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Do Norway pout (*Trisopterus esmarkii*) die from spawning stress? Mortality of Norway pout in relation to growth, sexual maturity, and density in the North Sea, Skagerrak, and Kattegat

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The mortality patterns of Norway pout (NP) are not well understood. It has been suggested that NP undergo heavy spawning mortality, and this paper summarizes and provides new evidence in support of this hypothesis. The very low–absent fishing activity in recent years provides a unique opportunity to analyse the natural life-history traits of cohorts in the NP stock in the North Sea. Based on the ICES trawl survey abundance indices, cohort mortality is found to significantly increase with age. We argue that this cannot be explained by selectiveness in the fishery, potential size-specific migrations out of the area, higher predation pressure on older individuals, or differences in survey catchability by NP age from before to after spawning and that it is higher in the main spawning areas than outside. We found that natural mortality (M) is significantly correlated with sexual maturity, sex, growth, and intraspecific stock density. All of this is consistent with a greater mortality occurring mainly from the first to the second quarter of the year, i.e. spawning mortality, which is discussed as being a major direct and indirect cause of stock mortality.

Introduction

The North Sea–Skagerrak–Kattegat Norway pout (NP; *Trisopterus esmarkii*) stock is an important food source for commercially important fish species, such as cod (*Gadus morhua*), saithe (*Pollachius virens*), haddock (*Melanogrammus aeglefinus*), mackerel (*Scomber scombrus*), and whiting (*Merlangius merlangus*). Therefore, this small, short-lived species is an important prey organism in the North Sea ecosystem (Sparholt *et al.*, 2002a; ICES, 2008; Rindorf *et al.*, 2010). In addition, the NP stock is usually a direct target of a significant small-meshed fishery for reduction (industrial) purposes (ICES, 2007a, b, c, 2010).

The time-series of the NP stock mortality shows substantial differences between natural mortality by age as estimated by Sparholt *et al*. (2002a), the MSVPA (multispecies virtual population

analysis) model, and the SURBA (survey-based assessment) model (ICES, 2004, 2006, 2008; Supplementary material). Despite these differences, constant values of natural mortality of $M = 0.4$ per quarter for all ages are still used in the ICES single-stock analytical assessment (ICES, 2010).

Although mortality by predation of the NP stock decreases or remains somewhat constant as fish grow older, based on documentation from existing stomach sampling programmes and MSVPA analyses (Sparholt, 1994; ICES, 2006, 2008; Rindorf *et al.*, 2010), total natural mortality increases with age (Sparholt *et al.*, 2002a, b). Total mortality is also substantially higher than the fishing mortality documented through the ICES single-stock assessments (Sparholt *et al.*, 2002a; ICES 2007a, b, c, 2008, 2010). As a result, total mortality (Z) cannot be exclusively explained by fishing activities and direct predation mortality;

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there is another important source of natural mortality. The highest total mortality rates have been observed between the first (Q1) and second (Q2) quarters of the year, which correspond to the spawning season (Sparholt *et al.*, 2002b; Lambert *et al.*, 2009).

Residual mortality, i.e. natural mortality caused by factors other than predation, is not well known or documented for fish in general nor are the processes contributing to it (Baur *et al.*, 2006; Bass *et al.*, 2007; Golubev, 2009; Gislason *et al.*, 2010; Partridge, 2010). Several small, short-lived fish species have adult natural mortalities of more than 0.6 that increase with age (e.g. Gislason *et al.*, 2010). The increase in M with age during the adult life stage is, however, not well investigated for fish because it is difficult to isolate M from fishing mortality (F), but it has been documented for some stocks of small fish species (Beverton, 1963; Caputo *et al.*, 2002; Cook, 2004; Terzibasi *et al.*, 2007; Golubev, 2009; Uriarte *et al.*, 2010). For several fish species, there is evidence of residual mortality as a result of active gene-directed and age-determined apoptosis, senescence, and diseases associated with spawning. For some short-lived fish species, this is associated with truncated ontogeny, accelerated gonad maturation, and spawning events (e.g. Caputo *et al.*, 2002; Terzibasi *et al.*, 2007). Mediterranean goby (*Aphia minuta*) seems to have an endogeneous timer-inducing adult mortality immediately after the first spawning season by causing irreversible intestinal deterioration (Caputo *et al.*, 2002). Age-dependent degeneration or the dysfunction of several organs and age-related pathological changes similar to those of mammals has been demonstrated for a variety of fish species (Woodhead, 1998; Kishi *et al.*, 2003; Reznick *et al.*, 2006; Buston and Garcia, 2007). The short lifespan of the fish *Nothobranchius furzeri* is associated with explosive growth, accelerated sexual maturation, and the expression of ageing-genes causing behavioural and histological changes (Terzibasi *et al.*, 2007). Spawning mortality is observed for other small, short-lived fish species such as capelin (*Mallotus villosus*) and anchovy (*Engraulis encrasicolus*; Uriarte *et al.,* 2010) and suggested for Northeast Arctic cod (*G. morhua*), where males mature earlier and have higher mature mortality than females (Jakobsen and Ajiad, 1999). Indirect spawning-related mortality may also originate from the abrupt and substantial energy loss with increased vulnerability and exposure to invertebrate scavengers and predators. However, to our knowledge, it has not been reported for small species of the Gadidae family. In the North Sea, small gadoids, such as blue whiting (*Micromesistius poutassou*), poor cod (*Trisopterus minutus*), pouting (*Trisopterus luscus*), silvery cod (*Gadiculus argenteus*), and NP, have been observed living up to ages 10–20, 5, 4, 3, and 5 years, respectively (www.fishbase.org), indicating that spawning stress and mortality might be an issue for some of these species.

Previously, data had been inadequate to investigate these dynamics for NP; however, there is a unique opportunity to estimate M for this normally exploited stock because fishing activity has been very low since 2003. The targeted fishery was totally closed in 2005 and 2007 as well as for the first half of 2006 because of a low stock level. In those periods, M approximately equals total mortality (Z).

It is essential, for both ecosystem and single-stock management, to investigate the natural mortality dynamics of NP, the periodical variability herein, and to provide accurate data on life-history traits influencing mortality rates used in ICES analytical assessments. Therefore, it is important to know whether this

small gadoid species dies abruptly and at a relatively young age from spawning stress (e.g. Ursin, 1963; Bailey and Kunzlik, 1984; Lambert *et al.*, 2009) and energy depletion, similar to some salmon species, capelin, anchovies, and gobies, or if there are other reasons for which they have a short lifespan. In the study by Lambert *et al.* (2009), maturity and growth dynamics were thoroughly investigated. In the present paper, we analyse the level of natural mortality in relation to maturity, sex, and growth dynamics on quarterly and geographically disaggregated bases. This is done by the use of long-term data time-series in an effort to understand the mechanisms behind the dynamics of mortality, including predation and fishing mortality. Lambert *et al.* (2009) and the present study have different objectives, but overlapping documentation, and some figures from Lambert *et al.* (2009) have, therefore, been used in the present study. We tested three null hypotheses: (i) H_01: natural mortality is constant over years (at a level of approximately $M = 1.6$) and quarters ($M = 0.4$) and independent of age; (ii) H_02: there is no relationship between natural mortality and reproduction-specific life-history traits of NP, such as sex, maturity, or growth and, thus, mortality is decoupled from spawning; and (iii) H_03: there is no density-dependence, neither intra- nor interspecific, in NP mortality.

Material and methods

To complete the objectives of this study, extensive disaggregated data were used, involving complex data compilation, manipulation, and analyses (see also Lambert *et al.*, 2009). The yearly abundance indices were computed from survey raw catch per unit effort (cpue) data by fish length combined with raw sex–maturity age–length keys (SMALKs). Data were available from the ICES coordinated International Bottom Trawl Survey (IBTS) for 1983–2006 covering the North Sea and Skagerrak–Kattegat (Anon., 2004). These indices were stratified by roundfish areas (RFAs) 1, 2, 3, 4, 7, 8, and 9 (see RFAs in Figure 1 in Lambert *et al.*, 2009). The total area differs and is wider than the combined index area covered for the standard calculation of the ICES IBTS abundance indices to assure the coverage of the full NP stock distribution area needed for the area-disaggregated analyses of geographical variability (Anon., 2001, 2004; Sparholt *et al.*, 2002a, b; ICES, 2004, 2007a, b, c). The NP stock is distributed mainly in the northern North Sea, Skagerrak, and Kattegat, and potential seasonal migrations do not result in the migration out of this shelf area because the NP stock is not distributed in areas with depths greater than 200–250 m (Sparholt *et al.*, 2002a, b). Data manipulation was necessary to perform the analyses of geographical variation because the SMALKs were not always complete for all areas for every year and quarter (i.e. for each cell). The initial data were taken from the ICES DATRAS database, and where information was missing, empty cells were filled with estimates based on the methods given in the IBTS manual and on biological and ecological knowledge (Anon., 2001, 2004; ICES 2007d). Such data filling was necessary in the SMALKs because there was a risk to bias data and results if valid and available cpue information were excluded from cells and not used in the analyses because there were no SMALK observations for these cells (Hoenig and Heisey, 1987). The manual provides standard substitution procedures for converting length data to age data when age–length keys (ALKs) are missing (for one RFA, 1 year, and one quarter) or are not reliable (e.g. an RFA with < 25 otoliths sampled). Following the IBTS manual, the ALKs of certain RFA were used to replace the missing observations of the neighbouring RFAs in

a given quarter and year, when needed. However, the same procedure for converting data to sex and maturity data used in Lambert *et al.* (2009) was not adequate for the present study because of the spawning migration out of Skagerrak–Kattegat and its related sex distribution patterns (Ursin, 1963; Poulsen, 1968; Lambert *et al.*, 2009). Maturity ratios have proven variable between years (Lambert *et al.*, 2009), whereas sex patterns are more consistent. Consequently, the missing observations in the SALKs were replaced by the average of all available years for the same quarter and RFA. Therefore, total abundance indices, both in total and by sex, were computed following the procedure described by ICES (Anon., 2001).

Total mortality (Z) was calculated from the cpue values (Ricker, 1975; Sparre and Venema, 1989):

$$Z = \frac{1}{t_2 - t_1} \ln \frac{\text{cpue}(t_1)}{\text{cpue}(t_2)}, \qquad (1)$$

where cpue is the catch in the number of individuals per trawl hour, and t_1 and t_2 represent ages, with $t_1 < t_2$.

To perform a robustness check and sensitivity analysis on the above described data-manipulation procedures for filling in gaps in SMALKs and SALKs, the yearly Z values by age were computed with Equation (1) using the revised area-disaggregated IBTS cpue data as described above (for age groups 1–4+) and compared with mortality estimates from abundance indices using the ICES standard calculation procedures and area. The comparison showed that the dynamics of the mortality from the revised cpue indices were very similar to those of ICES (Table 1). The present data compilation establishing more disaggregated data was thus determined to be valid and was preferred to investigate quarterly and sexual-disaggregated mortality patterns.

Table 1. Total mortality (Z) calculated based on IBTS cpue data according to ICES standard calculation procedures and according to the revised calculation procedure.

Cohort	Z_{1-2} ICES	Z_{1-2} (revised)	Z_{2-3} ICES	Z_{2-3} (revised)
1981	–	–	2.07	2.52
1982	0.83	0.84	2.60	2.56
1983	1.25	1.23	4.27	4.08
1984	1.81	1.74	1.84	1.91
1985	1.46	1.37	3.47	3.56
1986	1.48	1.38	1.43	1.58
1987	−0.72	−0.55	1.88	1.89
1988	0.99	1.03	1.75	1.35
1989	0.60	0.52	3.10	3.14
1990	1.02	0.96	1.23	1.26
1991	0.65	0.67	3.69	3.60
1992	1.97	1.89	1.58	1.53
1993	0.85	0.85	1.24	1.31
1994	0.81	0.84	1.37	1.44
1995	−0.47	0.26	1.72	1.75
1996	0.60	0.66	2.08	2.08
1997	0.53	0.60	2.22	2.14
1998	0.83	0.71	1.88	1.91
1999	1.04	1.02	1.18	1.18
2000	0.48	0.64	2.15	2.10
2001	1.14	1.00	2.83	2.81
2002	1.19	0.96	2.32	2.47
2003	1.92	1.79	1.58	1.81
2004	1.55	1.59	–	–

The disaggregated Z-values were, in a few cases, estimated to be negative, particularly from Q1 to Q2 and from Q3 to Q4, which is likely a consequence of incomplete spatial coverage in Q2 and Q4. ICES has evaluated the quality of the IBTS Q1 and Q3 to be high, and those quarters are estimated by ICES to be consistent with respect to coverage and catchability and are used in stock assessments (Fraser *et al.*, 2007; ICES, 2007a, b, c). Consequently, the indices from Q1 and Q3 were mainly used in this study.

For $H_0 1$, the IBTS estimates of Z by age were compared with the MSVPA and SURBA model estimates (ICES, 2004, 2006, 2008) and to the estimates from Sparholt *et al.* (2002a) to evaluate seasonal and long-term trends in mortality as well as its age-dependence. Emphasis was placed on the more recent period when fishing activity, and fishing mortality were very low or zero in the NP fishery.

For $H_0 2$, the evidence for linking mortality patterns to maturity and growth dynamics, i.e. indicating potential spawning mortality, was summarized based on Lambert *et al.* (2009). The mortality of mature individuals could not be computed directly because the percentage of fish maturing from one quarter to the next (from, e.g. histological studies) is unknown (Lambert *et al.*, 2009). Therefore, alternative multiple linear regressions and analyses of variances were performed to check for consistency between total mortality (Z) and sex and maturity ratios.

Concerning $H_0 3$, variation in growth and maturity has been shown to be dependent on both intra- and interspecific densities (Lambert *et al.*, 2009). The mortality rates were consequently analysed in the context of variations in density. Linear regressions of Z as a function of the NP stock numbers and biomasses were tested and were also tested as a function of the spawning-stock biomasses (SSBs) of the main predator stocks of cod, saithe, haddock, mackerel, and whiting (ICES, 2007a, 2009).

Results

### Magnitude and variability of mortality by age ($H_0 1$)

Z by age does not show periodical trends over the period 1983–2006, except seasonal trends, and Z increases with age for all years (Figures 1 and 2; Supplementary material), i.e. both in years with and without targeted fishery, so the fishery cannot explain the difference. This age-dependent mortality is consistent for Z_{age3}, but the few exceptions here may be artefacts because of the scarcity of age group 4 individuals observed. For 2005, Z corresponds to M, because the fishery was closed in that year (Figure 1). Here, M_{age1} (1.59) is equivalent to the value used in the assessment, $Z = 1.6$. M_{age2} and M_{age3} are higher at 1.81 and 2.11, respectively. This age-dependent mortality confirms the conclusions obtained from the SURBA model analyses performed by ICES (ICES, 2004; Supplementary material) and from Sparholt *et al.* (2002a), while contradicting the MSVPA outputs indicating constant natural mortalities by age (ICES, 2004, 2006, 2007a, 2008). Both the 2008 and the ICES WGSAM 2011 results show some annual variability in the rate of mortality by predation (M_2), but a similar level for M_2 at ages 1 and 2.

Dynamics of maturity, spawning time, and place in relation to mortality ($H_0 2$)

From Lambert *et al.* (2009), we know that the ratio of mature individuals at ages 2 and 3 decreases from Q1, i.e. spawning time, to Q3 (Figures 2 and 13 in Lambert *et al.*, 2009). In addition, very few post-spawning fish have been recorded despite extensive
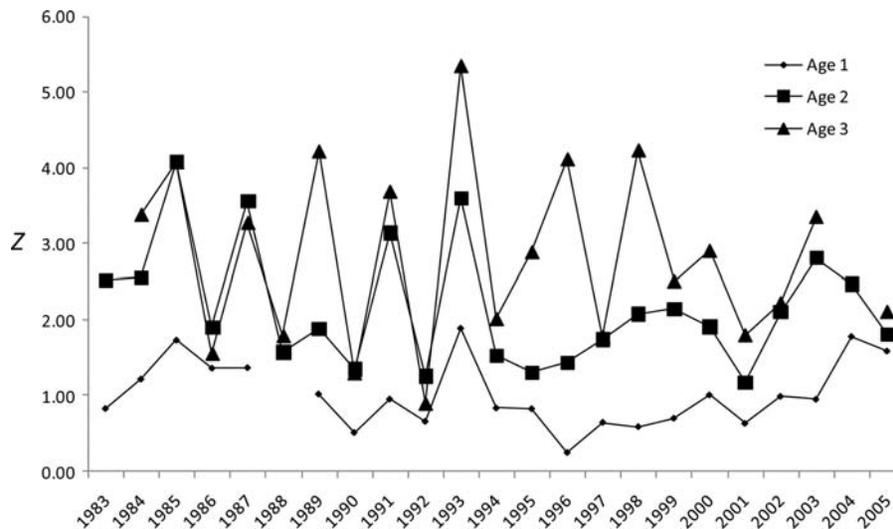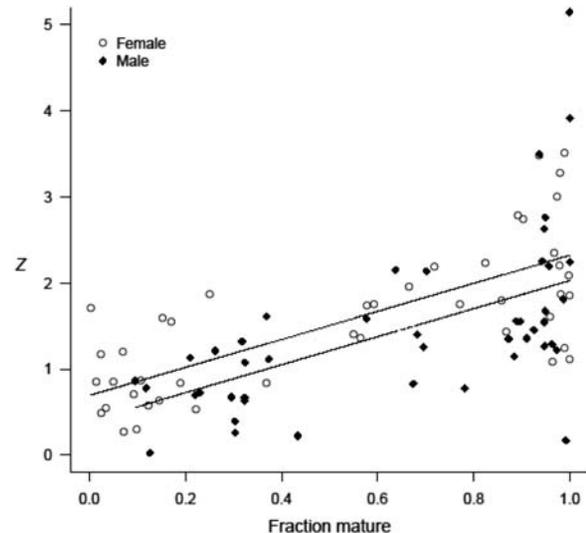
Figure 1. Total mortality (Z) by age over a 23-year period calculated according to Equation (1) based on revised IBTS Q1 cpue data. The negative value from 1988 age 1 was omitted from the calculation.
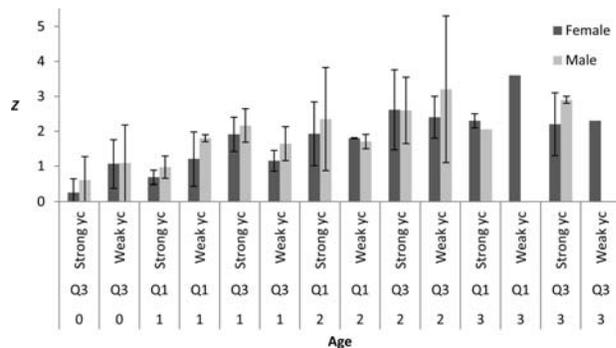
Figure 2. Seasonal total mortalities (Z) by sex and age for strong and weak year classes based on revised IBTS Q1 and Q3 cpue data. Z is calculated according to Equation (1). Error bars represent the standard deviations.

Figure 3. Total mortality (Z) of females (black dots) and males (white dots) as a function of the fraction mature for age groups 1 and 2. Z is calculated according to Equation (1) and based on the revised IBTS cpue data. Regression t-test statistics: $p < 0.001$ for females and $p = 0.058$ for males.

survey efforts, indicating a high mortality of mature individuals following the spawning event (Figure 2 in Lambert et al., 2009). The maturity ratio also increases with age for both sexes and shows a strong spatial pattern, reflecting likely effects of spawning, as explained below (Figures 2, 3, 13, and 14 and Table 3 in Lambert et al., 2009). Spawning areas of the NP stock are identified in Lambert et al. (2009), and the percentage of mature individuals is significantly higher in the main spawning areas RFA1 and RFA3, where the decrease in the maturity ratio from Q1 to Q3 is most evident (Figures 3 and 13 and Table 3 in Lambert et al., 2009). This strongly indicates a link between spawning and greater mortality during the breeding season, i.e. direct or indirect mortality caused by spawning stress. Although mortality cannot be directly calculated for the spawning areas during and just after the spawning period, the yearly total mortality for both sexes is positively correlated with the overall maturity ratio assessed during the spawning season (Figure 3 and Table 2; Figures 2, 3, and 13–15 and Table 3 in Lambert et al., 2009). Figure 3 shows a low mortality rate by sex until ~50% of the individuals are mature (with an unexplained gap between 0.4 and 0.6), a much higher rate above 60%

are mature, and a very high level above 90% are mature. The spread around the latter high level indicates that some other factors apart from the fraction mature potentially influence mortality.

Growth dynamics in relation to mortality ($H_0 2$)

The growth of NP shows strong spatio–temporal differences (Figure 8 and Table 5 in Lambert et al., 2009). Body weight is generally stable from Q1 to Q2, with a notable exception found in the western North Sea, where age group 2 loses considerable weight. This is likely to be spawning-related because this area covers the main spawning ground of the stock. Besides the loss in weight, a general decline in mean length-at-age from Q1 to Q2 is also

Table 2. Statistics: *F*-test and the corresponding *p*-values of the multiple linear regression of total mortality (*Z*) from Q1 vs. sex and fraction mature.

	Estimate	s.d.	*t*-value	$p(>|t|)$
Intercept	0.69	0.16	4.38	<0.001
Sex: female	-0.29	0.15	-1.92	0.06
Fraction mature	1.63	0.21	7.61	<0.001
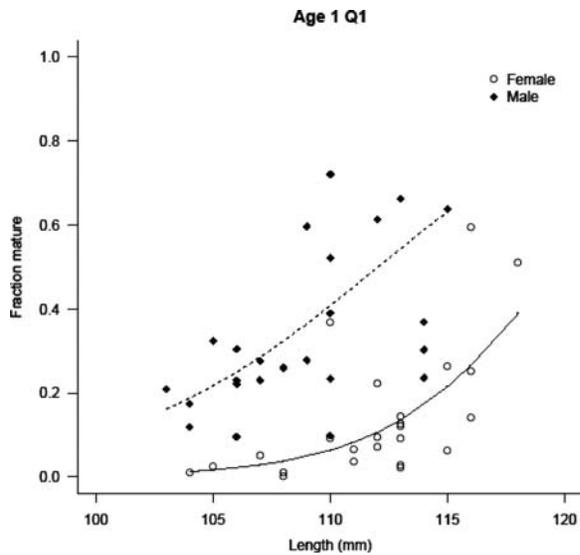
Figure 4. Relationship between the fraction mature and the mean length-at-age MLA (A1 Q1; males, $p < 0.001$; females, $p < 0.001$). Females, white dots and continuous curves; males, black dots and dashed curves (from Lambert *et al.,* 2009).

observed for both females and males (Figure 8 and Table 5 in Lambert *et al.*, 2009), implying that the proportion of large individuals has decreased from before to after spawning.

Integrated growth and maturity patterns in relation to mortality ($H_0 2$)

When recruits benefit from favourable growth conditions during their first year, i.e. reach relatively large mean length at age 1 in the first quarter (MLA1 Q1), more individuals will mature before the spawning season (Figure 4). This clear pattern is observed for both females and males. Males mature earlier and at smaller sizes than females (Figure 5). Consequently, males form the major part of the spawning stock during the first spawning season of a cohort. This pattern coincides with the age 1 and 2 mortalities for males being higher than for females in Q1 (Figure 2), where males undergo a significantly greater mortality than females by an average of 0.2 (paired *t*-test, $t = 3.059$, d.f. = 101, $p = 0.003$), potentially explained by spawning-associated mortality.

Density-dependence in mortality related to density-dependence in maturity and growth ($H_0 3$)

Early ages of less abundant cohorts show consistently higher mean mortality rates than the more abundant cohorts of both sexes, although the standard deviations are too high for this difference

to be statistically significant (Figure 2). The negative relationship between year-class strength and the mortality rate of young age groups was investigated further. It appears that total mortality of age 1 males and females (Figure 6) tends to be lower when density is higher, although not significantly. No intraspecific relationship between mortality and density was observed for age 2 or 3.

The decreasing pattern in mortality in relation to intraspecific density over time (Figure 6) is unlikely to be caused by predation, even if it is generally accepted that higher prey density usually results in overall lower predation mortality (ICES, 2006, 2008). No significant interspecific density-dependence in *Z* for age 1 or 2 was found in relation to SSB for the most important predator stocks in the North Sea known to prey upon NP (ICES, 2006, 2008), i.e. saithe, haddock, cod, and whiting (Figure 7), nor has this been found for *Z* by sex (not shown). A general pattern indicates that mortality tends to increase when the main predator stocks become more abundant (Figure 7). However, this is not significant, and no seasonal patterns have been found to explain the quarterly patterns observed in the increasing mortality by age (Figure 2).

Lambert *et al.* (2009) showed that the maturity rates of age 1 NP were also negatively influenced by density (Figures 5 and 15 in Lambert *et al.*, 2009). The age and the length at which 50% of the fish are mature increase with increasing recruitment (Figure 18 in Lambert *et al.*, 2009). Variations in natural mortality can consequently be explained by spawning mortality, i.e. maturity occurs later and, thus, spawning mortality is lower at high population densities.

This correlation is supported by the relationships between growth, density, and mortality. The mean length at age 1 (MLA1) Q1 is negatively correlated with density (Figure 8), and MLA1 Q1 is lower for strong year classes (female, $p = 0.05$; male, $p = 0.03$). At age 2, the decrease is only significant for females ($p = 0.04$).

Discussion

### $H_0 1$: natural mortality is constant over years and quarters and independent of age

This hypothesis is rejected. The present study shows that the annual NP total mortality *Z* varied over the last 25 years, but no overall periodical trend could be observed except seasonal variation. There is a distinct and consistent age difference in *Z*. *Z* increases significantly with age and, based on Sparholt *et al.* (2002a), the peak in the length distribution representing larger individuals disappears between Q1 and Q2. The total mortality from 2005 to 2006 shows the same age pattern as for the full period investigated in the present study, i.e. mortality increases from ages 1 to 3. For these years, mortality corresponds to the actual natural mortality because the fishery was closed at that time. Both in historical times of relatively higher fishing mortality and in the most recent years of low fishing intensity, total mortality was highest for the oldest fish. Consequently, the effect of higher fishing activity on the oldest age groups cannot explain the observed trend. Furthermore, fishing intensity and mortality (ICES, 2010) in the directed NP fishery are actually highest in Q3 and Q4, which cannot explain the higher *Z* in Q1 and Q2 (Lambert *et al.*, 2009), i.e. the seasonal patterns in *Z*. Also, no sex-selective fishery was evident from the biological sampling from the fishery (not shown) that would explain the sexual differences
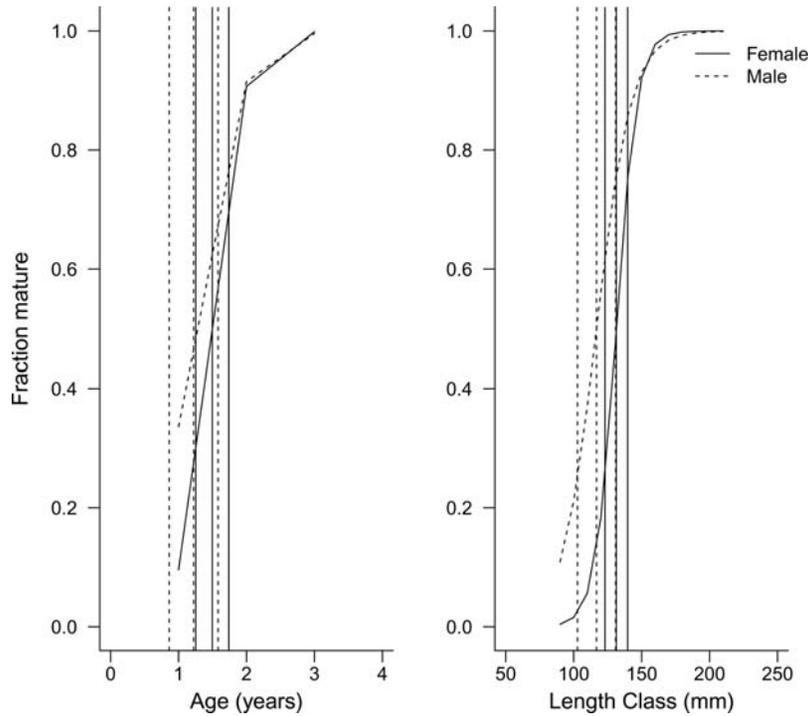
Figure 5. Fraction mature as functions of age [logit(p) = $a + b \times$ age] (left) and length [logit(p) = $a + b \times$ length] (right). Females, continuous lines; males, dashed lines; LC, length class. Vertical lines represent the age at 25, 50, and 75% maturity (from Lambert *et al.,* 2009).

observed in Z. Estimates of Z at age with confidence limits from a stock assessment with the full population dynamic SURBAR model (SURBA standard ICES assessment model in the statistical

software R) based on IBTS Q1 and Q3 NP cpue data at age confirm the increasing mortality with increasing age (Supplementary Figure S1). Bootstrap analyses of observation variability (*CV*) in
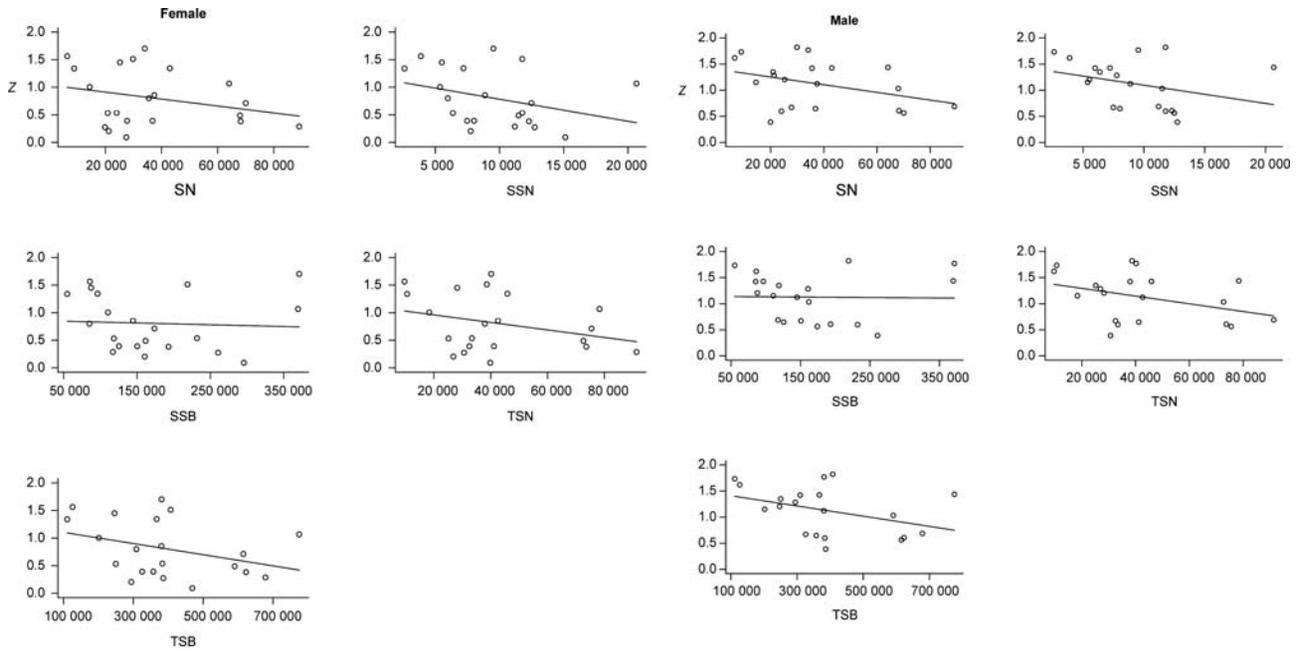
Figure 6. Total mortality (Z) based on revised IBTS Q1 cpue at age 1 vs. NP age 1 stock number (SN; $r_f^2 = 0.08$, $p = 0.222$; $r_m^2 = 0.14$, $p = 0.106$), spawning-stock number (SSN; $r_f^2 = 0.11$, $p = 0.145$; $r_m^2 = 0.10$, $p = 0.178$), SSB (t; $r_f^2 = 0.00$, $p = 0.807$; $r_m^2 = 0.00$, $p = 0.942$), total stock number (TSN; $r_f^2 = 0.09$, $p = 0.177$; $r_m^2 = 0.15$, $p = 0.096$), and total-stock biomass (TSB; t) ($r_f^2 = 0.12$, $p = 0.117$; $r_m^2 = 0.15$, $p = 0.089$). Female figures at left, and male figures at right; regression lines are shown; numbers in millions and biomass in tonnes (t). Z is calculated according to Equation (1).
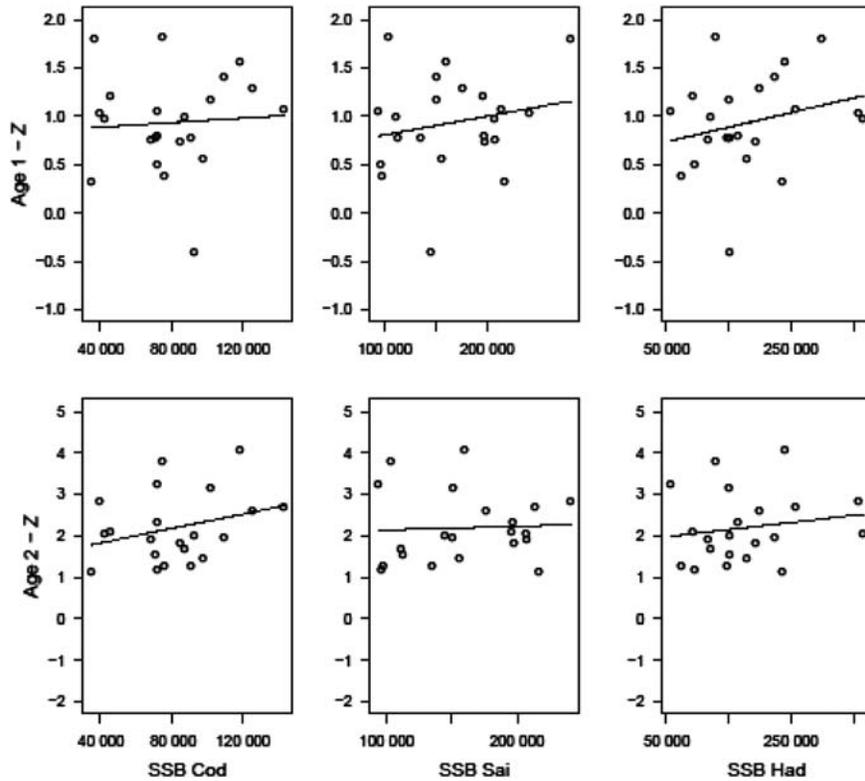
Figure 7. Total mortality (Z) based on revised IBTS Q1 cpue at age 1 (top panels) and age 2 (bottom panels) vs. SSBs (t) of three main predators on 1 January. Regression lines of the relationships shown for cod (Cod; age 1, $r^2 = 0$; age 2, $r^2 = 0.08$), saithe (Sai; age 1, $r^2 = 0.04$; age 2, $r^2 = 0$), and haddock (Had; age 1, $r^2 = 0.06$; age 2, $r^2 = 0.03$). Z is calculated according to Equation (1).
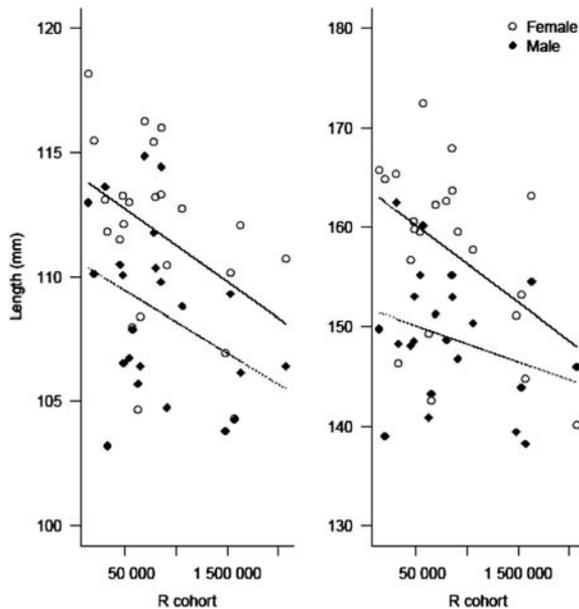
Figure 8. Mean length-at-age in Q1 of age 1 (left) and of age 2 in Q1 (right) vs. year-class strength [recruitment (R) of a cohort] showing statistically significant intraspecific density-dependence. Females, white circles and continuous lines; males, black dots and dashed lines; cohorts in millions (from Lambert *et al.*, 2009).

the same data support the differences in Z at age not being just random variability (Supplementary Table S1). In brief, the observed significant age- and season-specific mortality patterns can be directly explained by greater mortality associated with the spawning event for older fish in the first part of the year.

Survey coverage and catchability with respect to the hypotheses H_01–H_03

A potential problem resulting from the use of survey results is that the sample size is generally small, and hence the abundance estimates are likely to be noisy (Cook, 1997). However, the survey time-series used in the present study have extensive coverage, and enough individuals have been sampled to obtain statistically significant results. ICES has evaluated the IBTS Q1 and Q3 and has concluded that they have adequate coverage and consistent time-series information for use in NP stock assessments (ICES, 2007a, b, c, d). These data are widely used in similar fish population dynamic analyses on NP and other demersal, gadoid species (e.g. Cook, 1997; Cotter, 2001; Beare *et al.*, 2002; Lambert *et al.*, 2009). The robustness and sensitivity analysis of potential data compilation effects of SMALKs to include all available cpue data for a wider area showed similar dynamics of the mortalities calculated from the revised cpue indices compared with those from the ICES standard area. In both cases, the ICES standard calculation (summing and raising) procedures were used (Anon., 2001). The data filling has not been so extensive that it can influence

the overall results. Even if there were a potential effect, it would only affect the results and introduce noise concerning the geographically (spawning area) related analyses because the main data filling only concerned the geographical area disaggregation level.

The conclusions are based on the assumption that there is no significant difference or bias in NP catchability according to age (for the 1+ group) or year in the surveys, i.e. the sampling of each age group, especially the 1+ group, is representative for the stock. This assumption is assessed to be reasonable.

First of all, age group 1 NP has a mean length of 11–15 cm in Q1–Q4 varying with sex, maturity, and region (Lambert *et al.*, 2009), and the observed length range of age 1 in the full IBTS Q1 ALK time-series is 5–17 cm, of which only 0.6% are <8 cm, 1.6% are 8–9 cm, and 6.5% are 9–10 cm (DATRAS, www.ices. dk). Götz (1997) published the only available selection parameters and ogive for NP in the IBTS GOV trawl, and she estimated an L_{50} of 8.0 cm, with a very narrow selection range, where 100% of the NP are caught at length 9.2 cm, the length where North Sea NP are fully selected by the IBTS survey gear.

Second, there is no indication in the literature of lower catchability of the older age groups for the species covered by the IBTS survey, including NP (Cook, 1997; Cotter, 2001; Beare *et al.*, 2002; Anon., 2004). Cotter (2001), Cook (1997), and Anon. (2004) have indicated that survey catchability of 0-group gadoids, clupeoids, etc. may, in general, be relatively low due to the mesh-size selection in the small-meshed IBTS survey trawls, but this is not the case for the 1+ group. Cook (1997) found that the small gadoid whiting has equal catchability for all ages 1–6 in the IBTS survey. Furthermore, neither the surveys nor the commercial fleet have been able to find old NP (see below). Fraser *et al.* (2007) calculated the IBTS survey (GOV-trawl) catchability for NP. The results showed a constant catchability for NP in the length interval 12–20 cm, and the catchability was low for small fish of ~7.5 cm (the 0-group), which is similar to the length of the estimated L_{50} for NP for the GOV trawl (Götz, 1997). Fraser *et al.* (2007) estimated lower IBTS catchability for fish of lengths of ~20–23 cm. However, the confidence limits for this estimate were high and substantially overlapped those for the estimated catchability within the full size range 15–23 cm, i.e. this result was not significant. NP at age 2 has mean lengths of 12–15 cm (immature fish) and 15–18 cm (mature), whereas age 3 mean lengths are 14–16 and 18–20 cm for immature and mature fish, respectively (Lambert *et al.*, 2009). Therefore, the results of Fraser *et al.* (2007) did not indicate low IBTS catchability of the age and length groups for which we estimated high mortality, i.e. for ages 1–3.

Third, several scientists have suggested that the depth distribution of NP could increase with age (e.g. Poulsen, 1968; Raitt and Mason, 1968; Albert, 1994, in the Norwegian Deep). Sparholt *et al.* (2002a, b) analysed and discussed these potential catchability changes with age in relation to depth-dependent distribution and migration based on several sources, including IBTS data analyses and a literature review. They concluded that there was no evidence of vertical migration and associated age-specific migrations out of the NP population area and the IBTS area according to depth or topographical conditions, which could explain the very less number of old NP in the catches in the North Sea and Skagerak–Kattegat. Furthermore, Lambert *et al.* (2009) demonstrated that there is no basis for dividing the stock into several smaller stock components based

on analyses of variability in growth and maturity dynamics. In addition to the work of Fraser *et al.* (2007), fishery landings statistics do not indicate depth differences between sizes, and the number of individuals found in deeper waters remains very low. Fishers have found no signs of emigration of the stock out of the area, and they have not noticed size- or age-specific patterns in occurrence according to depth either in the bank areas or along the Norwegian Trench (Flemming Christensen, a long-time NP fisher and former Chairman of the Danish Commercial Fishery Association, pers. comm.). Finally, papers (Cook, 1997; Cotter, 2001) and reports (Beare *et al.*, 2002; ICES, 2004) find similar trends in age-specific mortality using independent sources, i.e. different North Sea surveys and commercial fishery data time-series.

Consequently, age-, season-, and area-specific mortality patterns cannot be explained by survey coverage and catchability or by age-specific migration out of the area or vertical distribution patterns by age. We have no objective information indicating that larger NP (at least age 1+) are not representatively sampled in the analysed IBTS surveys and that the constant catchability assumption is not valid.

$H_0$2: there is no relationship between natural mortality and the reproduction-specific life-history traits of NP, such as sex, maturity, and growth, and thus, mortality is decoupled from spawning

This hypothesis is also rejected. The present study and Lambert *et al.* (2009) provide evidence that spawning mortality impacts the life-history traits and population dynamics of the NP stock. The ratio of mature individuals declines significantly from before to after spawning, and only very few post-spawning NP have ever been observed despite extensive surveying and fishing in the North Sea. For the youngest age classes, the proportion of mature individuals is higher for males than for females, and total male mortality is higher. This is in accordance with Cooper (1983), who found an increasing numerical dominance of NP females with age. Maturity and growth dynamics (Lambert *et al.*, 2009) strongly indicate greater mortality in the spawning areas and during the spawning season, as further discussed below.

Geographical patterns and mortality dynamics pertaining to $H_0$2 and $H_0$3

Geographical patterns and subarea-dependent mortality have not been explored to the fullest extent in the present study using IBTS data because potential patterns therein might be flawed by subarea-specific NP migrations within the North Sea and Skagerrak–Kattegat. Although such internal migration patterns are not fully mapped, it is clear that Skagerrak–Kattegat is a nursery area and that NP migrate to the North Sea when maturing (Ursin, 1963; Poulsen, 1968; Lambert *et al.*, 2009). Geographically determined growth patterns of decreasing mean weight and length with age in the spawning areas during the spawning season have been observed (Lambert *et al.*, 2009). In addition, geographical maturity patterns have shown a significantly higher percentage of mature individuals in spawning areas RFA1 and RFA3, in which there were significant decreases in the maturity ratio from Q1 to Q3, and where more than 90% of the spawners were recorded in Q1 (present study and Figures 2 and 3 and Table 3 in Lambert *et al.*, 2009). This indicates that the larger, more mature individuals disappear after spawning. It is also observed

that total mortality is significantly correlated with the percentage of mature fish. Mortality cannot be directly calculated in the spawning areas during and just after the spawning period, but the results show that the yearly total mortality for both sexes is significantly positively correlated with the overall maturity ratio assessed during the spawning season (Figure 3). The above factors indicate a higher natural mortality associated with spawning.

Based on stomach-content data analyses disaggregated to ICES statistical square (area) and quarter of the year in the North Sea (1991), Rindorf et al. (2010) calculated biomass eaten and local predation mortality indices. They found that predated biomass (and predation mortality) of NP by cod, whiting, haddock, and saithe was high in the second half of the year (Q4 and Q3) and low in the first half (Q2 and Q1). In Q1, the small NP biomass eaten occurred in the most northern areas west of Orkney and south of Shetland. Based on Rindorf et al. (2010, Figures 2b and 5b), the areas of highest biomass predated and highest predation mortality were not in the main spawning areas during the spawning season (Q1) that were identified by Lambert et al. (2009, e.g. Figure 1). The latter study includes a review of previous studies on NP spawning and egg/larvae distribution and identifies the main NP spawning areas to be in proximity to the 120-m isobaths in RFA1 and RFA3 near Viking Bank along the Norwegian Trench and along the Scottish east coast (and in RFA7) in Q1. Consequently, predated biomass and predation mortality are low in the main spawning areas and during the spawning season, indicating that increased mortality cannot be explained by predation mortality.

$H_0$3: there is no density-dependence, intraspecific, or interspecific mortality in NP

This hypothesis cannot be conclusively rejected. The density-dependence, either intra- or interspecific, of NP mortality shows a distinct pattern. Mortality is significantly positively correlated with intraspecific population density. The NP population dynamics seem, therefore, to be influenced by density-dependence, which results in a lower growth rate and maturation when the stock is at a relatively high level. Thus, bringing together the varied information pertaining to NP mortality, it is likely that lower stock densities contribute to higher growth rates and higher maturity ratios and, consequently, greater mortality rates, which are most likely caused by spawning. Kempf et al. (2009) found no intraspecific relationship between NP SSB in the year of birth and the IBTS age 1 recruitment index of the following year, whereas the interannual variability in age 1 recruitment was found to be correlated with the Q2 sea surface temperature when taking predation impact into consideration. However, this was not highly significant and included the removal of years characterized as outliers.

Interspecific density-dependence and predation were not significant factors based on the available data at the scale of our study, but additional studies are necessary on more disaggregated coverage and overlapping distribution and density patterns between NP and its main predators by age or size group, especially during the spawning period. With regard to the overlap between NP and important predators in the North Sea, Rindorf et al. (2010) found low predated biomass and predation mortality in the main spawning areas during the spawning season. Kempf et al. (2009; Figure 10) found no strong correlation between the spatial overlap of NP age 1 abundance and certain NP predators

(saithe, haddock, and mackerel) in the IBTS Q3 survey. Both of these studies are based on extrapolations of the 1991 "Year of the Stomach Sampling" diet compositions of predators. However, strong predator–prey relationships do exist between some commercially important North Sea stocks and NP. Adult whiting is an important predator of small NP (Jones, 1954; Daan and Welleman, 1998). In recent years, a significant part of the western mackerel stock has migrated to the North Sea, resulting in a potential higher predation mortality of small/young NP (particularly of the 0-group). Further, the North Sea saithe stock has recently increased, leading to potentially higher predation mortality among larger NP (ICES, 2010). The stomach contents of the main predators should be analysed for the years beyond 1991 (ICES, 2006, 2008; Kempf et al., 2009; Rindorf et al., 2010) at the precise NP spawning time and place to determine whether NP are subject to increased predation when potentially weakened by spawning events.

Although our analyses indicate density-dependent mortality which can be associated with spawning and that available documentation on predation cannot explain the observed increase in Z at age, it is difficult to disentangle density-dependent mortality and size-selective mortality. Size-selective mortality will usually result in greater mortality of the smallest (youngest) fish, but for NP, we observe greater mortality rates for the largest (oldest) fish, and that spawning is not only associated with age, but also with size. We find evidence of spawning mortality where the fastest growing individuals mature faster and therefore spawn and die faster, but there may be other reasons for such reversal size-selective mortality, e.g. density-dependence. Density-dependence probably does not influence mortality directly, but rather indirectly as explained above, and can also be influenced by size-selective mortality other than spawning mortality, so no rigorous conclusions can be made on the rejection of hypothesis $H_0$3.

Conclusions and future studies

Our results indicate that a significant proportion of the NP stock most likely dies as a direct or indirect result of spawning. However, the variation in total mortality is high and cannot be exclusively explained by this one life-history trait, i.e. other types of size-selective mortality may also have an effect. In fisheries and ecosystem management, it is important to recognize the biological and ecological contexts and mechanisms that lead this small, short-lived gadoid to allocate so much energy to reproduction the first time it spawns and to produce a high likelihood of death as a result of spawning stress or increased exposure to other mortality associated with spawning. Ursin's (1963) studies on NP growth have indicated that a likely cause of the observed growth and energy allocation dynamics may be the mortality associated with spawning.

With respect to NP, future investigations should concentrate on (i) intensified surveying of NP and its predators during and just after the spawning event at the spawning localities to follow mortality and predation patterns, (ii) precise maturity patterns and histological gonad analyses during the spawning season to follow the mortality patterns of NP that are closely associated with development in the mature stages before and after spawning, (iii) histological analyses of NP gonads and other organs in relation to potential senescence associated with spawning, and (iv) tank experiments on spawning NP. With these approaches, it will be possible to evaluate some mortality mechanisms and to what

extent NP is weakened by the spawning event due to energy loss and increased vulnerability and exposure to fish and invertebrate predation, as well as senescence, sickness, and other residual mortality induced by spawning.

Supplementary material

The following supplementary material is available at the *ICESJMS* online version of the manuscript: bootstrap analysis and estimation of observation variability (*CV*) in the NP IBTS Q1 and Q3 cpue data by age, and total mortality (*Z*) at age with confidence limits from a SURBAR full population dynamic model assessment in 2011.

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