Oogenesis and reproductive investment of Atlantic herring are functions of not only present but long-ago environmental influences as well

Thassya C. dos Santos Schmidt¹,²,¹, Aril Slotte³, James Kennedy⁴,⁵, Svein Sundby⁶, Arne Johannessen⁷, Gudmundur J. Óskarsson⁷, Yutaka Kurita⁸, Nils C. Stenseth¹,²,⁹,¹⁰ and Olav Sigurd Kjesbu¹,²

¹Institute of Marine Research, N-5817 Bergen, Norway; ²Department of Biology, University of Bergen, N-5020 Bergen, Norway; ³Marine Research Institute, 121 Reykjavik, Iceland; ⁴Biopol, 545 Skagastølstråd, Iceland; ⁵Tohoku National Fisheries Research Institute, Miyagi 985-0001, Japan; ⁶Centre for Ecological and Evolutionary Synthesis, Department of Biosciences, University of Oslo, N-0316 Oslo, Norway; ⁷Institute of Marine Research, Fiskevægen, N-4817 His, Norway; and ⁸Centre for Coastal Research, University of Agder, N-4604 Kristiansand, Norway

Contributed by Nils C. Stenseth, January 13, 2017 (sent for review October 23, 2016; reviewed by Susan Lowerre-Barbieri and Peter J. Wright)

Following general life history theory, immediate reproductive investment (egg mass × fecundity/body mass) in oviparous teleosts is a consequence of both present and past environmental influences. This clarification questions the frequent use of season-independent (general) fecundity formulas in marine fish recruitment studies based on body metrics only. Here we test the underlying assumption of no lag effect on gametogenesis in the planktivorous, determinate-fecundity Atlantic herring (Clupea harengus) displaying large plasticity in egg mass and fecundity, examining Norwegian summer–autumn spawning herring (NASH), North Sea autumn spawning (NSAH), and Norwegian spring spawning herring (NSSH). No prior reproductive information existed for NASH. Compared with the 1960s, recent reproductive investment had dropped markedly, especially for NSAH, likely reflecting long-term changes in zooplankton biology and productivity. As egg mass was characteristically small for autumn spawners, although large for spring spawners (cf. different larval feeding conditions), fecundity was the most dynamic factor within reproductive investment. For the data-rich NSSH, we showed evidence that transient, major declines in zooplankton abundance resulted in low fecundity over several subsequent seasons, even if Fulton’s condition factor (K) turned high. Temporal trends in $K_{\text{slope}}$ (K on total length) were, however, informative. These results clarify that fecundity is defined by (i) dynamics of primary (standing stock) oocytes and (ii) down-regulation of secondary oocytes, both processes intimately linked to environmental conditions but operating at different timescales. Thus, general fecundity formulas typically understate interannual variability in actual fecundity. We therefore argue for the use of segmented fecundity formulas linked to dedicated monitoring programs.

Significance

Fish stock advice and management have a focus on protecting the reproductive capacity of a stock. Central to the associated research undertaken is whether spawning stock biomass is a proxy for total egg production. Here we demonstrate for the planktivorous Atlantic herring that the standard use of season-independent potential fecundity formulas may cause flaws in these interpretations. In particular, this would happen when the adults have experienced poor feeding conditions that negatively affect the reservoir of primary oocytes and thereby the future fecundity. Hence, females in excellent condition may show significantly lower-than-expected fecundity that could lead to errors in the judgment of reproductive capacity, especially under "red flag" situations.

The ultimate combination of factors determining the absence or presence of large classes of recruits entering the fishery is still enigmatic after a century of research (1, 2), in particular under climate change (3). The predictive power of useful relationships typically diminishes over time when the blend of influential abiotic and biotic drivers change (4, 5). Due to the high importance of getting a grip on the expected level of recruitment (REC) for quota decisions, one practical solution is to assume the same REC as in preceding years. Logically, this is a fragile approach as environmental conditions are per definition non-stationary (3). Although fully solving the “recruitment problem” seems unrealistic due to the chaotic nature of the multiple processes involved, the spawning stock biomass (SSB) can be regulated by humans through the degree of fishing intensity. In addition, individual body condition can be influenced by the level of harvest on important prey. Consequently, major efforts have been placed on studies of whether SSB properly reflects stock reproductive potential (SRP) (6–8). This might be specifically tested by delimiting SRP to total egg production (TEP) (7). [Note that “reproduction” and “recruitment” often are used synonymously (9)]. TEP values, however, are approximations because, among other aspects, general instead of season-specific potential fecundity ($F_P$) formulas are typically applied (8). Logically, this might not be a problem as long as the general $F_P$ formula sufficiently covers the full scope in actual $F_P$ dynamics, which, however, requires dedicated data collection programs. In addition to infrequent observations on fecundity, the quality of this type of exploratory recruitment-related analyses might be challenged by the use of independent datasets unsuited to advance understanding. Even for data-rich cases, further improvements may be possible as reproductive outputs are seldom seen as a function of past environmental influences (see below). In essence, we hypothesize that the current estimation practices may overlook underlying patterns in TEP that could contribute to early warning signals, “red flags” of impaired recovery during times of low SSB, and/or poor environmental conditions (10).

An extensive amount of information exists on oogenesis, including also for the present category of interest, the oviparous marine teleosts. The emphasis, however, is on physiogenetic...
Factors (11) rather than the quantitative nature of oocyte production per se, which is essential in recruitment-related studies. In particular, how early oocyte recruitment and thereby the foundation for future fecundity is affected by environmental fluctuations appears as a “black box” (i.e., without any knowledge of its internal workings), apparently because of methodological challenges in enumerating these tiny cells although progress has been made (12). Also, fecundity observations should not be studied in isolation but seen together with egg-size variations; reproductive investment (RI) \( RI = \text{mean egg dry weight (EDW)} \times F_p \) encapsulates the fundamental trade-off between egg size and fecundity (13). The lack of pairwise EDW and \( F_p \) data stands out, however, as typical in the marine literature. Taken together, a conceptual understanding of how immediate and past environmental drivers (14) affect RI and SRP (measured as TEP) is clearly required.

For both scientific and methodological reasons, the Atlantic herring \((SI\text{ Appendix, Fig. S1})\) was selected as a model species to address these issues. The sustainable harvest and well-being of this major player in the North Atlantic has recently been debated within the framework of the carrying capacity of pelagic ecosystems, with special reference to the Norwegian Sea due to the northerly shift in the migration of Atlantic mackerel \((Scomber scombrus)\) \((SI\text{ Appendix, Fig. S2})\). Major, transient falls in the abundance of prey (zooplankton) have been noted, but also seen before “the present mackerel era” \((SI\text{ Appendix, Figs. S1 and S2})\). Although trends in both directly and indirectly linked fish health and population-specific status under such situations, as for mackerel (16), corresponding RI responses remain unaddressed. In contrast to Atlantic mackerel or blue whiting \((Micromesistius poutassou)\), the third main planktivorous fish in question \((SI\text{ Appendix, Fig. S2})\), \( F_p \) in herring can be easily assessed as all developing oocytes grow in synchrony up to spawning, reflecting a clear-cut example of so-called determinate fecundity style (12). The fact that herring is a total spawner (all eggs shed at once) also simplifies the estimation of EDW as there is no batch effect on EDW (17). Finally, reproductive plasticity and, not least, adaptability also simplifies the estimation of EDW as there is no batch effect on EDW (17).

Specifically, we focus on three stocks of Atlantic herring (Fig. 1) with potentially different trade-offs between egg size and fecundity (26): Norwegian summer–autumn spawning herring (NASH), North Sea autumn–spawning herring (NSAH), and Norwegian spring–spawning herring (NSSH). No earlier reproductive information existed for NASH (27), comparably much smaller in stock size (28). As typical for these size-specific visual or filter feeders (15), gonad growth is fueled by preying on zooplankton in the upper water layers until overwintering (21, 22). Note that both North Sea herring (winter and autumn spawners combined) and NSSH collapsed in the late 1960s but recovered after management regulations \((SI\text{ Appendix, Fig. S1})\). Examples of published material on fecundity and egg size before these stock collapses are available (29–32). For NSSH, comprehensive datasets on fecundity exist from the previous 2 decades (21, 33, 34). To address RI variability, this information was systematically collated and supplemented by local sampling for all three stocks \((SI\text{ Appendix, Fig. S3})\). The resulting insights indicate that NSSH would be an ideal candidate to test the usefulness of general \( F_p \) formulas but also that a new conceptual framework for oocyte recruitment is paramount, including environmental lag effects. Thereafter, we examined how revised TEP values compare with corresponding standard values but also with larval abundance estimates (“larval index,” or LI), consulting the years from 1997 onward, i.e., when zooplankton data were regularly available \((SI\text{ Appendix, Fig. S1A})\). Such a study is appropriately timed due to the current downward trend in SSB of NSSH \((SI\text{ Appendix, Fig. S1A})\) related to poor REC \((SI\text{ Appendix, Fig. S4C})\), giving rise to concerns about the future fate of one of the largest fish stocks in the world.

**Results and Discussion**

**Overview of Stock-Specific Reproductive Cycles and Body Growth Patterns.** Our measurements \((SI\text{ Appendix, Table S1 and Fig. S3})\) of ovary \((SI\text{ Appendix, Fig. SSC})\) and oocyte-size development \((SI\text{ Appendix, Figs. SSD and S6})\), supported by earlier, similar types of datasets (see references in Fig. 1 and \(SI\text{ Appendix, Fig. S1})\), clarified collectively that the reproductive cycle of Atlantic herring differs markedly in length across stocks—lasting about 6, 9, and 12 mo for NSAH, NASH, and NSSH, respectively (Fig. 1). The appearance of the cortical alveoli stage was restricted to long days while the first vitellogenic cycle was timed due to the current downward trend in SSB of NSSH \((SI\text{ Appendix, Fig. S1A})\) related to poor REC \((SI\text{ Appendix, Fig. S4C})\), giving rise to concerns about the future fate of one of the largest fish stocks in the world.

**Fig. 1.** Schematic overview of the reproductive cycle of NASH, NSAH, and NSSH. Leading cohort oocyte diameter was used to reflect ovary development. Information on reproductive ecology was collated from published sources (19–24) and our own sources \((SI\text{ Appendix, Figs. S3, S5, and S6})\). Each stock experiences periods of intense summer feeding followed by overwintering. Note that NASH and NSAH spawn before overwintering whereas NSSH spawns afterward and that the length of the reproductive cycle varies by stock. The timing of the feeding season and overwintering of NASH were assumed to be equal to NSH due to overlapping distributions \((SI\text{ Appendix, Fig. S3})\). The annual cycle of zooplankton (prey) production in the North Sea and in the Norwegian Sea is illustrated (green bar) (25).

**Reproductive Investment Across Stocks.** Recent estimates standardizing reproductive investment either by total length \(RI_{TL} \) \((Fig. 2A)\) or by somatic weight \(RI_{WT} \) \((SI\text{ Appendix, Fig. S4A})\) were evidently highest for NSSH \((P \leq 0.001)\) and similar for NSAH and NASH \((P \geq 0.923)\). For both NSAH and NSSH, today’s values of \(RI_{TL} \) appeared markedly lower than those based on information dating back to the late 1950s/early 1960s \((Fig. 2A)\). Also, currently NSSH invests the most in reproduction whereas historically NSAH did so, in line with simulations showing a higher scope in RI for NSH \((Fig. 2A)\). The cold-water, productive zooplankton regime in the North Sea around 1960 \((SI\text{ Appendix, Fig. S1B})\) apparently boosted NSAH RI whereas the recent, opposite...
environmental situation in the Norwegian Sea (SI Appendix, Fig. S1A) should work the other way around for NASH and NSSH RI. The fact that recent NASH RI were markedly lowered despite normal temperature and zooplankton abundance situations (SI Appendix, Fig. S1B) supports the idea of a major regime shift in the North Sea, claimed to have happened in the mid-1980s (37). This regime shift also included altered key prey (copepod) biology (37). Note that only one historic fecundity sample was available for NSSH whereas three were available for NASH. However, also for NSSH indirect or direct environmental effects (see below) operating over large oceanic scales appear as plausible causes for the outlined changes in RI (37) whereas genetic bottlenecks effects related to the above-mentioned stock collapses seem less likely (38, 39). For quality assurance, RI were also regressed directly on TL, finding no evidence of any current difference between NSSH and NASH (slope, P = 0.934; intercept, P = 0.633; SI Appendix, Fig. S9B). This conflicting result, however, could be explained by differences in body allometrics (SI Appendix, Fig. S9C), i.e., higher W-at-TL for NSSH as well as NASH compared with NSSH (slope, P ≥ 0.766; intercept, P < 0.001) while similar for NASH and NASH (slope, P < 0.757; intercept, P = 0.120). Also, the consistent use of pre-overwintering RI	_{W} and RI	_{D} for all three stocks, using, in the case of NSSH, simulated individual weight data (40), reconfirmed that NSSH females presently allocate relatively the most to their gonads of the three stocks studied (P ≤ 0.045 and P ≤ 0.006, respectively). Generally, RI_{TL} was strongly correlated with RI_{I} (R ≥ 0.959; P < 0.001).

**Trade-Off Between Egg Size and Fecundity.** The three reproductive traits investigated, F_{P}, relative somatic fecundity (RF_{PS}), and EDW, were all well separated by stock in bivariate plots using TL as covariate (Fig. 2 B–D). EDW appeared (un)influenced by TL (P ≥ 0.123). NASH had the heaviest eggs (P < 0.001), whereas those of NASH and NSSH weighed the same (P = 0.617). NASH turned out to be among the most fecund Atlantic herring stocks reported so far (12, 22, 29). The presently seen trade-off between egg size and fecundity agrees with the general (13) and species-specific literature (26). However, unlike earlier herring studies, we used only pairwise fecundity and egg-size datasets as well as analyzed NASH. Also, for RF_{PS} of NASH, we found intermediate instead of expected high values (Fig. 2C) (cf. small egg size; Fig. 2D), obviously related to the small body size of these adults (SI Appendix, Fig. S7), balancing out RI_{D} (or RI_{TL}) at the same level as for the other, larger, highly fecund autumn spawner, NASH (SI Appendix, Fig. S9, and Fig. 24, respectively). Hence, the tactical pattern of small eggs in autumn spawners and large eggs in spring spawners of this species (26) was firmly confirmed, divergences thought to be related to spatiotemporal differences in zooplankton type and size (25). In contrast to general expectations of increased specific reproductive costs with growing body size (17), present RF_{PS} of NASH appeared unrelated to TL (P = 0.659) (Fig. 2C) (further elaborated on below). The same applied to NASH 2014 (P = 0.686) but is questioned due to the current short TL range (Fig. 2D). A period of half a century, F_{P} fluctuated markedly more than EDW, i.e., by 50–58 and 1–10%, respectively, reflecting collectively to NSAH and NSSH due to comparable trait responses (SI Appendix, Fig. S10). This suggests that not only time of spawning (36) but also the associated egg size are mainly genetically controlled, whereas varying levels of fecundity are widespread (17).

**Reproductive Ecology: The NSSH Case Study.** As F_{P} appeared strikingly more variable than EDW (SI Appendix, Fig. S10), and present data on RF_{PS} of NSSH displayed an exceptional downsizing with TL (Fig. 2C, cf. also SI Appendix, Fig. S4B), we aimed at understanding the full fecundity dynamics in NSSH. Historic F_{P}'s exceeded corresponding modern estimates (Fig. 3D). Ongoing down-regulation of vitelogenic oocytes due to atresia (21) probably explains why the relative position of the various F_{P} curves (Fig. 3) tended to vary with advancement in maturity represented by mean oocyte diameter (OD) (SI Appendix, Figs. S11 and S12 and Table S2, Eqs. SS–S12). Final (prespawning) F_{P} values, i.e., the standard point of reference in these respects, were evidently dissimilar (OD ≥ 1.200 vs. slope, P = 0.084; intercept, P = 0.001; RF_{PS} ≤ 0.123). This among-year difference was clearly body-size-dependent; the maximum/minimum factor increased from 1.50 at 32 cm to 2.02 at 38 cm for RF_{PS} (2007 vs. 2014). In other words, larger individuals were seemingly more sensitive to environmental influences. Note that this span in fecundity exceeded methodological difficulties in estimating annual SSB (factor: 1.20–1.49) (SI Appendix, Fig. S4A). Initial runs (GLM) showed that F_{P} in a given winter (prespawning situation) was an function of immediate body condition (individual W-TL pairs) and environmental temperature and feeding conditions experienced during preceding periods of oogenesis, explaining 69–77% of the variance depending on OD and model setting (SI Appendix, Table S3). The temperature impact across OD appeared unsystematic (SI Appendix, Table S3) requiring further analysis (see below). Importantly, whether sporadic cases of poor feeding situations, as in the summers of 1997, 2009, and 2010 (SI Appendix, Fig. S1A), appeared adjacent in time to the resulting winter F_{P} in question or during similar time windows of early oocyte recruitment (Fig. 1) in past reproductive cycles appeared of trivial importance (SI Appendix, Table S3 and Fig. S14). Therefore, females which had experimental little food at some adult stage were merged as “poor- and good-seasons females” (P&GSF) to be held against “good-seasons females” (GSF) only, considering up to three to four feeding seasons back in time (SI Appendix, Fig. S14). As density-dependent effects
also played a role (see below), these terms were not necessarily linked to zooplankton abundance only. Therefore, P&GSF could apparently display fecundity lag effects operating over several seasons (SI Appendix, Fig. S14). Down-regulation of fecundity was omnipresent, but, surprisingly, dampened down for P&GSF compared with GSF (SI Appendix, Fig. S15), indicating that cutbacks in early oocyte recruitment (SI Appendix, Fig. S16 E and F) caused these low $F_P$ for P&GSF (1999, 2014, and 2016; Fig. 3D) rather than prevalent atresia mediated by poor body conditions as such. Massive atresia (41) was unlikely an important issue as no samples had mean Fulton's $K < 0.7$ (SI Appendix, Fig. S17A), $K = 0.7$ being the critical threshold value at the individual level in these regards (33) (see details below). Use of the extensive Institute of Marine Research (IMR) Central Database (CDB) documented that 2014 (P&GSF) had the highest whereas 2007 (GSF) had the lowest W-at-TL (slope, $P = 0.080$; intercept: $P = 0.018$; all modern years included; SI Appendix, Fig. S17B), which again deviated from conventional expectations. The $F_P$ in 1998 was intermediate (Fig. 3B), perhaps because the detrimental effect of the poor 1997 feeding season was still developing and thereby causing bigger impacts in 1999, as observed (Fig. 3B). Altogether these lines of evidence called for increased attention on early oocyte recruitment dynamics. This view was encouraged by the predictive power ($R^2$) of $F_P$ weakened with advancement in OD from 300 to 500 $\mu$m (SI Appendix, Table S4, July), seen also partly from 900 to 1,200 $\mu$m (SI Appendix, Table S3, February). However, $R^2$ in July was generally low, probably due to rapidly changing body metrics at this time of peak feeding (15). In summary, P&GSF and GSF showed highly different size-specific $F_P$ and $RF_{PW}$ trajectories as a function of $K$, although collectively responding positively to increasing $K$ (SI Appendix, Fig. S18). The virtual lack of any effect of TL on $RF_{PW}$ for P&GSF was striking (SI Appendix, Fig. S18B). In essence, measured body condition failed to adequately categorize experienced feeding history but was useful as a proxy of $F_P$ within each P&GSF and GSF category. This meant that, for example, applications of GSF-segmented $F_P$ formulas (SI Appendix, Tables S5 and S6) on P&GSF biometric data gave overly optimistic estimates of P&GSF $F_P$ (SI Appendix, Fig. S14). This knowledge about lag between cause and effect questions the standard use of general fecundity (GF) formulas (SI Appendix, Tables SS and S6), not only for herring but probably also for other teleosts whose early oocyte recruitment is tightly tied to past seasonal fluctuations in food availability. Consequently, although we produced an extensive list of multiple regressions to predict $F_P$ (SI Appendix, Tables S2 and S5–8), one simple, main message emerged: P&GSF and GSF datasets were largely incompatible in these respects. As an example, subsequent exclusions of P&GSF 1999 and 2014 datasets from statistical tests on $F_P$ vs. TL and W increased $R^2$ abruptly from 0.39 to 0.83 (SI Appendix, Table S5; Eq. S23 vs. Eq. S29). These findings also showed that GSF $F_P$ could be more reliably predicted ($R^2 = 0.83$) than P&GSF $F_P$ ($R^2 = 0.43$) (SI Appendix, Table S5; Eq. S29 vs. Eq. S9). Also, GSF $F_P$ could be effectively given ($R^2 = 0.70$) by replacing W with age (SI Appendix, Table S5; Eq. S29), but this predictive power disintegrated ($R^2 = 0.17$) for P&GSF (SI Appendix, Table S5; Eq. S28). Selective use of the homogenous GSF material (SI Appendix, Table S5, Eq. S25) documented that environmental temperature during oocyte growth affected $F_P$ by about 10% but that this small, negative effect faded away in prespawners (SI Appendix, Table S9). A higher temperature is known to increase the atretic turnover rate and thereby accelerate down-regulation of vitellogenic oocytes (17, 21). Both body metrics were not necessarily reflected in $F_P$; therefore the establishment of any NSSH TEP series required answering which segmented $F_P$ formula (SI Appendix, Table S5) to use in a given situation (Q1) and, linked with this, how long a time will any lag effect last (Q2). Regarding Q1, the above remark that the positive influence of TL on prespawning $RF_{PW}$ was absent for P&GSF but present for GSF [P&GSF: $P = 0.627$; 1999, 2014, and 2016 (grouped data); GSF: $P < 0.001$; 1997, 2006–2008 (grouped data); SI Appendix, Fig. S13D] pointed to $K$ (SI Appendix, Table S10, 1994–2014 (IMR CDB)) regressed on TL as a way forward, i.e., the $K_{sp}$ (Fig. 4). Although $K$ and $K_{sp}$ were, as expected, positively related ($P = 0.0134$), the data points were highly scattered with low explanatory power ($R^2 = 0.06$) (SI Appendix, Fig. S19). The 71-y time series revealed the existence of successive “waves” of both mean $K$ and $K_{sp}$, but these reciprocal rhythms were clearly out of phase recently, i.e., $K$ turning extremely positive and $K_{sp}$ extremely negative (Fig. 4A). A contemporary drop has also been seen for Northeast Arctic cod liver index, attributed to ocean warming (42) (cf. temperature rise in SI Appendix, Fig. S6). Concentrating on $K_{sp}$ predominantly negative values appeared before the stock collapse and positive values peaked midway during the collapse followed by values fluctuating by large negative values, as also detected in the beginning of the series (Fig. 4). $K_{sp}$ was negatively related with SSB when SSB was $\geq 8$ million tonnes (t), as seen before 1960 (SI Appendix, Fig. S1) ($R^2 = 0.43$; $P = 0.006$; SI Appendix, Fig. S20), but not later when SSB turned <8 million t ($P > 0.136$; SI Appendix, Fig. S20). In cases of no fecundity information being available, P&GSF and GSF could in principle be split apart by $K$ and $K_{sp}$, were largely incompatible in these respects. As an example, sub-
years later (Fig. 4A). This noted pattern agrees with that younger classes of spawners are successively entering and the older, affected ones are leaving the population, assuming here that TL effectively reflects age (SI Appendix, Fig. S6A). Although within-seasonal developments in body condition (e.g., K) of P&GSF and GSF were comparable (SI Appendix, Fig. S16A and B), the corresponding trends in Kslope were apparently not (SI Appendix, Fig. S23). For repeat spawners (TL ≥ 32 cm), the P&GSF Kslope (season 2013–2014) remained negative during the length of vitellogenesis whereas the GSF Kslope (season 2006–2007) turned positive before spawning (SI Appendix, Fig. S23). Similar trends were seen for somatic K, i.e., KS (SI Appendix, Fig. S24). These individual details reconfirmed that massive atresia was not the underlying cause for the low P&GSF FK and none of the P&GSF showed K < 0.7 during the main atretic window in October–November (21) (Fig. 1).

We argue that traditional proof-of-concept evaluations on SSB as proxy for TEP should be treated with caution. This was seen by applying GSF but also GF formulas on one single year of data (2014) referring to a clear-cut P&GSF situation (Fig. 3D): TEP vs. SSB split by age class gav in every case a strong relationship (R² ≥ 0.94; P < 0.001) (Fig. 4B). However, use of the GSF formula inflated TEP of 10-year-old herring (cf. the strong 2004 year class; SI Appendix, Fig. S4C) by 31 and 11% by the GF formula. Compared with the real P&GSF situation, both these regressions reflected a significantly different TEP picture (GSF formula: slope, P = 0.004; intercept: P < 0.001; GF formula: slope, P = 0.076; intercept: P = 0.023). In the following time-series analysis (1997–2014; Fig. 4C) using either segmented formulas or one general formula altogether, both approaches indicated significant relationships between TEP and SSB, although dampened in the first case (segmented formulas: R² = 0.56; P < 0.001; general formula: R² = 0.74; P < 0.001), but otherwise similar (slope, P = 0.722; intercept: P = 0.590). The fact that the GF formula smoothed out trends was also seen in a 16% reduction in the interannual variance in TEP (P = 0.055) compared with the de facto situation. For unknown reasons survey abundances of first-feeding NSSH larvae (LI) were poorly correlated with our quality-secured, segmented TEP estimates (r = 0.304; P = 0.168; SI Appendix, Fig. S25A). The relative survival index (RSI; LI/TEP) ranged from 6 to 28% (SI Appendix, Fig. S25B). Based on the fact that TEP, LI and RSI values following the last strong year class of NSSH in 2004 (SI Appendix, Fig. S4C) are rather ordinary relative to 1997–2004, we can safely reject that the present poor recruitment situation of NSSH is due to inferior egg and/or first-feeding larval production. This might seem surprising as P&GSF have been frequent contributors, but a typical P&GSF still produces thousands of eggs (Fig. 3D). Obviously, the dominating factor counteracting the fall in stock productivity has been major cuts in landings, falling steadily from about 1.7 million t in 2009 to 0.3 million t in 2015 (28). Mean TL has increased in parallel (SI Appendix, Fig. S4B), putting Fp upward (Fig. 3). Altogether, the current recruitment problem of NSSH should be investigated between later larval stages and the 0-group stage, possibly related to mackerel predation (44) (SI Appendix, Fig. S2) or to shifts in spawning grounds (45) in warmer waters (46).

Our findings of P&GSF switching to a low reproductive investment modus required conceptual insights in early oocyte recruitment (EORn). Generally, poor seasons lead to decreased oogonial proliferation (fewer oogonial nests) and increased apoptosis and vice versa in good seasons (11). As apoptosis also affects follicular cells, apoptosis might actually trigger atresia (47); atresia is seen for both small and large oocytes (48). Evidence shows that oogonial proliferation and folliculogenesis happen shortly after spawning (49). Hence, EORn of NSSH should be particularly prevalent in March–April (Fig. 1), i.e., near the spring bloom (40). Although low EORn indicated episodes of low zooplankton abundance, P&GSF changed this downturn in oocytic production into a characteristic property. Thus, the usual splitting into unfavorable and favorable environmental conditions as overlying frames in oogenesis studies becomes inadequate. Our conceptual EORn model points to...
negative cascading effects of a poor feeding season on the different developmental phases of primary (previtellogenic) oocytes (PVOs) (17, 30) (Fig. 5 and SI Appendix, Fig. S26). Hence, fecundity studies, including experimental ones (51), limited to one season only will notably underestimate the potential dynamics. As for the sophisticated neuroendocrinological pathways involved (52), much are still unknown, but this article documents that the standard focus on secondary oocytes in marine laboratories needs to be supplemented with EORX studies if Fv dynamics is to be better understood.

Materials and Methods

This section is detailed in SI Appendix, SI Materials and Methods covering the following subject areas: data repositories on adult population demography, environmental temperature, and zooplankton abundance; published reproductive information (including data bases); additional field sampling of reproductive information; manuals for processing of samples onboard and in the laboratory; automated methodology to determine fecundity; routines for egg dry weight recording; estimation of total egg production and consulted data on larval abundance and recruitment at age 0; definition of various reproductive indices; statistical analyses and models; and a list of abbreviations. SI Appendix, SI Materials and Methods includes 27 graphical illustrations, 2 data inventories, and 9 detailed statistical appendixes, all from this study.

ACKNOWLEDGMENTS. We thank researchers Dr. A. Thorsen for expert advice on ImageJ and Dr. Richard Nash for constructive comments; technicians J. Røttingen and Ø. Sørensen for help during field surveys; and B. Njå Strand, M. Tolleshaug, and V. Mangerud for laboratory assistance performed at Institute of Marine Research (IMR). The work was supported by PhD Grant 240467/2012-4 (to T.C.D.S.S.) from the Brazilian National Council for Scientific and Technological Development and by IMR Project No. 14861 (to O.S.K.).