



Fecundity of flounder, *Pleuronectes flesus*, in the Baltic Sea – Reproductive strategies in two sympatric populations

Anders Nissling*, Gry Dahlman

Ar Research Station, Gotland University, SE-624 60 Lärbo, Sweden

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ABSTRACT

Two sympatric flounder populations with different reproductive strategies, offshore spawning at 10–20 psu producing pelagic eggs and coastal spawning at 5–7 psu with demersal eggs respectively, inhabit the brackish water Baltic Sea. Salinity governs the reproductive success by irregular saline water inflows and hence stock abundance and distribution. The potential fecundity (the standing stock of vitellogenic oocytes in the pre-spawning ovary) was assessed for fish sampled at five locations (two for offshore spawners and three for coastal spawners) along the salinity gradient (ICES SD 25, 27/28, 28 and 29). Multiple linear regression analysis resulted in r^2 -values of 0.698–0.894 for the respective sampling location with somatic weight or total fish length as the main predictor, and otolith weight (proxy for age) and oocyte density (by gravimetric counting) as additional predictors. Analysis by univariate regressions using GLM revealed significantly higher fecundity for coastal spawning- than offshore spawning flounder (~69% more oocytes for an intermediate sized fish) but no intra-population differences. Similarly, gonad dry weight was significantly higher for coastal spawning flounder. Further, growth estimations indicated higher growth in offshore spawning- than in coastal spawning flounder suggesting that the coastal spawning population allocate relatively more resources into reproductive growth than somatic, potentially a result of strong selection for high fecundity of flounder producing demersal eggs due to poor egg survival for this spawning strategy. Earlier studies on fecundity of Baltic flounder are reviewed and discussed with consideration of inter-population differences questioning the idea of in general higher fecundity of flounder in the Baltic Sea.

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1. Introduction

Depending on variability in environmental conditions affecting the likelihood of progeny survival there is a trade off between investment in gonad production vs. somatic growth influencing current vs. future reproductive potential, and between production of few but large eggs or many but small eggs, as well as between few or many egg batches (e.g. Rijnsdorp and Vingerhoed, 1994; Wootton, 1998; Stearns, 2000; Kjesbu and Witthames, 2007). The majority of commercial marine fishes, including flounder, *Pleuronectes flesus*, display a high longevity and batch spawning. Obviously, high egg production over a long period of time increases fitness in response to varying conditions during the spawning season (cf. window of survival) and between years (often several years between strong year classes; e.g. Hjort, 1914; Cushing, 1990). Accordingly, in an environment with varying environmental conditions, selection for many but small eggs in several batches over few but large eggs spawned in few batches can be expected.

The Baltic Sea, a large brackish water area, is inhabited by both marine and freshwater species. Water exchange is restricted by shallow straights in the Sound and the Belt-Seas (ICES SD 22 and 23). Accordingly, salinity in the surface layer decreases from ~8 psu in the southwest (SD 24) to merely ~3 psu in the north (SD 31) (ICES SDs shown in Fig. 1). Moreover, salinity varies vertically with a halocline at 50–70 m depth in the deep basins in SD 24, 25, 26 and 28 with a salinity ranging between ~10 and ~20 psu. Exchange between the surface and bottom water is restricted and renewal of the bottom water occur mainly following irregular inflows of saline water from the North Sea (the Kattegat–Skagerrak area). Stagnant conditions in the bottom water accompanied with decreasing salinity and oxygen conditions may prevail for years (Franck et al., 1987; Matthäus and Lass, 1995). Thus, the system is strongly affected by irregular major inflow events determining e.g. the salinity and hence species composition with effects on ecosystem level (e.g. Segerstråle, 1969; Voipio, 1981). Hence, depending on spatial (south–north) and temporal (inflow events) variability in salinity conditions, the reproductive success varies, affecting species, flounder included, abundance and distribution (e.g. Ojaveer et al., 1985; Drews, 1999; Nissling et al., 2002).

For marine fishes adapting to the Baltic Sea following the last glacial period (10,000 years before present; see Voipio, 1981), salinity represents a major evolutionary force. Species that succeeded to

* Corresponding author. Tel.: +46 498 224630.

E-mail address: anders.nissling@hgo.se (A. Nissling).

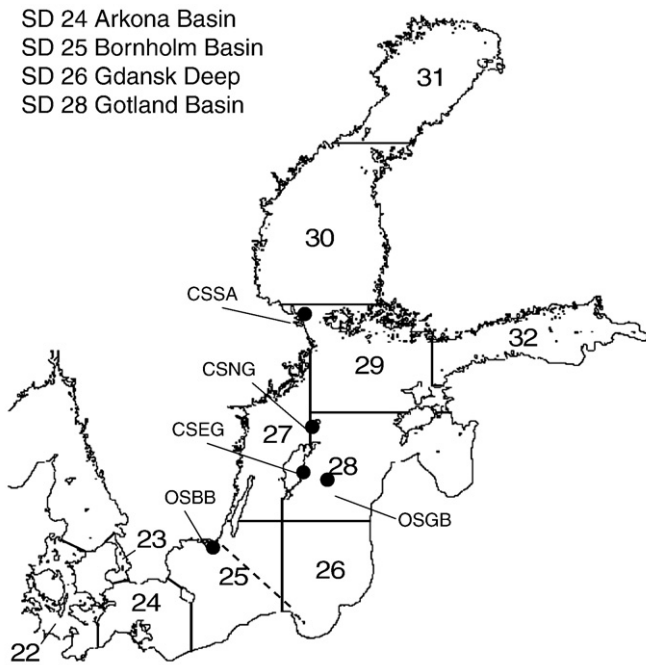


Fig. 1. The Baltic Sea with ICES subdivisions (SD) and positions of sampling locations; OSBB and OSGB (~53–90 m depth), and CSEG, CSNG and CSSA (~5–13 m depth). Dashed line indicates the distribution of coastal spawning flounder in the inner Baltic Sea according to Molander (1954).

colonise the Baltic Sea display different salinity requirements compared to their counterparts outside the Baltic Sea in terms of potential for fertilisation and egg development, i.e. form specific populations. Adaptations to the less saline conditions in the Baltic Sea involve changes in egg specific gravity by increased water content allowing for neutrally buoyancy for fish spawning pelagic eggs (e.g. Thorsen et al., 1996; Nissling et al., 2002), but additionally the strategy of producing demersal eggs has evolved (see Lönning and Solemdal, 1972).

Flounder is the most common flatfish in the Baltic Sea, distributed in almost all parts of the Baltic except for in the eastern part of the Gulf of Finland (SD 32) and the Gulf of Bothnia (SD 31). Both types of spawning strategy occur; flounder producing pelagic eggs occur in SD 24 and 25 but also in SD 26 and 28, whereas flounder producing demersal eggs inhabit SD 25–30 and SD 32 (see Sandman, 1906; Solemdal, 1971; Nissling et al., 2002). Fish using the respective spawning strategy share feeding areas in coastal waters during summer–autumn but utilize different habitats for spawning; pelagic eggs at higher salinities in the deep basins vs. demersal eggs at low salinities in coastal areas and on banks, i.e. form two sympatric populations. Despite similar egg dry weights (see figures in Solemdal, 1970) egg characteristics of the respective population differ in terms of egg diameter and specific gravity; higher egg diameter and lower specific gravity for flounder with pelagic eggs allowing for neutral egg buoyancy at 15.2 ± 1.9 (sd) psu in SD 25 and 13.9 ± 1.5 psu in SD 28 (Nissling et al., 2002). Further, spermatozoa mobility at different salinities differs between the populations; spermatozoa for the flounder population with demersal eggs showing mobility also at low salinities (≥ 3 –4 psu) (Nissling et al., 2002). Recent investigations have shown significant genetic differences between the two flounder populations in the Baltic Sea (Florin et al., 2005; Hemmer-Hansen et al., 2007). Occurrence of hybridisation is unknown.

Fecundity may vary not only between species but among populations within species. E.g. Rijnsdorp and Vingerhoed (1994) found a latitudinal trend in fecundity in common sole, *Solea solea*, partly explained by a reversed trend in egg size. Bagenal (1966), studying

plaice, *Pleuronectes platessa*, suggested that size specific annual fecundity varies, with lower fecundity in the centre and higher fecundity to the edges of the distribution. However, this pattern has been questioned by Rijnsdorp (1991) and Rijnsdorp and Witthames (2005), who argue that fecundity of plaice is fairly constant but with the Baltic Sea as an exception with considerably higher fecundity, as suggested by Kändler and Pirwitz (1957). Brackish water and varying salinity conditions of the Baltic Sea may therefore involve selection for high fecundity. Hence, as spawning of flounder in the Baltic Sea occurs along a salinity gradient influencing the reproductive success (e.g. Nissling et al., 2002) the number of eggs produced can be assumed to vary between populations/areas to optimise fitness.

The present study includes flounder from the offshore spawning population (pelagic eggs) spawning at ~13–18 psu and at ~10–12 psu and fish from the coastal spawning population (demersal eggs) spawning at ~6–7 psu, with the main aim to evaluate potential differences in fecundity between the populations. The potential fecundity was assessed, i.e. the standing stock of vitellogenic oocytes in the pre-spawning ovary, as opposed to “realized fecundity” (the number of eggs spawned). To reduce the risk of biased data from differences in maturity levels among fish potentially hampering comparisons of fecundity, data standardization (see Thorsen et al., 2006) was conducted by consideration of discrepancies in oocyte density (number of oocytes per gram ovary) among samples.

Fecundity of flounder in the Baltic Sea has been assessed previously (Kändler and Pirwitz, 1957; Ciegiewicz and Musial, 1964; Kuczyński and Zaporowski, 1992; Kosior et al., 1996), but, to our knowledge, this is the first time that fecundity has been estimated for both the offshore- and the coastal spawning population, i.e. allowing comparison of egg production between these sympatric populations.

2. Material and methods

Coastal spawning flounder were sampled at three locations, off Eastern Gotland [Coastal Spawning Eastern Gotland (CSEG); SD 28], Northern Gotland (CSNG; SD 27/28) and in Northern Stockholm archipelago (CSSA; SD 29), and offshore spawning flounder were sampled at two locations, the Bornholm Basin (OSBB; SD 25) and the Gotland Basin (OSGB; SD 28) (Fig. 1). Fish were caught with gill-nets (CSEG, CSNG and CSSA) or by trawling (OSBB and OSGB). The sampling was carried out shortly prior to the expected spawning period of flounder at the respective location; offshore spawning flounder commencing spawning somewhat earlier than coastal spawning flounder, and earlier spawning in the south compared to in the north, e.g. onset of spawning in March at OSBB and OSGB, from April at CSEG and CSNG and from May at CSSA (see Bagge, 1981; own observations) (Table 1). Fish from CSEG, CSNG and CSSA were caught in coastal areas at ~5–13 m depth and fish from OSBB and OSGB,

Table 1

Sampling locations, date and depth range of catches of coastal- and offshore spawning flounder *Pleuronectes flesus* in the present study.

Sampling location	Acronym	ICES SD	Positions	Date	Depth (m)
<i>Offshore spawners</i>					
Bornholm Basin	OSBB	25	N 55 44–55 51 E 15 33–16 28	March 16–20 2006	~53–63
Gotland Basin	OSGB	28	N 57 06–57 31 E 18 52–19 16	March 2–9 2005 and 2006	~55–90
<i>Coastal spawners</i>					
Eastern Gotland	CSEG	28	N 57 14 E 18 40	March 30–31 2005	~5–8
Northern Gotland	CSNG	27/28	N 57 57 E 19 04	March 30–31 2005	~5
Stockholm archipelago	CSSA	29	N 60 02 E 18 50	April 25–May 03 2006	~7–13

caught offshore at 53–65 and 55–90 m depth respectively, were considered as belonging to the offshore spawning population (according to information about depth distribution of the respective population in the area, fish from the coastal spawning population should not occur deeper than 30–40 m depth; Molander, 1954). To ensure similar size/age distribution among fish from the respective sampling location, fish were selected according to three size classes, <250, 250–300 and >300 mm total length. Despite this procedure some discrepancies in size/age distribution between sampling locations occurred (see below) depending on the size distribution in the catches.

Selected fish were in pre-spawning late vitellogenesis condition (ovary filling most of the body cavity with individual oocytes clearly visible). The fish were frozen onboard (OSBB and OSGB) or after landing (CSEG, CSNG and CSSA) and transported to the Ar Research Station. After thawing fish length (± 1 mm total length; Lt), somatic weight [± 1 g (intestine and gonad removed); Ws], gonad weight (± 0.01 g; Gw) and gonad dry weight (48 h at 60 °C; Gdw) were assessed, and otoliths removed and weighted (± 0.0001 g; OTw) and a number of fish from the respective sampling location aged by otolith readings. The total number of fish analysed from the respective location is shown in Table 2a.

Flounder represent a capital spawner, i.e. the reproductive investments are covered by energy reserves stored in the soma during the previous feeding season, with unimodal vitellogenesis, i.e. display only one stage of vitellogenic oocytes during development that after hydration are released successively in batches. Thus, the annual potential fecundity (Fp) can be determined by assessment of the number of advanced yolked oocytes (e.g. Janssen et al., 1995). Fecundity was estimated gravimetrically. Two samples, one from each gonad lobe, were weighted (± 0.0001 g) and the oocytes separated by gently shaking of the sample in isotonic water. Oocytes still occurring in aggregations were separated under a stereo-microscope at 10.5 \times magnification and the total number counted. In accordance with Kuczynski and Zaporowski (1992) no differences in the number of oocytes per weight unit in different parts of the gonad were assumed. Fecundity was calculated as the ratio between total gonad weight and weight of the respective oocyte sample times the number of oocytes counted in the respective sample. The on average Fp of the two samples was used in further analysis; difference between sub-samples averaged 5.8, 4.5, 11.5, 8.9 and 9.0% for CSEG, CSNG, CSSA, OSBB and OSGB respectively (no difference among locations; $df=4$, $F=0.531$, $p=0.713$).

Discrepancies in maturity levels of fish may hamper comparisons of the Fp as the standing stock of vitellogenic oocytes may be down-regulated by atresia during the maturation process (e.g. Kurita et al., 2003; Kennedy et al., 2007). Obviously, differences in maturity levels may occur among sampling locations and between years within locations, but differences in maturity status also exist among individual fish sampled at the same occasion (see Thorsen et al., 2006). Thus, standardization of data is required to provide unbiased fecundity comparisons, i.e. to ensure similar levels of maturity among analysed fish. Ultimately oocyte diameter of the leading cohort shows the maturation status (Kjesbu, 1994), but the on average oocyte size may be used as an indication of maturity status (Thorsen et al., 2006). Further, Thorsen and Kjesbu (2001) showed that there is a strong relationship between the mean diameter of oocytes and oocyte density in a sample. Thus, lacking data on mean oocyte diameter, densities (n oocytes/g gonad weight; Od) were used as an indicator of maturity level; high Od involving risk for not yet down-regulated Fp, and low Od eventually resulting from the presence of already hydrated eggs, i.e. fish post pre-spawning conditions, affecting Fp estimation. Further, mean oocyte dry weight (Odw), estimated as the quota between Gdw and assessed fecundity, was used for comparisons of maturity status. However, as a result of unintentionally changed routines in assessing gonad dry weights, estimations of Odw

for fish from OSGB sampled in 2006 and from CSSA were excluded in further analysis. Additionally, as there is normally a relationship between fecundity and fish size poor relationships were used as an indication of doubtful data. Finally, the significance of potential differences in maturity status on Fp-estimations was elucidated by plotting Od against the relative potential fecundity (Fp per Ws; Frp); the latter for reducing effects related to variation in fish size. Positive relationships between Frp and Od indicate effects of fish in different maturity status, i.e. require inclusion of Od in further analysis of Fp (see Thorsen et al., 2006).

Statistical treatments were conducted using the SPSS 17.0 software. Apart from in analyses of potential relationships between Od and the relative potential fecundity all data were ln-transformed before statistical analyses.

The relationship between fish length (Lt), somatic weight (Ws), otolith weight (OTw; as proxy for age), condition [Cf; Fulton's condition factor; (somatic weight/length³)*100] and oocyte density (Od) respectively, and Fp was analysed for each of the sampling locations to evaluate significant variables. Further, multiple regressions with stepwise addition of variables were applied to assess the major predictors of Fp.

Intra- and inter-population comparisons of Fp (dependent factor) were analysed by univariate regressions using GLM with sampling location as fixed factor and Lt, Ws, OTw, Cf and Od, as well as the potential interaction between sampling location and the respective variable, as covariates. The model (based on the lowest residual sum of squares) was run stepwise with subsequently removal of non-significant ($p>0.05$; starting with the highest) variables until only significant predictors were included in the respective model.

Further, as an inter-population difference in Fp was found, Gdw (dependent factor) was analysed with population as fixed factor and Lt as well as Lt*population as covariates, as described above, to reveal if observed differences in Fp were reversed by differences in Odw.

3. Results

3.1. Standardization of data

In Table 2a r^2 -values for the relationship between potential fecundity (Fp) and somatic weight (Ws) for the respective sampling location are shown together with intra-location oocyte density (Od) values. Poor relationships as well as large differences in Od for in particular OSGB and CSSA, suggest discrepancies in maturity among sampled fish potentially biasing estimations of Fp, i.e. demand for a closer examination.

Firstly, potential intra-location differences among the OSGB samples were evaluated by comparing Od and estimated mean oocyte dry weights (Odw) according to depth distribution; ~55 m, ~65 m and deeper (~80–90 m), referred to as OSGBa, OSGBb and OSGBc, respectively (Table 2b). Both significantly higher Od ($df=3$, $F=61.20$, $p<0.001$) and lower Odw ($df=3$, $F=20.25$, $p<0.001$) for OSGBa and OSGBb compared to OSGBc and OSBB (no difference in Od and Odw; $df=1$, $F<0.01$, $p=0.994$ and $df=1$, $F=0.63$, $p=0.430$, respectively)

Table 2a

R-square values for the relationship between potential fecundity and somatic weight (ln-transformed values) and the distribution in oocyte density (n oocytes/g gonad weight) of coastal- (CSEG, CSNG and CSSA) and offshore spawning (OSBB and OSGB) flounder *Pleuronectes flesus*, respectively at different sampling locations (Fig. 1).

	n	r^2 fecundity–somatic weight	Δ (max–min) n oocytes/g gonad weight
CSEG	41	0.702	7916
CSNG	43	0.844	6680
CSSA	60	0.632	14,527
OSBB	52	0.814	8655
OSGB	102	0.632	15,427

Table 2b

Oocyte density (n oocytes/g gonad weight) and estimated mean oocyte dry weight (μg) for flounder *Pleuronectes flesus* from different sampling depths at OSGB (OSGBa ~55 m, OSGBb ~65 m and OSGBc ~80–90 m) in comparison to at OSBB (offshore spawning population) and CSEG, CSNG and CSSA (coastal spawning population).

	n	Oocyte density ($\times 10^3$) average \pm sd	Oocyte dry weight average \pm sd
OSGBa	34	14.40 \pm 2.13	21.7 \pm 2.9
OSGBb	38	12.95 \pm 1.92	24.2 \pm 4.6
OSGBc	30	8.37 \pm 3.19	27.3 \pm 6.9 ^a
OSBB	52	8.37 \pm 2.49	28.7 \pm 4.3
CSEG + CSNG + CSSA	144	11.63 \pm 2.06	26.2 \pm 4.0 ^b

^a $n = 9$.

^b $n = 84$; CSEG and CSNG only.

strongly indicate fish with not fully ripen oocytes at OSGBa and OSGBb. Moreover, estimated mean Odw of OSGBa and OSGBb were lower than those of CSNG and CSEG ($df = 2$, $F = 7.75$, $p < 0.001$) as opposed to for OSGBc ($df = 1$, $F = 0.608$, $p = 0.439$), and Od exceeded those of coastal spawners. Hence, sampling location OSGBa and OSGBb were omitted in further analyses.

Secondly, the risk for biased comparisons of Fp due to potential discrepancies in maturity levels among the remaining sampling locations was evaluated by comparing Od within the respective population. Based on the criterion, on average Od $\pm 2 \times$ sd (standard deviation) some fish (6 from the coastal spawning population and 2 from the offshore spawning population) were considered outliers and omitted in further analysis. Despite this, when plotting Od against the relative potential fecundity (Frp) of remaining fish significant positive relationships were found for both the coastal spawning population ($df = 1$, $F = 15.08$, $p < 0.001$) and the offshore spawning population ($df = 1$, $F = 34.12$, $p < 0.001$) (Fig. 2). Hence, as discrepancies in maturity levels affect individual Fp estimates (Thorsen et al.,

2006) Od was included as a covariate to fish size in analysis of potential intra- and inter-population comparisons of Fp (see below).

The use of otolith weight (OTw) as a proxy for age was validated by strong relationships between ages determined from otolith readings and OTw; $r^2 = 0.6895$, $df = 1$, $F = 159.9$, $p < 0.001$ ($n = 74$) and $r^2 = 0.7234$, $df = 1$, $F = 94.1$, $p < 0.001$ ($n = 38$) for the coastal spawning- and the offshore spawning population, respectively.

3.2. Description of analysed fish

In Table 3 length (Lt), somatic weight (Ws), otolith weight (OTw) and condition (Cf; Fulton's condition factor) of analysed fish from the respective sampling location are shown. Some discrepancies in the material occur. E.g. the location OSBB included comparatively more small/young fish and few large/old, whereas fish from CSNG and in particular OSGBc where on average larger/older with only few small/young individuals. Further, differences in Cf of the fish occurred. Fish from CSNG displayed on average poorer Cf (ANOVA; $df = 4$, $F = 4.27$, $p < 0.01$) than fish from OSBB, OSGB, CSEG and CSSA ($df = 3$, $F = 0.84$, $p = 0.472$).

Analysis of growth, expressed as the relationship between OTw and fish size (Lt and Ws), revealed significant differences among locations ($df = 4$, $F = 9.27$, $p < 0.001$ and $df = 4$, $F = 11.89$, $p < 0.001$ when expressed as Lt and Ws, respectively) with higher growth for fish from location OSBB compared to the other locations ($p < 0.001$ –0.009; pair wise comparisons) as shown in Fig. 3. When expressed in Lt no significant differences in growth occurred between location OSGBc, CSEG, CSNG and CSSA ($p = 0.068$ –1.000), whereas when using Ws growth differed significantly also between OSGBc and CSNG ($p = 0.008$).

3.3. Fecundity

The relationship between length (Lt) and somatic weight (Ws) respectively, and measured Fp for the respective sampling location is shown in Fig. 4, and in Table 4 the r^2 -values for the relationships between fish size (Lt and Ws), otolith weight (OTw), condition (Cf) and oocyte density (Od), respectively and Fp, are shown. In general,

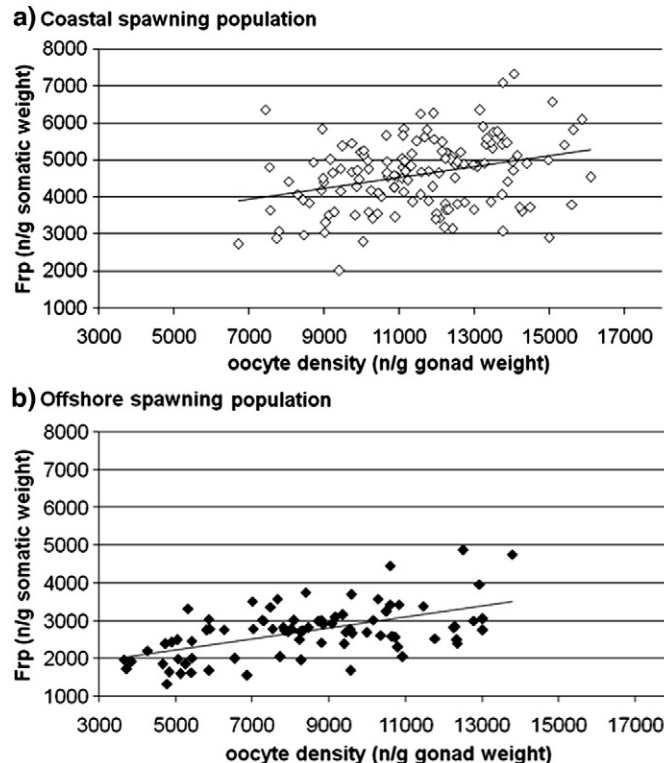


Fig. 2. The relationship between oocyte density (n oocytes/g gonad) and relative potential fecundity (Frp; n oocytes/g somatic weight) for a) coastal spawning- and b) offshore spawning flounder *Pleuronectes flesus* in the present study.

Table 3

Fish length- (total length; mm), weight- (somatic weight; g) and otolith weight (μg) statistics, and estimated condition (Fulton's condition factor) for coastal- (CSEG, CSNG and CSSA) and offshore spawning (OSBB and OSGBc) flounder *Pleuronectes flesus* in the present study (for locations see Fig. 1).

	CSEG	CSNG	CSSA	OSBB	OSGBc
Length					
Average	296	303	288	296	319
Sd	32	41	29	50	31
Median	294	292	295	289.5	321.5
Min-max	225–378	235–390	234–345	210–448	252–385
Weight					
Average	237	239	211	251	289
Sd	63	95	59	133	84
Median	229	216	208	213.5	287
Min-max	130–384	106–462	122–356	70–778	138–492
Otolith weight					
Average	31.0	32.4	27.3	23.6	32.7
Sd	10.5	10.9	9.4	7.6	7.6
Median	29.9	31.85	25.25	22.2	32.35
Min-max	14.1–56.5	16.9–54.6	13.2–51.2	12.5–50.0	20.1–50.6
Condition					
Average	0.902	0.824	0.874	0.894	0.872
Sd	0.108	0.072	0.120	0.081	0.093
Median	0.884	0.820	0.867	0.891	0.870
Min-max	0.711–1.231	0.646–1.014	0.628–1.280	0.675–1.074	0.661–1.130
n	40	43	55	52	28

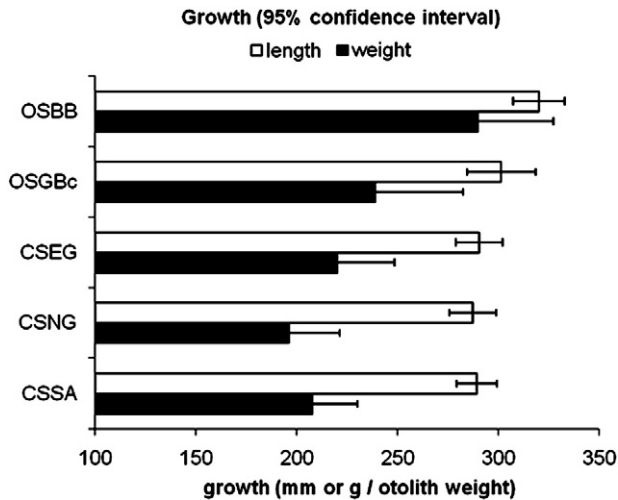
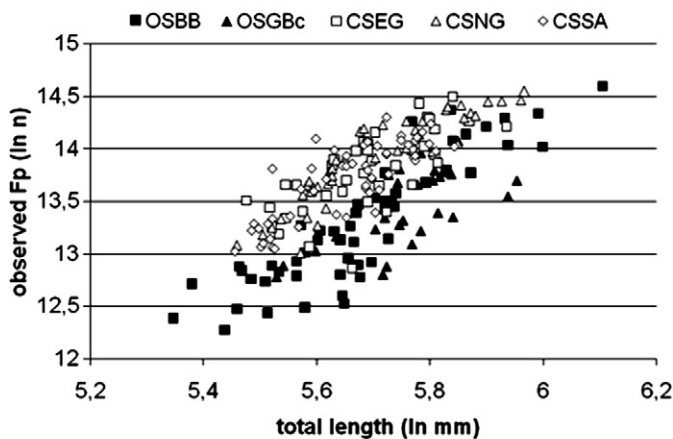


Fig. 3. Growth, expressed as total length and somatic weight respectively, in relation to otolith weight, of coastal- (CSEG, CSNG and CSSA) and offshore spawning (OSBB and OSGBc) flounder *Pleuronectes flesus* from different sampling locations (Fig. 1).

significant positive relationships occurred between Fp and Lt and Ws, respectively. Additionally, OTw yielded positive relationships for all locations apart from OSGBc. Further, poor relationships occurred between Fp and Od indicating low risk for results being biased from differences in maturation levels. The strongest relationships were

a) Fecundity - Length



b) Fecundity - Weight

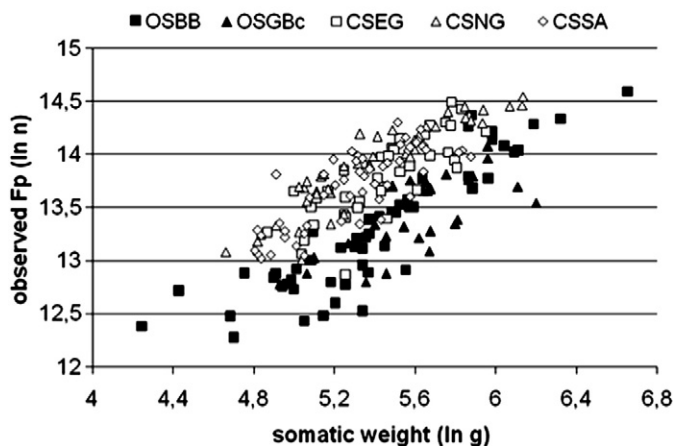


Fig. 4. Observed potential fecundity (Fp) in relation to a) total length and b) somatic weight of coastal- (CSEG, CSNG and CSSA) and offshore spawning (OSBB and OSGBc) flounder *Pleuronectes flesus*.

obtained for locations OSBB and CSNG, whereas the relationships for in particular OSGBc but also CSEG were lower. Multiple linear regression analysis resulted in r^2 -values of 0.698–0.894 with Ws (CSNG, CSEG, OSGBc and OSBB) or Lt (CSSA) as the main predictor, and OTw (CSEG and OSGBc) and Od (CSSA, OSGBc and OSBB) as additional predictors (Table 4).

The outcome of the univariate regression-analyses of both intra- as well as inter-population comparisons in Fp is given in Table 5. Within the respective population there was no effect of location on Fp for the offshore spawning population ($p = 0.205$), nor for the coastal spawning population ($p = 0.134$) despite somewhat lower Fp for fish from CSEG compared to CSSA and CSNG. Inter-population comparisons (locations for the respective population pooled) revealed a highly significant difference in Fp between the offshore- and coastal spawning population ($df = 1$, $F = 120.3$, $p < 0.001$) with considerably higher fecundity for the coastal spawning population. Inclusion of also omitted outliers (see above) did not affect the observed inter-population difference in Fp ($df = 1$, $F = 10.93$, $p = 0.001$).

Additionally, to further elucidate potential inter-population differences in Fp, the relationship between Frp and Od was used to compare relative fecundity at a similar maturation status. Based on the regression lines (Fig. 2), considerably higher Frp of the coastal spawning population was evident at both low Od (5000), ~3650 vs. ~2200, and at high Od (15,000), ~5100 vs. ~3650. Further, analysing Frp at overlapping Od, [on average Od of the offshore spawning population + $1 \times sd$ (standard deviation) and on average Od of the coastal spawning population – $1 \times sd$ (Fig. 2)], revealed significantly higher (~50%) Frp of the coastal spawning population, $df = 64$, $t = 2.0$, $p < 0.001$ (t -test), i.e. strengthening the main finding of significantly higher Fp of the coastal spawning population.

Finally, the relationship between gonad dry weight (Gdw) and Lt was considered (Fig. 5) to elucidate the potential for observed differences in Fp between the respective populations being reversed by differences in oocyte dry weights. A univariate regression analysis revealed a highly significant effect of population on Gdw with higher Gdw for the coastal spawning population, $df = 1$, $F = 86.35$, $p < 0.001$ [ln Gdw on average 3.26 (3.20–3.32, 95% c.i.) for coastal spawners and 2.85 (2.78–2.91, 95% c.i.) for offshore spawners], suggesting considerable differences in energy allocation for gonad production between the two populations.

In summary, the study did not reveal any major differences within the respective population potentially reflecting adaptations to decreasing salinity, but between the respective population using different spawning strategies. According to the model, Fp was best described by the function $Fp = e^{2.376} \times Ws^{1.180} \times Od^{0.502}$ (r^2 -value = 0.868) for the offshore spawning population and $Fp = e^{4.684} \times Ws^{1.042} \times Cf^{-0.469} \times Od^{0.368}$ (r^2 -value = 0.746) for the coastal spawning population (size range; Lt ~210–450 mm, Ws ~70–780 g for offshore spawning fish and Lt ~225–390 mm, Ws ~105–460 g for coastal spawning fish). Plotting obtained residuals against Lt yielded no relationships, $r^2 \sim 0$, $df = 1$, $F = 0.006$, $p = 0.941$ and $r^2 \sim 0$, $df = 1$, $F = 0.048$, $p = 0.827$ for the coastal spawning

Table 4

R-square values for relationships between potential fecundity (dependent variable) and fish parameters (total length, somatic weight, otolith weight, condition and oocyte density, respectively) of coastal- (CSEG, CSNG and CSSA) and offshore spawning (OSBB and OSGBc) flounder *Pleuronectes flesus* at different sampling locations (Fig. 1). Predictors in multiple linear regression analysis applied are indicated by *.

	CSEG	CSNG	CSSA	OSBB	OSGBc
Length	0.520	0.828	0.659*	0.787	0.440
Weight	0.626*	0.844*	0.652*	0.814*	0.553*
Otolith weight	0.207*	0.784	0.410	0.663	0.102*
Condition	0.033	0.016	0.021	0.005	0.082
Oocyte density	0.004	0.069	0.041*	0.000*	0.040*
n	39	43	54	52	28
Multiple	0.698	0.844	0.755	0.894	0.811

Table 5

Results of the univariate regression analysis of potential fecundity in relation to fish size (somatic weight) for flounder *Pleuronectes flesus* from different sampling locations, CSEG, CSNG and CSSA (coastal spawning population), and OSBB and OSGB (offshore spawning population), and the in average potential fecundity (ln) with 95% confidence interval for the respective location/population (see Fig. 4).

	<i>n</i>	Coastal spawners		Offshore spawners		Coastal vs. Offshore	
		<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
		2.045	0.134	1.631	0.205	120.3	<0.001
		Average	95% c.i.	Average	95% c.i.	Average	95% c.i.
CSSA	54	13.82	13.76–13.87				
CSNG	43	13.85	13.78–13.91				
CSEG	39	13.67	13.61–13.74				
OSGBc	28			13.30	13.22–13.37		
OSBB	52			13.36	13.30–13.41		
CS	138					13.77	13.73–13.80
OS	80					13.38	13.33–13.43

population and the offshore spawning population respectively, i.e. the model (close correlation between modelled *F_p* values and observed for both the populations; $r=0.8405$ and $r=0.9315$, respectively), was considered to produce unbiased *F_p* estimates irrespective of fish size.

Fecundity may be given either as in relation to length or to weight. The latter often yielding the highest correlations (e.g. the present study). However, as argued in Thorsen et al. (2006), length varies less than weight during the pre-spawning period, and used in combination with Fulton's condition factor often yield r^2 -values of similar level as weight in models describing *F_p*. Hence, in Fig. 6 the relationship between modelled *F_p* and *L_t* in combination with *C_f* (treated as a constant) and in relation to *W_s*, respectively are shown (all other variables kept constant using on average values). For an intermediate sized fish, e.g. *L_t* 300 mm, *F_p* averaged ~633,000 and ~1,066,000 for offshore spawning- and coastal spawning fish respectively, i.e. a coastal spawning flounder display on average ~68% higher *F_p* than an offshore spawning flounder. Similarly, for a fish with *W_s* 250 g *F_p* amounted ~671,500 and ~1,141,000 for an offshore spawning- and a coastal spawning fish respectively, i.e. on average ~70% higher *F_p* for coastal spawning flounder.

4. Discussion

Population egg production is the basis for stock–recruitment relationships. Rather than the spawning stock biomass the total annual stock fecundity represents the reproductive potential and varies between species and among populations as well as with age/size of maturity and age/size structure of the stock, and with fish condition depending on food availability. Maturity and stock structure

are strongly influenced by fishing mortality involving both phenotypic and genotypic changes (Trippel et al., 1997; Conover and Munch, 2002; Grift et al., 2003), e.g. early maturity and truncated age/size distribution. Hence, as maturation, growth and condition within a population are governed by environmental conditions, varying in space and time, the reproductive potential of a stock varies over years and is influenced by the spatial distribution of the spawning fish (e.g. Morgan and Rideout, 2007). Moreover, in the Baltic Sea opportunities for reproduction differ strongly between areas depending on salinity and oxygen conditions affecting the viable egg production (MacKenzie et al., 2000; Köster et al., 2001; Nissling et al., 2002, 2006). Accordingly, information about egg production in different areas is a prerequisite for understanding stock development mechanisms and for description of stock–recruitment relationships, and thus, for appropriate management measures. The present investigation includes estimations of the potential fecundity (*F_p*) in two sympatric populations of flounder in the Central Baltic Sea spawning along a salinity gradient with different spawning strategies. However, to fully understand egg production processes of the respective population, including estimations of realized fecundity, future studies should focus on timing and level of oocyte regulation, now possible by new methodology (e.g. Kurita and Kjesbu, 2009; Witthames et al., 2009).

According to our results, *F_p* differed between the coastal- and the offshore spawning populations at a given length (*L_t*) or weight (*W_s*), with the former population being significantly more fecund. Further, the results revealed no major differences in *F_p* within the respective population, i.e. no evidence for an increase in fecundity within populations along the salinity gradient. Whether coastal spawning flounder further north, e.g. in the Bothnian Sea spawning at ~5 psu

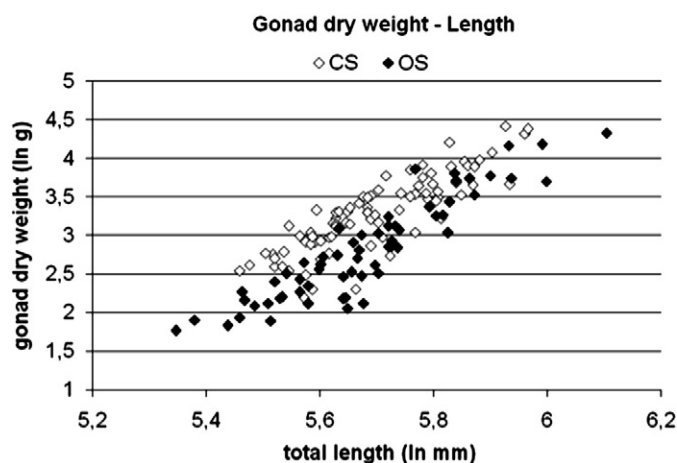


Fig. 5. Gonad dry weight in relation to total length of coastal- (CS) and offshore spawning (OS) flounder *Pleuronectes flesus*.

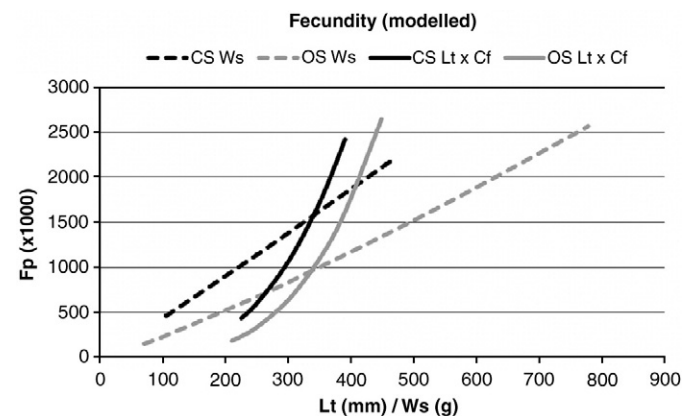


Fig. 6. Modelled potential fecundity (*F_p*) in relation to total length (*L_t*) in combination with fish condition (*C_f*) and to somatic weight (*W_s*) respectively of coastal- (CS) and offshore spawning (OS) flounder *Pleuronectes flesus*.

(compared to at 6–7 psu for fish in the present study), display higher fecundity remains an open question for future investigations.

Why are coastal spawning flounder more fecund? Regarding salinity conditions in the respective spawning habitat, coastal spawning flounder reproduce at 5–7 psu as opposed to at 10–20 psu for the offshore spawning population. Although, yet not fully elucidated, both fertilisation rates and egg survival rates can be expected to be lower for coastal spawning flounder due to the lower salinity conditions (Molander, 1954; Solemdal, 1970; Nissling et al., 2002). Further, production of demersal eggs probably involves higher mortality due to e.g. predation, infestation of bacteria etc.

Higher egg production demands for allocation of more energy in gonad production and consequently reduced somatic growth. This is in accordance with our findings; significantly higher gonad dry weights in relation to Lt of the coastal spawning population but somewhat lower growth. Investigating growth of flatfishes in the Baltic Sea, Sager and Berner (1989) found decreased growth with decreasing salinity [fish from the Belt-Seas (SD 22), the Bornholm basin (SD 25) and the Gotland basin (SD 28) respectively]. Concomitant to this, fish sampled at OSBB (SD 25) in our investigation displayed significantly higher growth. Further, fish sampled at OSGBc (at ~80–90 m depth), identified as offshore spawning fish, showed somewhat higher growth contrasting with fish from CSNG but also from CSEG and CSSA. Hence, offshore spawning fish displayed somewhat higher growth rates than coastal spawning, indicating that more energy is invested in somatic growth. Furthermore, differences in migration pattern between coastal- and offshore spawning flounder, limited migration for coastal spawning whereas offshore spawning flounder perform migrations between shallow coastal areas (for feeding) and deep areas (for spawning) (Molander, 1954; Bagge, 1981), imply higher energy reserves for coastal spawning fish allowing for higher investment in gonad production.

Differences in energy allocation between the spawning strategies complicate, however, the comparison of Fp as the maximum size (L_{∞} ; von Bertalanffy function) of flounder differ between areas and/or populations (Bagge, 1981; Sager and Berner, 1989) with higher sizes in the southwest compared to in the northeast. Hence, differences in maximum size imply that a full grown offshore spawning flounder may produce a similar amount of eggs (or even more) as a full grown coastal spawning flounder as indicated in Fig. 6. The available information on L_{∞} is, however, scattered and without consideration of differences between spawning strategies. Bagge (1981), summarising earlier investigations,

mention 35 cm in SDs 26 and 28, Sager and Berner (1989) report 32 cm for flounder in SD 28 and 60 cm in the Bornholm area (SD 25) whereas, in a recent investigation, Gårdmark and Florin (2007) report similar L_{∞} , ~34.5 cm, for flounder in SD 25 and 28. Thus, more comprehensive data on differences in size at age as well as in maximum size between populations/areas is required to fully evaluate differences in Fp, and to allow estimations of stock fecundity.

Assessed mean oocyte dry weights (Odw) at both OSBB and OSGBc (28.7 and 27.3 μg , respectively) as well as for coastal spawners (on average 26.2 μg) are in agreement with egg dry weight measurements by Solemdal (1970); 25.5–29.2 μg (fish from SD 24 and 29), i.e. indicate that fish included in analysis were close to spawning. Contrary, evaluation of oocyte densities (Od) and mean Odw at OSGBa (~55 m depth) and OSGBb (~65 m depth) suggest that fish at these sampling stations were yet not fully mature as indicated by higher Od and lower mean Odw (i.e. not fully ripen oocytes) compared to both OSGBc (~80–90 m depth) and OSBB as well as CSEG and CSNG. This raises the question whether the fish at OSGBa and OSGBb actually belonged to the offshore spawning population; Od values obtained exceeding those of coastal spawners. The high Od values observed at OSGBa and OSGBb may reflect that the Fp has yet not been adjusted by down-regulation from atresia, or perhaps, may result from that a number/the majority of fish at OSGBa and OSGBb, sampled at intermediate depths, were coastal spawning fish not yet at the spawning ground? Sampling at OSGB was conducted in March, i.e. about one month prior to onset of spawning of coastal spawning flounder in the area (Molander, 1954; own observation). According to available literature coastal spawning flounder are known to occur down to 30–40 m depth (Molander, 1954). Depth distribution may, however, have changed. Deteriorated conditions in the deep basin following eutrophication, exaggerating since the 1950s (Larsson et al., 1985; Elmgren, 1989; Karlson et al., 2002), have affected spawning conditions and thus recruitment and stock development of offshore spawning flounder in the area negatively (mostly low reproductive volumes in recent years; Didzis Ustups, personal communication). Hence, poor spawning conditions for offshore spawning flounder nowadays may have favoured the coastal spawning population. The above reflect the risk for blurred results in areas where mixed populations may occur. The persistence of spawning at certain locations over time (cf. homing), and spatial and/or temporal differences in spawning habitats between populations, suggests that sampling of fish close to spawning diminishes the risk of mixed population samples.

Table 6

Estimations of size specific fecundity (35 cm fish) of flounder, *Pleuronectes flesus*, from the Atlantic, the North Sea, the Kattegat and different areas in the Baltic Sea (ICES SD areas) derived from available literature, in comparison to results from the present study; modelled potential fecundity [Fp; based on Lt (mm) in combination with Cf and Od treated as constants using on average values; Fig. 6].

	Atlantic VIIIa	North Sea IV	Kattegat SD 21	Belt-Seas SD 22	Baltic Sea SD 24–25	Baltic Sea SD 25	Baltic Sea SD 26	Baltic Sea Present study
Fulton (1891) and Ehrenbaum (1936)		1,178,000 ^a						
Kändler and Pirwitz (1957)		920,000 ^b	1,190,000	1,120,000	1,310,000		1,035,200 ^c	
Cieglewicz and Musial (1964)							1,001,000	
Deniel (1981)	1,245,000 ^d							
Kuczynski and Zaporowski (1992)						1,120,000 ^e	1,300,000 ^e	
Kosior et al. (1996)						1,433,000 ^f	1,636,000 ^f	
Kosior et al. (1996)						1,059,000 ^g	1,307,000 ^g	
Offshore spawners								1,097,000 ^h
Coastal spawners								1,726,000 ⁱ

^a Calculated from values given in Kändler and Pirwitz, 1957; r-squared value = 0.9194, n = 5.

^b n = 45.

^c Calculated from the formula in Table 7 (coincides with figure given in Table 6) in Kändler and Pirwitz, 1957; n = 27.

^d Calculated from values in Table 40 in Deniel, 1981; r-squared value = 0.5860, n = 17.

^e From Fig. 1 in Kuczynski and Zaporowski (1992).

^f Fish sampled in 1993.

^g Fish sampled in 1995.

^h Based on $Fp = e^{-11.498 \times Lt^{3.564} \times Cf^{0.954} \times Od^{0.515}}$ (Cf = 0.8866 and Od = 8232).

ⁱ Based on $Fp = e^{-7.307 \times Lt^{3.125} \times Cf^{0.572} \times Od^{0.368}}$ (Cf = 0.8666 and Od = 11,607).

According to available information (Bagge, 1981 and references therein) coastal spawning flounder occur east and north of the boundary Torhamn, Sweden–Rosewie, Poland (shown in Fig. 1), and offshore spawning flounder mainly in SD 24–26 and SD 28.

In Table 6 the results from the present investigation, including fecundity estimations of coastal spawning- and offshore spawning flounder respectively, and size specific fecundity data from the literature covering different areas in the Baltic Sea, the North Sea and the Atlantic, are summarised. The hypothesis of higher fecundity of flounder in the Baltic Sea than outside (Kändler and Pirwitz, 1957) is not obvious. The estimation of 920,000 oocytes for a 35 cm fish in the North Sea is somewhat lower compared to the results in SD 22–26 (Kändler and Pirwitz, 1957). However, some of the fecundity estimations from sampling in SD 25–26 are similar to values from the Atlantic–North Sea–Kattegat area. In comparison to the results in our investigation, estimated fecundity in the Atlantic, the North Sea, the Kattegat and the SD 22 are similar to estimated fecundity for offshore spawning flounder, 1,097,000 (1,049,600–1,146,400, 95% c. i.), and some values from SD 25–26 are in agreement with estimated fecundity of the coastal spawning population, 1,726,000 (1,668,700–1,785,600, 95% c.i.) (based on Lt in combination with Cf and Od). As both coastal- and offshore spawning flounder occur in SD 25–26 (Molander, 1954), mixed population samples may occur. Examination of discrepancies in obtained Od in SD 28W (present investigation) revealed that homogeneity of samples was dependent on sampling depth and, furthermore, probably also on sampling time. In the majority of investigations referred to above, sampling has been conducted on pre-spawning fish, in January–February, and without information of sampling depth. From Fig. 1 in Kosior et al. (1996) it can be concluded that samples have been obtained from both shallow and deep areas suggesting fish from both the coastal- and offshore spawning population in the samples.

The above cannot, however, be regarded as a fully evaluation of the question concerning higher fecundity of flounder in the Baltic Sea. Apart from methodological discrepancies between studies, fecundity may have changed over time due to selective effects of fishing (Rijnsdorp et al., 2005). However, we conclude that earlier investigations, resulting in varying fecundity estimations in the area SD 25–26, may be a consequence of that the occurrence of two sympatric flounder populations in this area has been disregarded. In fact, our findings are in agreement with the genetic population structure; little differences (although significant) between flounder samples from the North Sea to the western Baltic, clearly isolated from flounder in the inner Baltic Sea spawning demersal eggs (Hemmer-Hansen et al., 2007).

To summarize, in the brackish water Baltic Sea two, sympatric, flounder populations have evolved. These populations occur mixed during the feeding season but utilize different habitats for spawning. Present study suggest that different spawning strategies have resulted in differences in reproductive investment; the coastal spawning type displaying considerably higher resource allocation into gonad growth than the offshore spawning population, and lower growth. This specific population, producing demersal eggs, displayed considerably higher size specific fecundity than flounder populations producing pelagic eggs, i.e. the offshore spawning type in the Baltic Sea as well as flounder in the Kattegat–North Sea–Atlantic area.

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