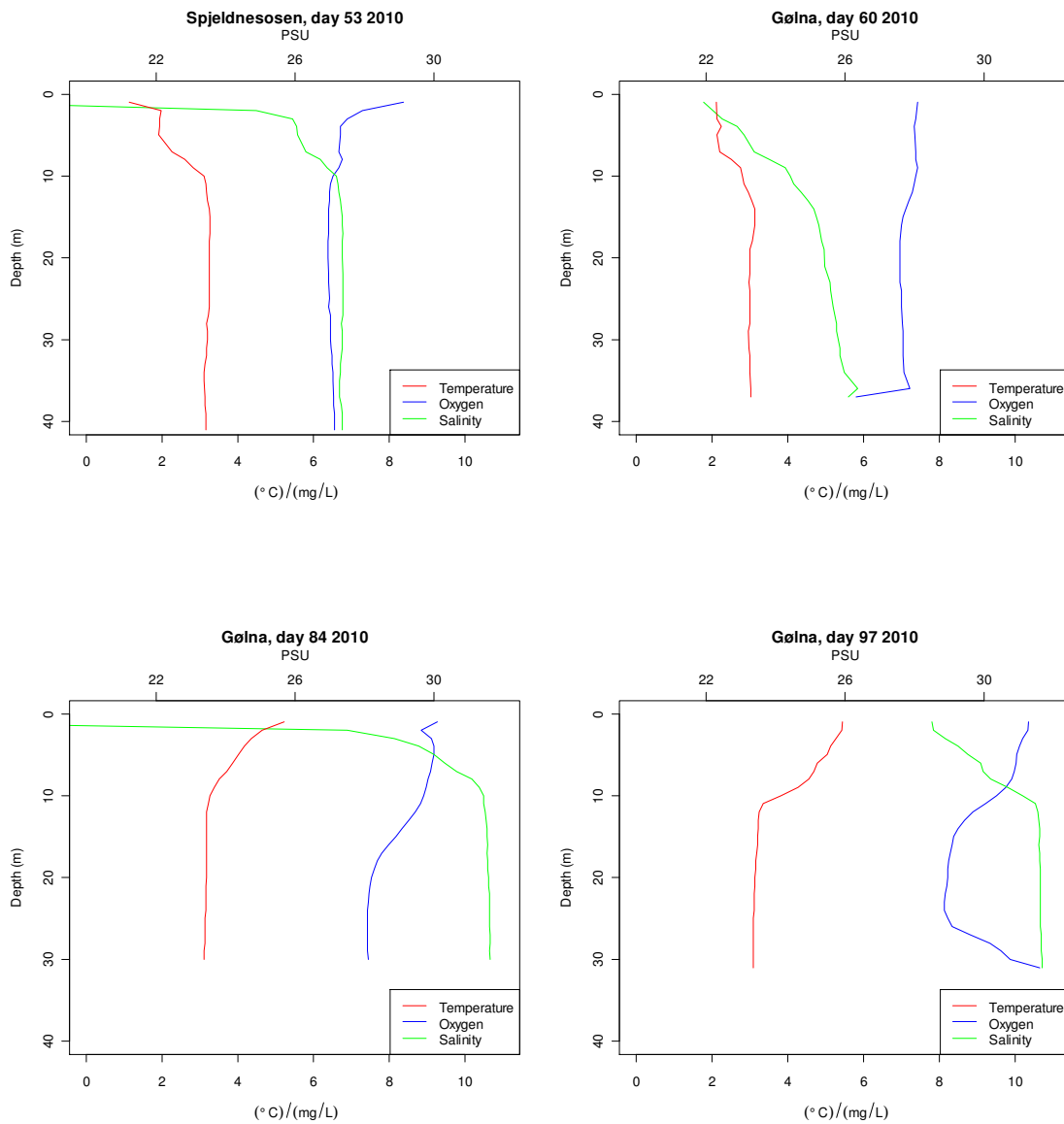


Figure A-1: CTD-profiles each survey during the study (except the profiles in the results chapter).

Appendix B

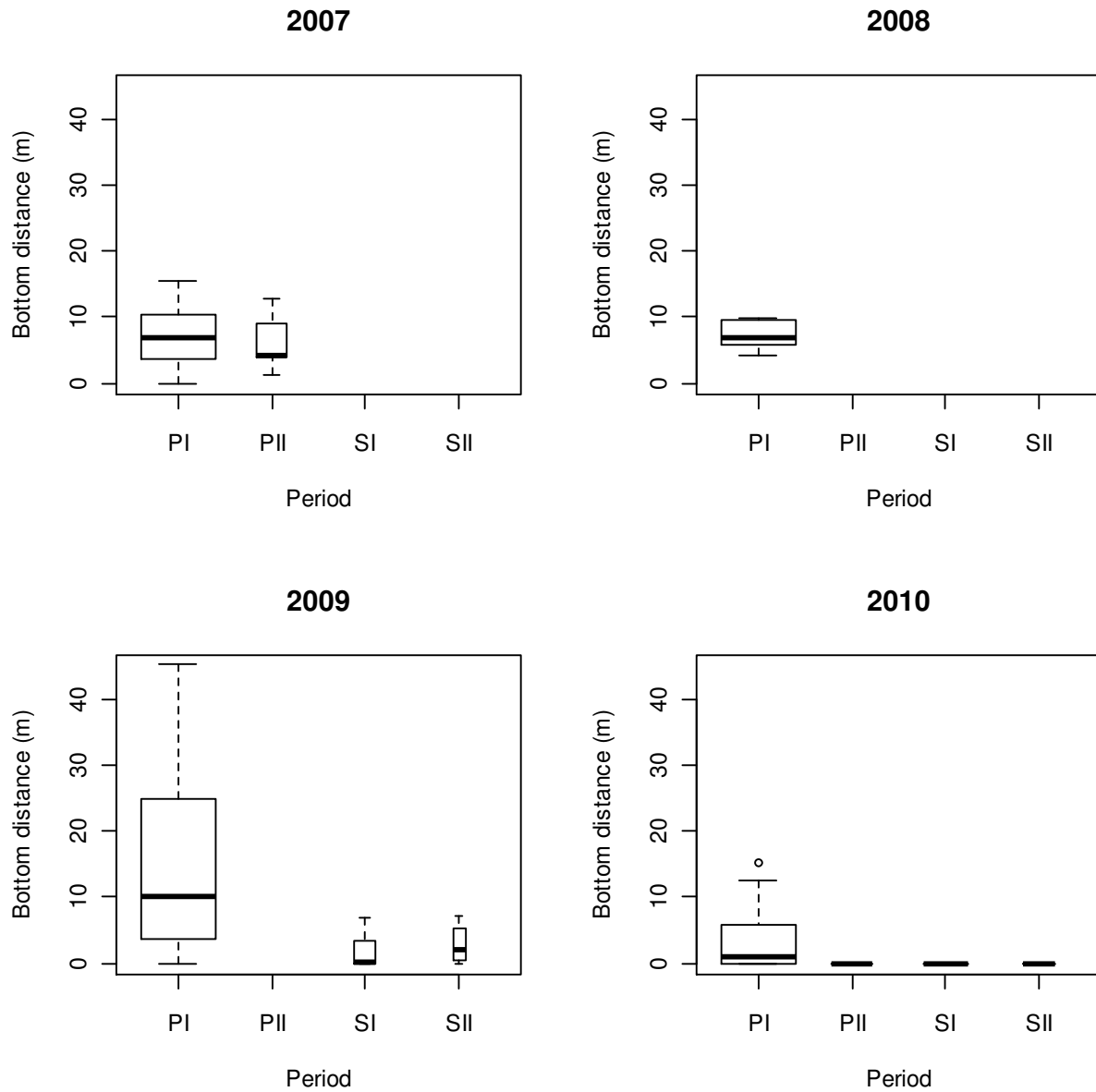


Figure B-1: The distance from the main school to the bottom for the different periods in 2007-2010.

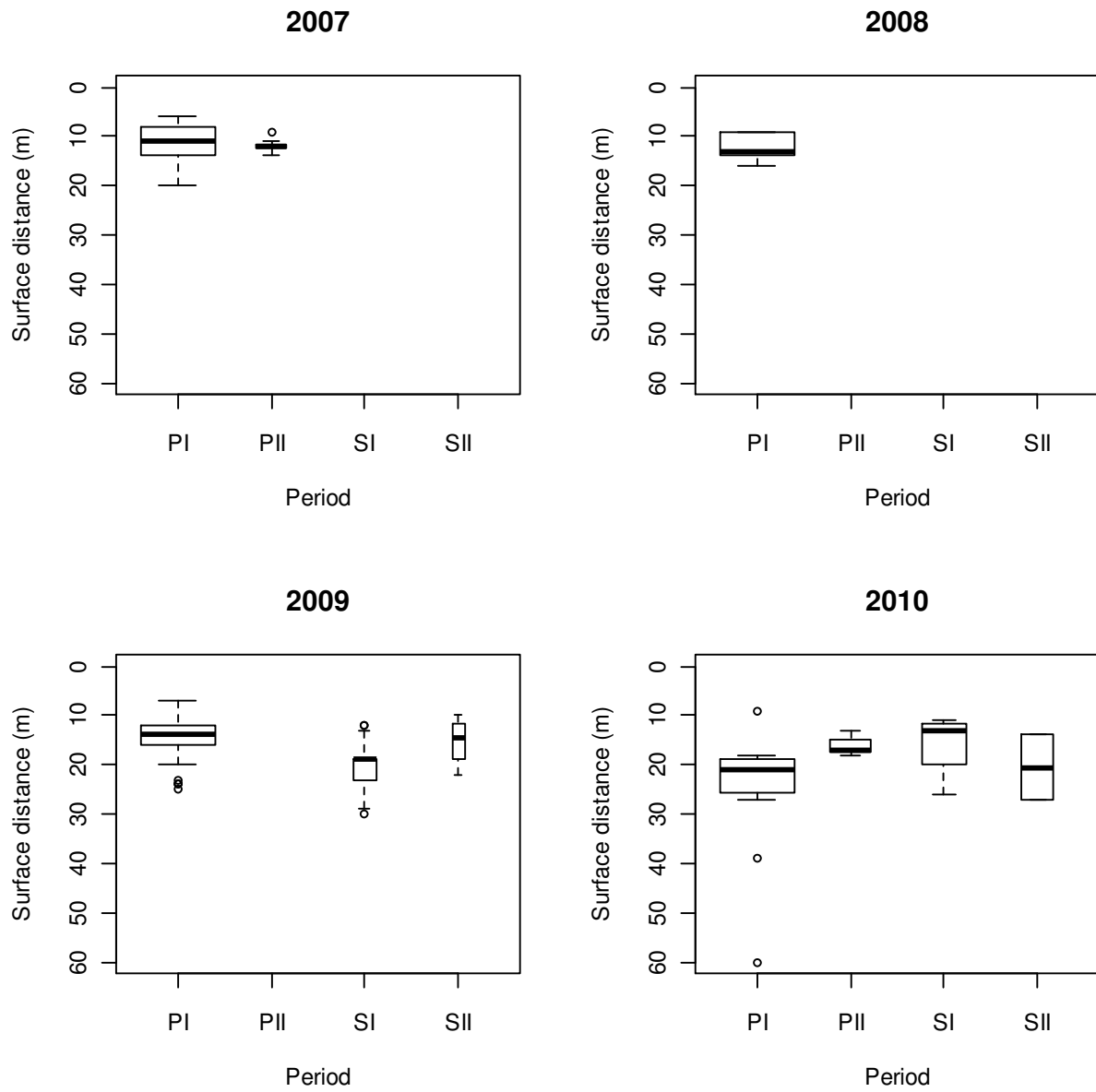


Figure B-2: The distance from the main school to the surface in the different periods in 2007-2010.

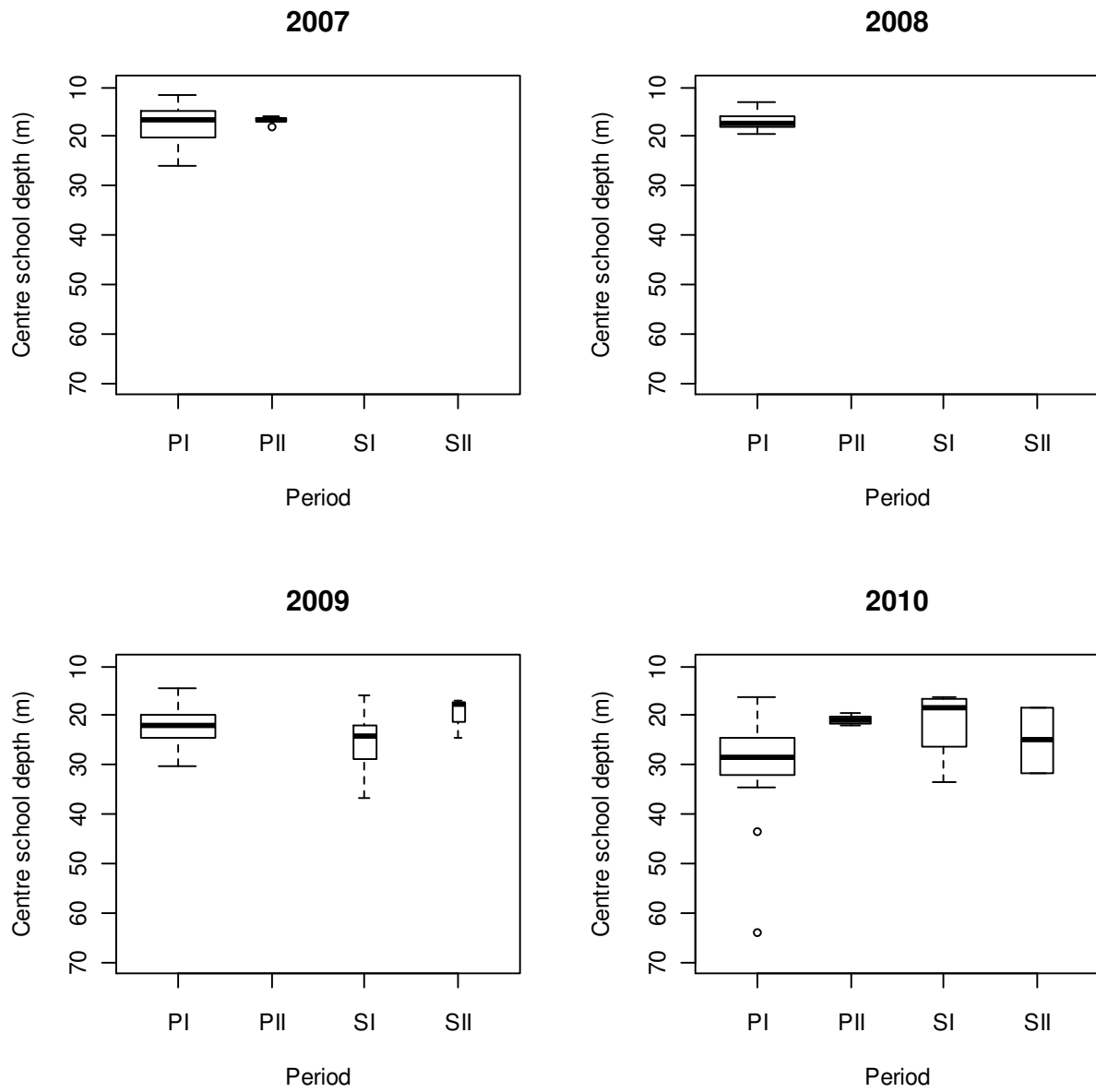


Figure B-3: The centre school school depth in the different periods I 2007-2010.

Appendix C

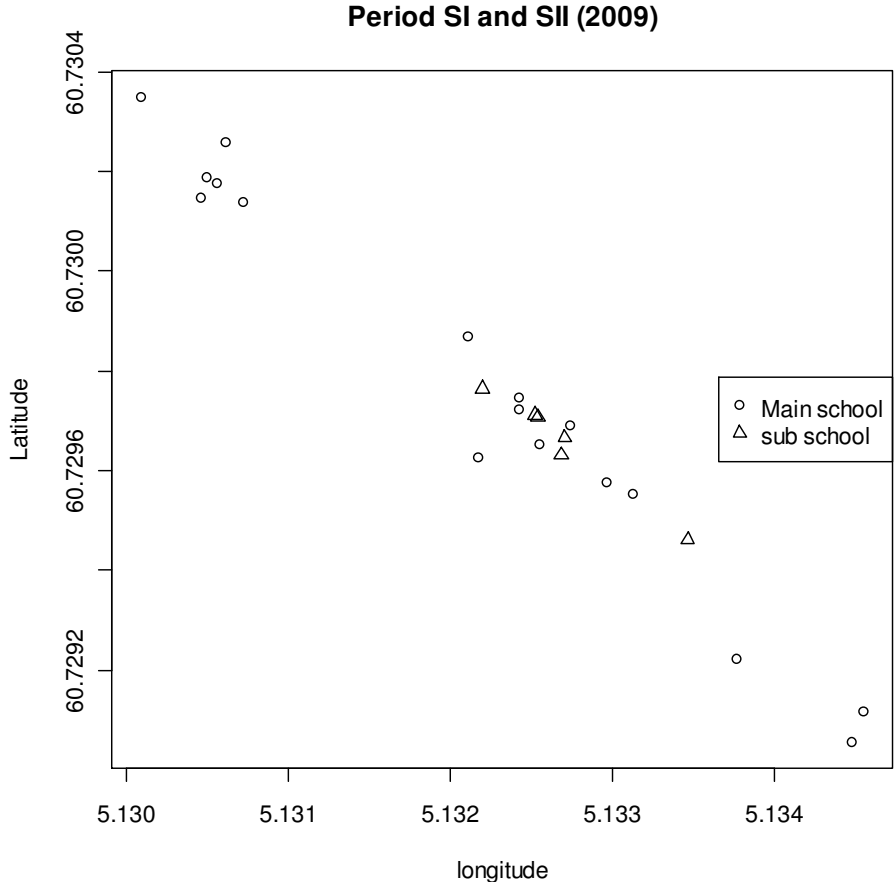


Figure C-1: The horizontal position of the demersal main school and the pelagic sub-school during spawning in 2009.

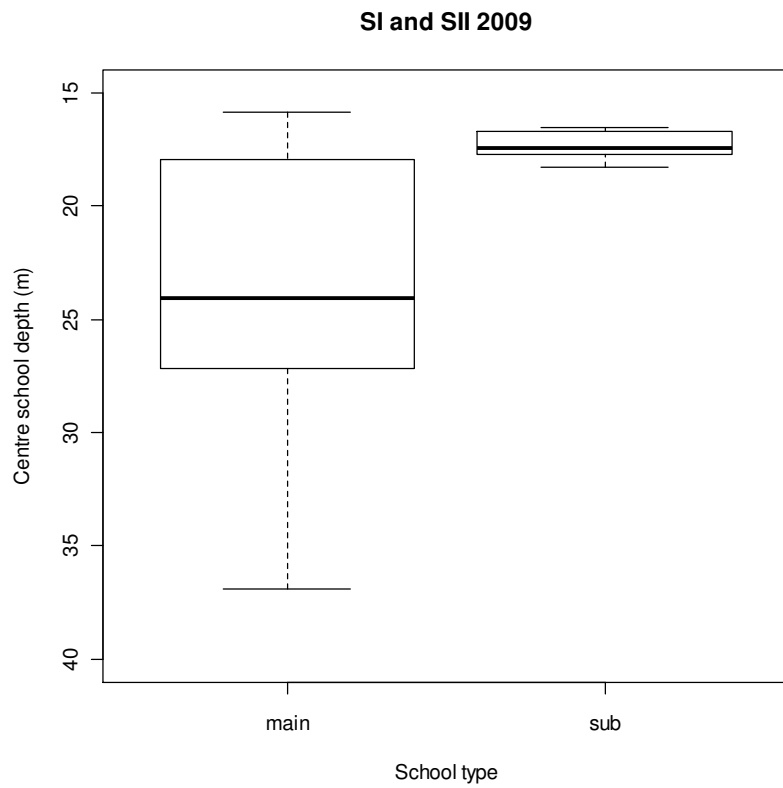


Figure C-2: The difference in centre school depth between the main school and sub-school during spawning in 2009.

Appendix D

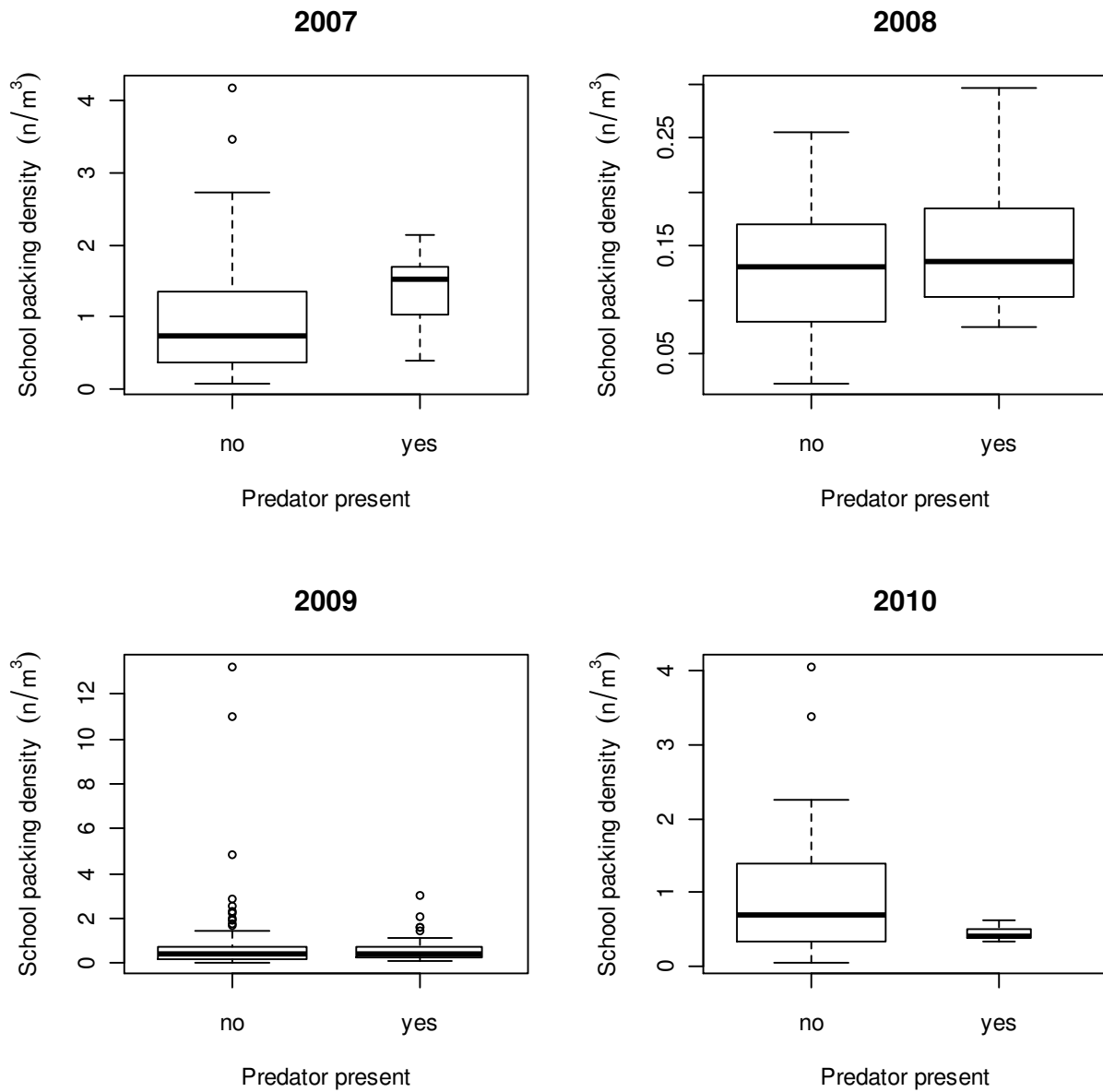


Figure D-1: Predator presence versus the school packing density (n/m^3) in 2007-2010.