Author(s): Marjomäki, Timo J.; Valkeajärvi, Pentti; Karjalainen, Juha

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FEATURE ARTICLE

Males die young, which may cause an Allee effect during a population collapse of the Vendace *Coregonus albula*

Timo J. Marjomäki[1] | **Pentti Valkeajärvi**[2] | **Juha Karjalainen**[1]

[1]Department of Biological and Environmental Sciences, University of Jyväskylä, Jyväskylä, Finland

[2]Natural Resources Institute Finland, Jyväskylä, Finland

Correspondence
Timo J. Marjomäki
Email: timo.j.marjomaki@jyu.fi

Abstract

Objective: We estimated the difference in mortality between mature male and female Vendace *Coregonus albula* based on a large data set of catch samples from 25 locations in Finland. We then used this estimate and age distribution data from Lake Etelä-Konnevesi to illustrate how the sex ratio (females per one male) might decrease as the average age of spawners increases during a several-year-long period of recruitment failure.

Methods: We estimated mortalities first from sex-specific age–ln(catch) curves and second from the average age-specific proportions of different sexes.

Result: The estimate of the additional mortality of males was around 0.2–0.4, depending on the method of estimation, and assumed true proportions in the population at age 1 (two growing seasons), when Vendace reaches sexual maturity. When using the additional mortality estimate and age distribution data from Lake Etelä-Konnevesi, the hypothetical sex ratio in the most extreme year was even as skewed as four females per one male.

Conclusion: If the lack of males per female spawner during a population decline reduces the per capita recruitment success of females, this is a depensatory density-dependent effect, the Allee effect. This phenomenon may partly explain the rapid population collapses and contribute to 2-year cyclicity typical of the dynamics of Vendace populations.

KEYWORDS

depensation, mortality, population dynamics, recruitment, sex ratio, stock assessment

INTRODUCTION

Higher mortality and thus a shorter life span of males than females, for various reasons ranging from behavioral differences to the effects of unguarded sex chromosomes, is a typical phenomenon in many animal groups (Xirocostas et al. 2020). In fishes, sex-specific differences in mortality have been observed for many species (Bunnell et al. 2012), with causes that can be natural or human induced, such as environmental changes and sex-selective fishing (Kendall and Quinn 2012; Wedekind 2012; Geffroy and Wedekind 2020).

The sex ratio of the spawning stock may affect the reproductive success of the population. An experimental study by Rowe et al. (2004) showed the effect of sex ratio on reproduction success in Atlantic Cod *Gadus morhua*:

several males per female in a tank guaranteed a higher fertilization rate than only one male. A female-dominated sex ratio has been observed in many coregonid fish populations (Selgeby 1985; TeWinkel et al. 2002; Yule et al. 2008; Pratt and Chong 2012), especially during periods of low abundance. In Lake Michigan, a sex-specific difference in natural mortality of Bloater *Coregonus hoyi* (Bunnell et al. 2012) resulted in some years with a considerable female dominance in spawners, which has been shown to be associated with poor recruitment (Bunnell et al. 2006; Collingsworth et al. 2014).

If the sex ratio becomes skewed in connection with the reduction of the spawning stock, the combined effect on the production of offspring may be more prominent. Depensation, analogous to the Allee effect (Allee 1931; Allee and Bowen 1932; Odum 1953, detailed description, e.g., in Rowe and Hutchings 2003) in population dynamics, is a phenomenon in which the per capita population growth rate decreases as the abundance decreases. This may be due to a reduction in growth in size or reproduction rate or an increased natural or fishing mortality. Depensation has been detected, for example, in collapsed Atlantic Cod stocks and may be one of the mechanisms preventing their recovery (Shelton and Healey 1999; Frank and Brickman 2000).

One of the mechanisms causing the decline in reproduction rate with population decline may be a reduction in mating success at low spawner densities (Møller and Legendre 2001; Rowe and Hutchings 2003; Rowe et al. 2004): the probability of encountering well-matched mating partners may decrease, especially if the local density of spawners decreases with their abundance. At low densities, individuals may either cease breeding, their reproductive behavior related to mate choice may change, and/or copulation with less well-matched mates may be more frequent, leading to lowered egg release, fertilization rate, or offspring viability. To better understand the potential Allee effect, Rowe and Hutchings (2003) emphasized the need for more detailed knowledge on the mating systems of exploited fish species, especially at low densities.

Vendace *Coregonus albula* is a short-lived freshwater Coregoninae species with a typical life span of less than 5 years. Population recessions lasting even more than a decade, with a density of less than 1% of the abundant phase and followed by a gradual recovery, are typical for Vendace in Finland (Järvi 1919, 1920, 1942a; Valkeajärvi and Marjomäki 2004, 2013). The occurrence of a few consecutive years of low reproduction success (e.g., due to environmental factors) followed by a predation-regulated regime has been suggested as one of the reasons for the collapse and the following prolonged recession (Heikinheimo 2001; Valkeajärvi and Marjomäki 2004). Spatial synchrony of recruitment success of Vendace has been observed between nonconnected lakes up to the range of a few hundred kilometers (Marjomäki et al. 2004), confirming that some environmental factors affecting a wide area similarly have a strong influence on Vendace recruitment. The collapse in recruitment of Vendace is usually rapid and severe and the prolonged depression is obviously accompanied by an increase in the mean age of spawners in the next few years. In addition to prolonged recession periods, a tendency for 2-year cyclicity has also been observed in several stocks (see references in table 1 in Marjomäki et al. 2021a), implying that within-population density-dependent mechanisms also significantly regulate Vendace recruitment.

Impact statement

In the short-lived coregonid fish Vendace, the mortality of males is considerably higher than that of females. During a period of low recruitment, this leads to a strongly skewed sex ratio, with female dominance in the spawning stock. Population decline accelerates if the increase in female dominance during stock decline reduces reproduction success (Allee effect). In stock assessment, attention should be paid to the sex ratio of the spawning stock, not just the spawner biomass.

In practice, every Vendace, both male and female, reaches maturity in Finnish lakes at the age of two growing seasons (one full year; Järvi 1919, 1920; Karjalainen et al. 2016). No sexual dimorphism, such as differences in size at age (e.g., data by Järvi 1919, 1920, 1942a; Viljanen 1986) or age at maturity or any secondary sexual characteristics, has been detected in Vendace. Despite being a pelagic schooling species for most of the year, Vendace spawn in pairs (Karjalainen and Marjomäki 2018) in the littoral–sublittoral zone from a depth of a few meters to more than 10 m (Heikkilä et al. 2006; Karjalainen et al. 2021). Spawning takes place in late autumn in the dark. Vendace catches from spawning sites are usually male dominated (Lahti 1992). This implies that males stay at spawning sites longer than females. Females move to the spawning site when they are ready to lay eggs (Lehtonen 1981). The actual spawning period lasts from 1 to 2 weeks (Karjalainen and Marjomäki 2018).

The spawning behavior of Vendace in natural conditions has not yet been documented. According to a laboratory study of Vendace spawning behavior (Karjalainen and Marjomäki 2018), males and females actively cruise close to the bottom. When they encounter a suitable mate, they ascend side by side towards the surface and the female

releases a couple of dozen eggs. Despite the high density of fish in the laboratory tank, only one male typically (98% of rises) participated in the rise and no tendency for satellite males or group fertilization was observed. Currently, it is not known whether any kind of mate choice takes place during the spawning of Vendace. The fecundity of a female Vendace is typically a few thousand eggs, so it must copulate tens to even more than a hundred times to release all eggs (Karjalainen and Marjomäki 2018). Spawning is therefore a very active and stressful period for both sexes, and it is probably more so for males, who have to be alert and active for a long time. Observations by Finnish Vendace fishers and our laboratory monitoring have indicated considerable mortality after spawning, and the mortality of males seemed to be higher than that of females (Karjalainen and Marjomäki 2018).

Already Järvi (1919, 1920) noted that in his catch, samples from Lake Keitele the proportion of males in Vendace decreases with age and that the oldest (age 5 and older) individuals were all female. Thus, although Järvi did not explicitly mention this, there must be considerable differences in mortality between the sexes. The fishing mortality of Vendace was primarily induced by seining, and it was not sex selective, except during the spawning season, which lasted about 2–3 weeks. Even during the spawning season, female fish were targeted as much as possible, for example in gill-net fishing, due to the high commercial value of Vendace roe. Therefore, the majority of the difference in mortality between sexes is likely due to differences in natural mortality. Lehtonen (1981) in his study of Vendace in the Baltic Sea also observed an increasing proportion of females with age and estimated that the instantaneous total mortality (Z; per year) of males was about 0.1 unit higher than that of females, likely due to higher natural mortality in males. To our knowledge, no other quantifications of the difference in Vendace mortality between males and females have been published.

Lehtonen (1981) also observed that the sex ratio of Vendace varies according to the age structure of the population; when the population consists mainly of young individuals, the sex ratio is even. However, when old fish predominate in the population, females become dominant. Interestingly, a witty piece of traditional knowledge shared by Lake Keitele fishers highlights the variation in the sex ratio in relation to the population dynamics of the Vendace: "There is a stock collapse coming when the male and female Vendace spawn at different times" (senior Vendace seiner Otto Minkkinen, oral communication in the 1990s). This statement encapsulates the phenomenon where, at the beginning of the spawning season, the catches are dominated by males, but in autumns when recruitment has been low in recent years and the spawning stock consists of exceptionally old, mostly female individuals, females can outnumber males significantly in the spawning sites during the actual spawning period to the extent that the males go practically unnoticed. It appears as if the females are spawning without partners.

Previous studies and traditional local knowledge thus suggest that there is typically a female dominance in older age-groups of Vendace, and the sex ratio of the spawning stock may vary considerably between years. In this study, our first aim is to quantify, in a general sense, the difference in the mortality between Vendace males and females, as well as the expected average sex ratios in different age-groups. We accomplish this by utilizing an extensive data set collected from various locations in Finland (Järvi 1924, 1942a, 1942b, 1947, 1950; see Appendix Table A.1.1). Secondly, we combine these estimates with the observed age distribution of Vendace in different years during the period of extremely large Vendace population fluctuation in Lake Etelä-Konnevesi. Our objective is to illustrate the potential variability in the sex ratio of the spawning population based on the observed variation in the age distribution of the population. Additionally, we consider the potential effects of the sex distribution on the reproductive success of Vendace.

METHODS

We used extensive Vendace catch sample data by Järvi (1924, 1942a, 1942b, 1947, 1950) from various locations (lakes, lake basins, and the Baltic Sea coast) in Finland from one or several years (Table A.1.1). The samples were representative of catch (Järvi 1919, 1920) and were collected by local fishermen in autumn prior to spawning. The majority of the samples were obtained from seine catches, although some were from gill nets and fyke nets. Järvi considered the seine samples to be highly representative of the population, except for the young-of-the-year juveniles that do not accumulate at spawning sites (Järvi 1919, 1920). In the same study, he compared seine and gill-net catches from his test gill-net series and concluded that both methods provided a fairly similar depiction of the population size structure. However, since gear information was not always reported for the samples and gear dimensions were not provided, we were unable to select samples based on gear type or assess and compensate for the potential effects of sex or size selectivity of the gear.

Since the samples were collected shortly before spawning, the sex of the fish could be visually determined by examining their gonads (Järvi 1919, 1920). The sex of every individual age 1 (two growing seasons) and older was recorded in every sample.

The age of the fish in each catch sample was determined from scales, following the method described by

Järvi (1919, 1920). Järvi's publications also included images of scales that were used to determine the ages (Järvi 1919, 1920, 1924, 1942a, 1942b, 1947). These determined ages align with our interpretation. Honkanen (2006) demonstrated that an experienced researcher can estimate the age of Vendace from scales with high reliability. However, there is a possibility of underestimating the age of extremely slow-growing Vendace. A detailed study of the coregonid population (Yule et al. 2008) revealed that systematic underestimation of age can introduce bias in the estimation of the sex difference in mortality.

We pooled catch samples from the same location from different years. We used all pooled samples consisting of at least 50 age-1+ (age 1 and older) mature individuals. The analyzed data consist of 169 Vendace catch samples containing 35,679 age-1+ individuals from 25 locations.

We employed two approaches to estimate the male-specific additional instantaneous mortality, which in this article we refer to as "dude penalty" or D.

$$D = Z_{\mathrm{m}} - Z_{\mathrm{f}},$$

where Z = instantaneous total mortality (a^{-1}), m = male, and f = female.

First, we estimated the proportional (%) age distribution for males and females separately in each pooled sample and calculated the average proportions to provide a broad representation of the average sex-specific age distribution of Vendace. Next, we generated Heincke's (1913) natural-logarithm-transformed catch curves for both sexes: x = age and y = ln (proportion at age). Assuming a constant Z across different age-groups, we used linear regression to estimate the mean $Z = -$slope (Ricker 1975; Jensen 1985) for the age-groups 1–5. It is worth noting that this method results in slightly downward biased estimates of the mortality but the bias does not affect the estimation of D very much because it remains relatively constant across a wide range of true Z values (see Appendix 2 for more detailed description of the potential biases). Due to the expected nonlinear relationship in the data, the residuals do not obey the assumptions of regression analysis. Therefore, we were unable to estimate the confidence intervals of the sex-specific Z estimates and test the significance of their difference between males and females.

Our second approach does not assume a constant Z across different age-groups. For each pooled sample from different locations, we estimated the proportions of both sexes ($p_{\mathrm{m},i}$ and $p_{\mathrm{f},i} = 1 - p_{\mathrm{m},i}$) by age-group ($i$). We then calculated the average age-specific proportions (P_{m}, P_{f}) by taking the simple arithmetic mean of p. Assuming an asymptotically normal distribution of random error for a sample of proportions following the central limit theorem, we tested the P estimates against the H_0 hypothesis of equal proportions (50%:50%) for both sexes.

Assuming (1) a constant male-specific additional instantaneous mortality, the dude penalty D for mature (age 1+, where age 1 = two growing seasons) Vendace, and (2) certain proportions at age 1, we can calculate the expected age-specific proportions of males and females (eP_{m}, eP_{f}). It is important to note that Z can be any number and have a different value in different age-groups since it does not affect the age-specific eP values (Appendix 3). This allows us to utilize data from multiple populations at various time points.

We performed iterations of this simple model using the observed proportions of sexes at age 1, as well as for adjusted proportions assuming 50%:50% and 40%:60% true proportions of males and females at age 1 ($aP_{\mathrm{m},1}$, $aP_{\mathrm{f},1}$). We estimated the values of the constant D that provided the best fit to the observed ($P_{\mathrm{m},i}$, $P_{\mathrm{f},i}$) and 50%:50% and 40%:60% adjusted proportions. Our criterion for determining the "best" fit was simply the minimum sum of the squared differences between the model-calculated expected proportions and observed/adjusted proportions without any transformations:

$$\min\left[\Sigma\left(P_{s,i} - eP_{s,i}\right)^2\right],$$

where subscripts i = age and s = sex.

Only age-groups 1–3 were utilized for this estimation to mitigate the bias resulting from limited sample sizes affecting the sex ratio of older age-groups (see Appendix 2 for more detailed description of the bias).

In an example illustrating the predicted hypothetical changes in the age distribution of the spawning stock (age-groups ≥1) during a severe population decline, we employed the observed age distribution of catch samples from Lake Etelä-Konnevesi spanning the years 1980–2010. By combining the best-fitting predicted estimated proportions of the sexes from Järvi's data (adjusted to a 50%:50% ratio at age 1 in Table 1) and the spawning stock age distribution data from Etelä-Konnevesi, we aimed to demonstrate the potential effect of recruitment failure and the resulting increase in average age on the sex ratio (number of females per male) of the spawning stock. The age distribution of the Etelä-Konnevesi spawning stock was estimated based on unselected catch samples obtained just before the spawning season. From 1980 to 1997, samples were collected from gill-net catches, while in subsequent years from seine catches. The catch samples from both gear are assumed to adequately represent the age distribution of the mature subpopulation. The samples were processed at the Finnish Game and Fisheries Research Institute. Ages were determined from scales. We did not utilize the annual age-specific sex ratio of the Etelä-Konnevesi catch sample data, as we consider the large data set by Järvi to be more comprehensive and less susceptible to random errors compared with a small annual number of observations from a single lake (typically only

TABLE 1 The average proportion of female and male Vendace at different ages in autumn (data by Järvi; Table A.1.1), the standard error (SE) of the proportions, the number of observations (n; different locations), and the significance (p) of the difference in the proportion from 50%. The sex ratio (number of females per male) is given as observed and predicted using a male-specific additional mortality $D=0.43$ (best minimum least-squares fit). The predictions are also given assuming 50%:50% (female:male) distribution at age 1 and the best-fitting value $D=0.37$, as well as 60%:40% distribution and the best-fitting value $D=0.33$ (see Figure 2).

	Proportion (%)					Females : male			
Age	Female	Male	SE	n	p	Observed	Predicted	Adjusted 50% predicted	Adjusted 60% predicted
1	41.8	58.2	3.9	24	0.048	0.72	0.72	1.00	1.50
2	51.2	48.8	4.7	24	0.794	1.05	1.10	1.45	2.07
3	63.3	36.7	5.1	25	0.015	1.73	1.70	2.10	2.84
4	73.7	26.3	6.4	19	0.002	2.81	2.61	3.03	3.92
5	73.7	26.3	6.5	11	0.005	2.81	4.01	4.39	5.39
6	75.5	24.5	2.5	3	0.009	3.08	6.17	6.36	7.43
7	100.0	0.0		1			9.48	9.21	10.23

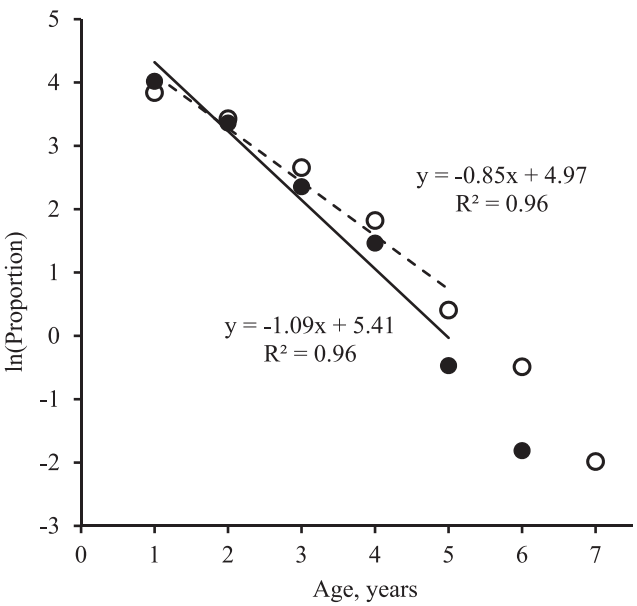

FIGURE 1 Catch curves plotted separately for male (black circles, solid line) and female (white circles, dashed line) Vendace based on ln(average proportions) of different age-groups. A linear regression is fitted to the data of age-groups 1–5. Data from Järvi (Table A.1.1).

a few individuals in old age-groups, especially during the recession). Therefore, it is essential to emphasize that this example is not exclusive to Etelä-Konnevesi, but serves as a more general illustration of the dynamics of the sex ratio.

We utilized data from Lake Etelä-Konnevesi spanning the years 1980–2010 to provide an illustration of the population dynamics of Vendace during a period of stock collapse and low abundance. The abundance of Vendace population was assessed using the catch per unit effort (CPUE; kg/haul) in seine fishing. The CPUE in seine fishing was monitored through fishing records. A group of seine fishers (three to five seines annually) voluntarily recorded their daily fishing effort (number of seine hauls) and the yield by species (kg) to the Finnish Game and Fisheries Research Institute (Valkeajärvi and Marjomäki 2013). The fishing licenses for seine fishing did not impose any temporal or local restrictions on fishing activities or the quantity or quality of the Vendace catch. Seine fishing for Vendace occurred throughout the year, but the annual average CPUE was calculated specifically for the most regular fishing period from July to October. The CPUE data were further divided into age-groups based the catch samples described earlier. The CPUE (kg/haul) of age-1+Vendace was used as an index of the spawning stock biomass in autumn y, while the CPUE (individuals/haul) of age-1 fish in year $y+2$ served as an index of age-0 recruitment from that spawning for year $y+1$.

RESULTS

Estimated from the extensive data set by Järvi, the catch curve regression analysis yielded Z estimates of 1.09 for males and 0.85 for females (Figure 1). The male-specific additional mortality, the dude penalty, was estimated to be $D=0.24$.

The average sex ratio of Vendace in the catch samples displayed a shift towards higher female dominance with age (Table 1). At age 1 (two growing seasons), the catch samples exhibited a slight male dominance, which was expected as the samples were typically collected near the spawning period. In age-groups 6 and 7, only a few males were found, with only 4 out of total of 19 in the raw data.

Based on the age-group-specific proportions of sexes within the range of ages 1–3, the estimated D is about 0.43 for the observed 42%:58% sex ratio at age 1 (females : males; Table 1). For the adjusted sex ratio 50%:50% and 60%:40% (Table 1; Figure 2), the estimated D values were

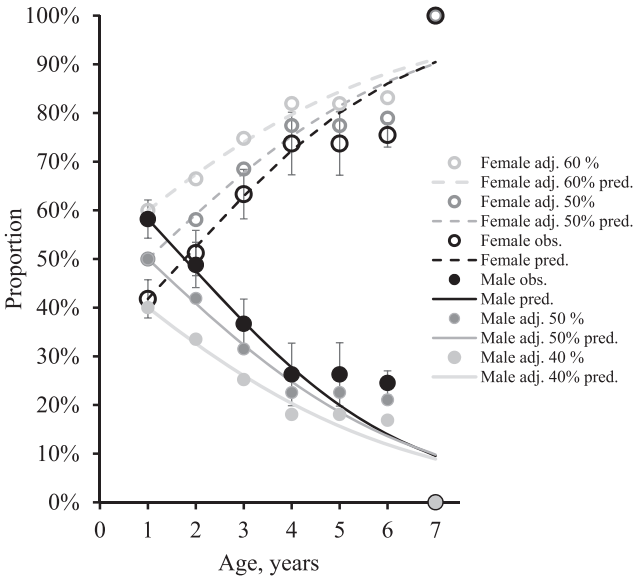

FIGURE 2 Observed average proportions (error bars show SE) of female and male Vendace by age (age 1 = two growing seasons in autumn) and predicted proportions assuming sex-specific additional instantaneous mortality $D = 0.43$ in males (best fit to the observed proportion of females and males at age 1; see Table 1). Gray circles represent the proportions assuming a 50%:50% sex distribution (female : male) at age 1 and best-fitting $D = 0.37$. Light gray circles show the same, assuming a 60%:40% sex distribution at age 1 and best-fitting $D = 0.33$. Data are from Järvi (Table A.1.1).

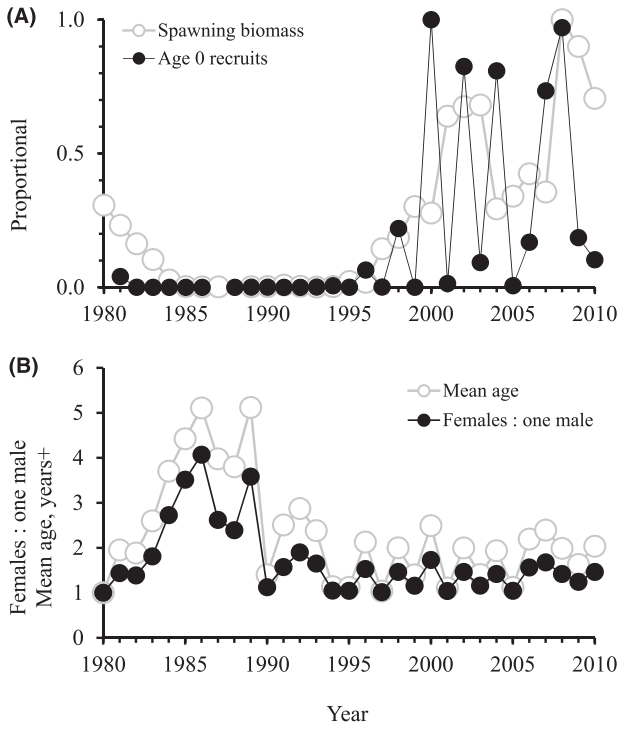

FIGURE 3 Graphs of (A) the proportional index of the spawning stock of Vendace in autumn and the index of recruitment (age 0) from that spawning 1 year later in Lake Etelä-Konnevesi for 1980–2010 (data from Valkeajärvi and Marjomäki 2013; Marjomäki et al. 2021c) and (B) the average age of the spawning stock given in full years (1 = two growing seasons in autumn) of mature (age ≥1) Vendace in Lake Etelä-Konnevesi and the hypothetical sex ratio (estimated number of female spawners per one male based on the 50%:50% adjusted predicted sex ratio in Table 1).

0.37 and 0.33. As age increased, the predicted number of females per male increased rapidly, reaching more than four females per male in age-groups for age 5 and older (Table 1).

In the case of recruitment failure, as exemplified by the data from Lake Etelä-Konnevesi, the recruitment of Vendace was negligible from 1982 to 1995, originating from spawning in autumn 1981–1994 (Figure 3A). Consequently, the index of spawning stock biomass experienced a drastic decline, plummeting to less than 1% of the year 1980 level by 1985. The recovery commenced gradually in the second half of the 1990s, with subsequent year-classes exhibiting increasing abundance every other year. Due to the prolonged absence of recruitment, the average age of spawners surged during the early years of the Vendace population recession, reaching the level of age >4, before returning to a "normal" range of age 1 to about age 2 once the remnants of the last abundant year-class from the spawning in autumn 1978 gradually diminished within the population (Figure 3B). Based on the age distribution and the predicted sex ratio (adjusted 50% prediction in Table 1), the estimated sex ratio exceeded two female spawners per male for several years, peaking to around four (80% females) at the most extreme case in 1986 (Figure 3B).

Since 1990, the estimated sex ratio of the spawning stock ranged from one to about two females per male and remained mostly at that level in later years, when the population maintained abundant levels. However, in accordance with the 2-year recruitment cycle in the period 1995–2006 (Figure 3A), the average age of spawners exhibited considerable variation even within the more abundant population. During that period, spawning in autumn characterized by assessed higher female dominance (Figure 3B; years 1998, 2000, 2002, 2004) resulted in low recruitment levels (Figure 3A; age-0 recruits in 1999, 2001, 2003, 2005).

DISCUSSION

The quantification of the difference in mortality between male and female fish has been relatively rare, although age-specific proportions of sexes have been regularly reported in various studies. Some examples include direct observations by Quinn and Buck (2001) and mortality estimates for each sex separately from stock monitoring data by Lehtonen (1981), Yule et al. (2008), and Bunnell et al. (2012). In this study, we first employed Heincke's (1913) catch curve method to estimate the sex difference in mortality.

Additionally, we developed a simple method to provide a rough estimate of this difference, assuming that the age-specific proportions of the sexes in the samples primarily depend on the constant sex difference in mortality (D). Due to the data set comprising samples from multiple locations and years, our estimates should be considered rough approximations. Both methods may also introduce bias, as demonstrated in Appendix 2, but we mitigated these to the best of our ability by selecting the appropriate age range for analysis in order to obtain unbiased estimates of the dude penalty, D.

However, some natural biases can arise due to the potential differences in sex ratio within the samples compared to the population. These biases can be attributed to sexual dimorphism; behavioral differences between sexes, such as the proportion of individuals at spawning site; and gear selection. To mitigate these, it would be important to know the true proportions of the sexes in the youngest age-groups studied. While the sex ratio of immature Vendace has not been studied, the sex ratio of larval Bloater, another Coregoninae species with a fairly similar life cycle to Vendace, did not differ from 50%:50% (Eck and Allen 1995). In catch samples of Vendace from winter seining, which is least likely to be sex selective, from Lake Puula (25 samples, 2414 individuals; T. J. Marjomäki, unpublished data), the average proportion of 2- and 3-year-old males did not differ significantly from 50%, but it was significantly lower in older age-groups. This suggests that assuming an approximately even sex ratio for age-1 Vendace in the previous autumn is a realistic assumption and that the additional male mortality and skewed sex ratio do not manifest notably at the immature stage. For simplicity, a constant D was assumed for all ages from the onset of maturity. However, the precision of the data in this study, especially at older ages, does not allow any more precise analysis than the assumed constancy.

Our estimates of additional sex-specific instantaneous mortality in mature male Vendace, ranging from about 0.20 to 0.4 per year, are considerable. As previously mentioned, Lehtonen (1981) estimated the instantaneous total mortality (M; per year) of males to be about 0.1 unit higher than that of females in Baltic Sea coast Vendace. Similarly, Bunnell et al. (2012) estimated a difference of about 0.1–0.2 for the Lake Michigan Bloater. Our mortality estimates are broad averages, and the male-specific mortality may vary across populations and years, potentially exhibiting density-dependent patterns as in Bloater (Bunnell et al. 2012). These factors warrant further analysis.

As mentioned in the introduction, the difference in Vendace mortality between sexes is unlikely to be primarily caused by sex-selective fishing gear because both male and female Vendace grow similarly in length and the Vendace populations in Finland were fished with mainly seining that was assumed practically nonselective by Järvi (1919, 1920), except for immature young-of-the-year individuals, for most of the year. The difference in mortality is likely attributed to the higher natural mortality of males as suggested by Lehtonen (1981) and Bunnell et al. (2012). Vendace total mortality estimates (Z) for both sexes combined range from 0.4 to 1.8, apparently depending on the intensity of fishing, most typically around 1.0 (Viljanen 1986), which aligns with the average of both sexes in our data. According to Viljanen (1986), the instantaneous natural mortality (M) estimates for both sexes combined range from 0.3 to 0.9, most typically around 0.6. Assuming our estimate of $D = 0.2$–0.4, the natural mortality (M) of males could be up to twice the mortality for females.

Several potential reasons for higher natural mortality in males of many animal species have been identified (Xirocostas et al. 2020; for fishes, Beverton 1992; Bunnell et al. 2012). In the case of Vendace, we can rule out the effect of sex-specific differences in age at maturity because practically every individual of both sexes reaches maturity after two growing seasons; for example, in the Järvi's data, no immature two-growing-seasons-old (age-1) individuals were found. One possible reason for higher natural mortality in male Vendace may be the greater stress and energy consumption they experience, especially during the spawning season. However, there is no available in situ data to quantify sex-specific differences in activity or postspawning mortality. Predation rates can differ between sexes, especially in species with sexual dimorphism (Kendall and Quinn 2012). Male Vendace may be exposed to greater predation or feed less than females due to their longer active periods in shallow littoral and sublittoral spawning sites as well as their daily migrations between spawning sites and daytime refuges in deeper areas (Lahti 1992). The behavior of Vendace, not to mention the differences between the sexes, particularly during the spawning season or in general during different seasons, is not well understood. Additionally, the seasonal distribution of natural mortality is unknown. If considerable additional male mortality occurs during a short spawning season of a few weeks, it could roughly add up to 1–2% additional mortality per day $[1 - \exp(D/21\,\text{days})]$, assuming negligible other mortality during this short period. In a laboratory study of Vendace spawning, postspawning mortality was found to be high, exceeding 50% (Karjalainen and Marjomäki 2018), but only slightly higher in males compared with females. However, the very high density and probably also the activity in the test tanks may have caused a higher mortality for both males and females than what would be expected in nature. Support for a greater decline in physiological condition of males compared with females during the spawning season was found in the closely related Bloater by Bunnell et al. (2012). They concluded that although there were

differences in growth and age at maturity, the differences were too small to account for the detected difference in mortality.

The sex ratio has not often been considered in the context of population regulation of Coregoninae fishes (but see Bunnell et al. 2006, 2012; Collingsworth et al. 2014), specifically in relation to the spawning stock–recruitment relationship, although both the age distribution of spawners and the mortalities of the sexes can vary considerably, resulting in very different sex ratios in different years. In species with a short life span, recruitment failure over several consecutive years leads to a substantial increase in the average age of spawners. We demonstrated that when mortality differs between sexes, the sex ratio of spawners can undergo dramatic changes during a decline in the stock. This can boost the decline due to depensation (Allee effect) in the density-dependent rate of reproduction in addition to other things, such as lower actual spawner density and higher predation intensity per unit prey, as suggested by Heikinheimo (2001) and Valkeajärvi and Marjomäki (2004). The temporary change in the sex ratio is expected to be most pronounced during the period of a steep decline in the spawning stock, when recruitment failure is initially triggered by another agent (e.g., weather, Marjomäki et al. 2004) and there are still spawners from the last abundant year-class. Once the population enters a more stable phase of low abundance regime, the sex ratio is expected to return to a less extreme level while the low regime is maintained due to some other factors affecting prerecruit mortality (Marjomäki et al. 2021b). Therefore, the dynamics of the sex ratio may be one of the factors contributing to the very dramatic collapse in recruitment during the transition from the abundant to the sparse regime.

In the population dynamics of Vendace, the sex ratio may contribute to the observed 2-year cyclicity in recruitment. Marjomäki et al. (2014) modeled the dynamics of Lake Puula Vendace and found that the rate of reproduction was consistently very low every second year, even though the abundance of the spawning stock did not vary much. A similar pattern can be observed in the time series of Lake Etelä-Konnevesi (Figure 3B): the variation in spawning stock does not explain the extreme variation in recruitment. However, the sparse year-classes (y) stem from the autumns ($y-1$) when the sex ratio of the spawning stock is expected to be more female dominated, although these expected differences are not particularly large. If the sex ratio indeed affects the rate of reproduction, it could be another mechanism working in conjunction with the other factors to amplify the strong fluctuations in Vendace year-classes (see Marjomäki et al. 2014, 2021a). However, this effect may not necessarily be real; the 2-year oscillation of the sex ratio in the spawning stock could equally be interpreted as the consequence of the strong 2-year oscillation of recruitment from past years, with a spurious association between the sex ratio of spawners and emerging recruitment.

Unfortunately, the year-specific reproduction rate (e.g., recruits per spawner unit) cannot be quantified from the Etelä-Konnevesi data during the low abundance phase with reliable precision because both the fishers' log-book-based recruitment and spawning stock indices are at a level of less than 1% of the normal levels (i.e., seine yield per unit effort is less than 0.2 kg/haul, less than 10 large old individuals instead of dozens of kg/haul, more than 1000 individuals and the number of seine hauls very low). The low level of information contained in the data at very low abundance is a chronic problem rendering quantitative studies of depensation or Allee effect difficult (Liermann and Hilborn 1997). Assessing the effect of the sex ratio is difficult because there are two other potential factors contributing to the low reproduction rate and depensation: the spawning stock itself was extremely low and the predatory population of European Perch *Perca fluviatilis* was increasing rapidly (Valkeajärvi and Marjomäki 2004). However, more understanding of the effect of sex ratio on reproduction rate can be obtained from laboratory experiments (Rowe et al. 2004). Recently, we have also succeeded in sampling spawned Vendace eggs from the spawning sites (Karjalainen et al. 2021), which enables the estimation of the fertilization rate in situ and the comparison of fertilization rates under different spawner densities and sex ratios in different years.

There are several mechanisms through which a skewed sex ratio, particularly one that is female dominated, can regulate the rate of reproduction, especially under conditions of low abundance. A simple proportional prediction suggests that when the number of males per female is extremely low, it numerically limits encounters and spawning rises or fertilization rate if there is insufficient sperm production. Rowe et al. (2004) showed that several male Atlantic Cod per female in an experimental tank guarantees better fertilization success than only one male. Atlantic Cod is a broadcast spawner, which differs from Vendace in its spawning behavior: in Atlantic Cod, several males typically participate in fertilization during the egg release, while Vendace spawns in pairs, according to current knowledge (Karjalainen and Marjomäki 2018). In the case of Vendace, a low density of spawners, particularly when the proportion of males is small, can result in a limited number of spawning acts and, in addition, a shortage of available sperm. In our fertilization experiments, we have observed that male Vendace have a very low instantaneous volume of sperm available for fertilization (50–200 μL; author's unpublished data). This suggests that the potential reproductive rate ("the maximum number of independent offspring that parents can produce per unit time" [Clutton-Brock and Vincent 1991], the inverse being "time-out" for

males and females [Clutton-Brock and Parker 1992]) of a male Vendace is lower compared with a female, although the proportion of sperm is practically innumerable compared with fish eggs. The potential reproductive rate affects the operational sex ratio, "the ratio of potentially receptive males to receptive females at any time" (Emlen 1976).

Both potential reproductive rate and operational sex ratio require further attention because, in addition to population-level numerical proportions of individuals and gametes, at the individual level they can also impact the direction and intensity of competition for mates and, consequently, sexual selection, with consequences for individual fitness and genetic variation in offspring. These phenomena can be important determinants of the Allee effect (Møller and Legendre 2001; Rowe and Hutchings 2003): individuals may refrain from spawning or reproduce at a low rate if only mates of an incompatible or nonpreferred phenotype are available. If individuals have to mate with partners that are not well matched, the quality or quantity of offspring may be compromised. As mentioned earlier, in the case of Vendace, it is still unknown whether mate selection plays a role in spawning and which sex, if either, is more selective. However, during a population collapse, the proportion of males decreases reducing their competition (if any) for females and the choosiness of females (if any) should be less. This can lead to increased reproduction between suboptimal partners, potentially resulting in less viable offspring or lower rates of spawning rises and fewer offspring. Alternatively, if there is no mate choice and spawning rises occur spontaneously in any random encounter between ripe female and male, females can still challenge the male fitness by allowing only about 1% of their eggs to be fertilized at a time, with a probable "time-out" effect after ejaculation, as observed in laboratory monitoring of Vendace spawning behavior (Karjalainen and Marjomäki 2018). In such a situation, the fittest males should have the highest reproductive rate and, consequently, the highest likelihood of siring offspring. If female dominance is high, males would need to allocate more resources to fertilize all the eggs, which should intensify this fitness test and potentially increase the fitness of the offspring. However, even the fittest males may be unable to fertilize all the eggs if there is a critical shortage of available males. Our fertilization experiments (Karjalainen et al. 2014; Jokinen 2015) have shown that using a mixture of milt from several males results in a higher fertilization rate on average compared with using just one male. Thus, if females cannot choose their mates, it may be advantageous to spawn with multiple individuals to avoid issues like inbreeding (Jokinen 2015). Overall, there are still many unknown features that warrant investigating in the future. However, the existing evidence suggests the possibility of depensation or an Allee effect during population decline.

CONCLUSIONS

Especially for schooling pelagic species, there is a tendency to assume that the mortality rates and, consequently, the proportions of both sexes remain relatively constant, or at least sufficient to ensure successful fertilization. However, in short-lived species with highly variable recruitment, this assumption may not always hold true. The sex ratio can vary widely due to variation in average age, induced by fluctuating recruitment. The multiple effects of the sex ratio on reproduction success, especially at low population abundance, warrant further population monitoring and experimental studies.

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CONFLICT OF INTEREST STATEMENT

There is no conflict of interest declared in this article.

DATA AVAILABILITY STATEMENT

Data used in this article are available in cited reports.

ETHICS STATEMENT

There were no ethical guidelines that were applicable to this study.

ORCID

Timo J. Marjomäki https://orcid.org/0000-0002-0563-3099

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APPENDIX 1

VENDACE CATCH SAMPLE DATA

TABLE A.1.1 Vendace catch sample data from T. H. Järvi used in this study by study locations, sampling years, number of samples, number of individuals studied that were age 1 and older, and data source.

Location	Sampling years	Number of samples	Number of individuals	Reference
Iso-Kaarnijärvi	1929, 1931	2	50	Järvi (1950)
Kallavesi	1922	2	72	Järvi (1950)
Keitele Keski	1906, 1907, 1912–1931	22	7254	Järvi (1942a)
Keitele Ylä	1904–1941	38	17,652	Järvi (1942a)
Kivijärvi	1913, 1914, 1916	4	670	Järvi (1950)
Kolkkajärvi	1934	1	84	Järvi (1950)
Muuruejärvi	1908, 1914, 1915, 1917	6	517	Järvi (1950)
Niinivesi	1916, 1917	2	92	Järvi (1950)
Nilakka	1914, 1916, 1917, 1920–1923, 1924	14	1111	Järvi (1924)
Oulujärvi	1914, 1915	2	430	Järvi (1950)
Pielavesi Iso	1916, 1920, 1922, 1923	5	493	Järvi (1924)
Pielavesi Keski	1916, 1921, 1923	7	397	Järvi (1924)
Pielisjärvi	1914, 1915	2	200	Järvi (1950)
Porovesi	1929	1	72	Järvi (1950)
Puruvesi	1914–1917, 1934–1935	19	1725	Järvi (1950)
Puulavesi	1915	1	121	Järvi (1950)
Pyhäjärvi, Karelia	1914–1943	24	2981	Järvi (1942b)
Pyhäjärvi, O.l.	1931	1	52	Järvi (1950)
Raanujärvi	1915	1	290	Järvi (1950)
Suininki	1931	1	259	Järvi (1950)
Vankavesi	1946	1	71	Järvi (1950)
Vesijärvi	1914–1916, 1919, 1920, 1929, 1940, 1943	8	255	Järvi (1947)
Vuosijärvi	1908, 1914	2	238	Järvi (1950)
Baltic Sea, Kemi	1929, 1948	2	246	Järvi (1950)
Baltic Sea, Olhava	1949	1	140	Järvi (1950)

APPENDIX 2

BIASES IN THE METHODS OF ESTIMATION OF ADDITIONAL MALE MORTALITY, *D*

Method 1

In method 1, D was estimated based on the difference in the instantaneous total mortality estimates between females and males.

The age distribution of a population was simulated:

$$N_1 = \mathrm{C} \times \exp(-\varepsilon), \varepsilon \sim N\left(0, \sigma^2\right),$$

where N_1 = number at age 1 (two growing seasons, age of maturity), C = constant, and ε = normally distributed random component with σ = standard deviation.

Then,

$$N_{i+1} = N_i \exp(-Z),$$

where Z = constant instantaneous total mortality.

A long sequence of annual abundances was generated. The abundances were ln transformed annually, and the average transformed numbers were calculated (referred to as "Population" in Appendix Figures A.2.1–A.2.3). Additionally, the annual proportional (p_i %) age (i) distributions were calculated. These distributions were averaged over years with no rounding, thus unrealistically assuming an unlimited sample size. The average p_i values were ln transformed ("Sample average" in Figures A.2.1–A.2.3). When estimating the rounding effect of the realistic limited sample size on age distribution, the average annual proportions were rounded to the nearest full individual, considering different sample sizes ("Sample n = ..." in Figures A.2.1–A.2.3). These rounded values were averaged and the averages ln transformed.

The instantaneous total mortality was estimated by the slope of linear regression of the above-described variables on age for different sequences of ages, ranging from age 1 to age 7 to shorter age ranges (e.g., ages 2–4).

The process of estimation of Z was simulated 5000 times for a sequence of 100 samples to gain average results.

Two biases emerge in this method. The first one stems from the fact that recruitment is not constant but typically very variable with large nonnormal distribution (Marjomäki et al. 2014), as simulated, leading to variability in annual p_i.

If $\sigma = 0$, the ln(average p_i) yields unbiased linear regression estimate of Z, but with the increase in σ, the relationship between ln(average p_i) and i becomes an increasingly nonlinear concave function (example Figure A.2.1). Consequently, the slope becomes less steep and therefore the estimate of Z will be underestimated. While this bias is considerable for large σ, it does not strongly depend on the value of true Z (Figure A.2.2). Therefore, this bias does not significantly affect the estimate of D, the additional mortality of males.

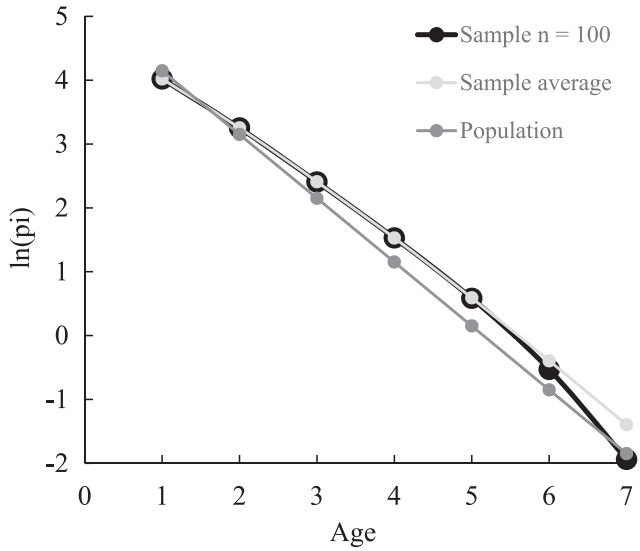

FIGURE A.2.1 The effect of sampling on the relationship between age and ln(proportion). See explanations in Appendix 2: Method 1.

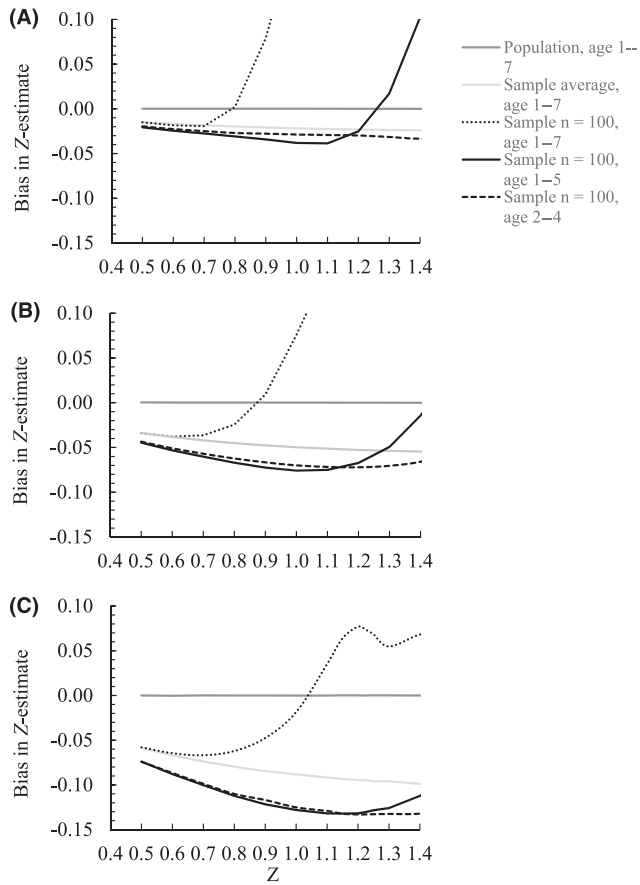

FIGURE A.2.2 The bias in Z in different linear regression estimates of Z for (A) $\sigma = 0.5$, (B) $\sigma = 0.75$, and (C) $\sigma = 1$. Sample sizes = 100 individuals.

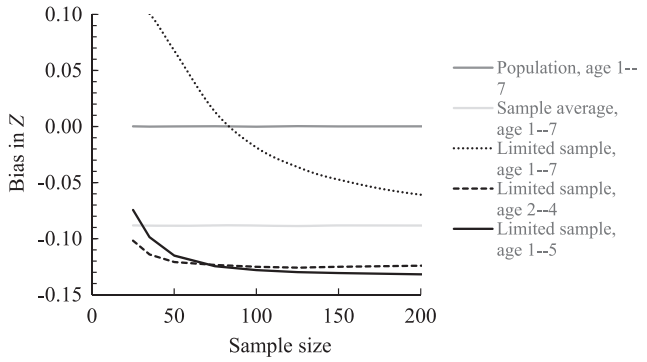

FIGURE A.2.3 The effect of sample sizes on the bias in different regression estimates of Z ($Z=1$, $\sigma=1$).

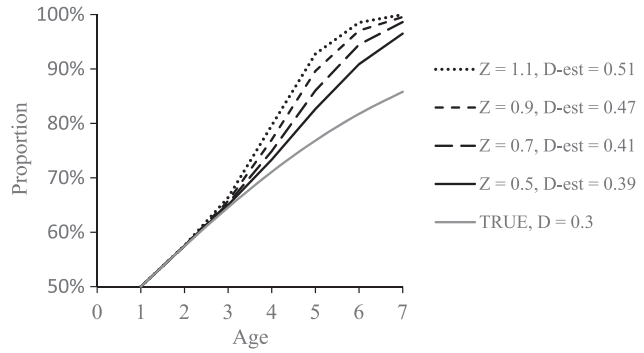

FIGURE A.2.4 The effect of Z on the average proportion of females in different age-groups in the limited sample size of 100 individuals (true $D=0.3$, proportion of females 50% at age 1).

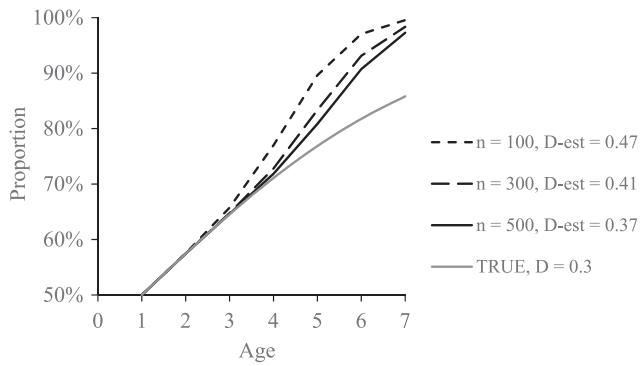

FIGURE A.2.5 The effect of sample size on the average proportion of females in different age-groups (true $D=0.3$, $Z=0.9$, proportion of females 50% at age 1).

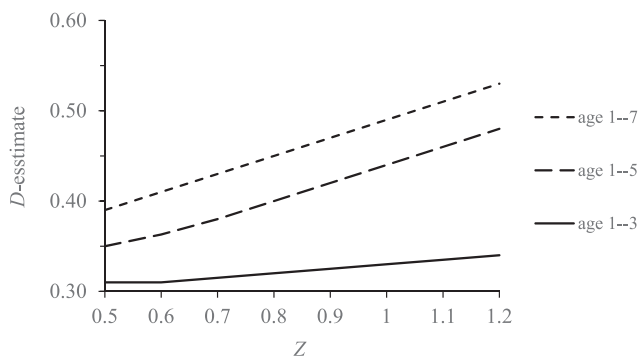

FIGURE A.2.6 The effect of Z and age range utilized in fitting on the estimate of D from method 2 (true $D=0.3$, sample sizes = 100, proportion of females 50% at age 1).

The second bias stems from the limited sample size leading to full individual-level rounded age distribution. There is obviously an increasing likelihood with the increase in age and decrease in p_i that this rounding leads to zero individuals in the sample. Thus, the downward bias in average abundance of several samples increases with age (Figure A.2.1) and Z. Consequently, the linear slope-based estimate of Z becomes biased. Importantly, the bias changes rapidly with Z if the regression contains old age-groups, which will strongly bias the estimate of D.

However, if the linear slope estimate is limited to the younger age-groups only, the bias in Z, although considerable in magnitude, depends much less strongly on Z (Figure A.2.2). If the regression estimation is limited (e.g., to the age-groups 1–5 or 2–4), the bias in the estimate of Z does not depend much on Z at reasonable Z levels and does not induce a considerable bias in the estimate of D. The most suitable age range for analysis is a compromise between low and rather constant bias versus the number of observations (age-groups) used for the slope estimate. We considered the age range 1–5 optimal due to reasonably constant bias and five data points for regression. For this age range, the sample size does not have much effect on the level of bias (Figure A.2.3).

The simulations also showed that there is no effect of the dependence of age distributions of consecutive years within a population on the estimate of Z.

Method 2

Samples were generated from a simulated population with the constant instantaneous total mortality of Z for females and the additional total mortality D for males. The average proportions of sexes were estimated, and method 2 was applied to these.

The average sex ratio was biased for the realistic limited sample sizes. Due to the fact that the proportion of males in the population declines with age, their probability of appearing in limited samples decreases with age faster than their proportion in the population (Figure A.2.4). Thus, the average proportion of females is overestimated, and importantly, this bias increases with the mortality Z. This leads to a strong overestimation of D in high mortality. The bias is obviously lower at larger samples sizes (Figure A.2.5) but is still prominent with an average sample size of 500 individuals.

Depending on the sample size, the bias in sex ratio emerges clearly at the age of 4–5 years (Figures A.2.4 and A.2.5), when the rounding effect starts to decrease the probability of males appearing in the sample. When method 2 is applied only to the proportions of sexes in age-groups 1–3, the bias in D is low even with high Z (Figure A.2.6).

APPENDIX 3

PROPORTIONS OF FEMALES AND MALES AT AGE $i+1$ BASED ON PROPORTIONS AT AGE i AND MORTALITY

If at age i the proportions are $p_{\mathrm{f},i}$ and $p_{\mathrm{m},i}=1-p_{\mathrm{f},i}$, then at age $i+1$ the proportion of females is

$$\begin{aligned} p_{\mathrm{f},i+1} &= p_{\mathrm{f},i}\mathrm{e}^{Z}/\left[p_{\mathrm{f},i}\mathrm{e}^{Z}+p_{\mathrm{m},i}\mathrm{e}^{Z+D}\right] \\ &= p_{\mathrm{f},i}\mathrm{e}^{Z}/\left[p_{\mathrm{f},i}\mathrm{e}^{Z}+\left(1-p_{\mathrm{f},i}\right)\mathrm{e}^{Z+D}\right] \\ &= p_{\mathrm{f},i}\mathrm{e}^{Z}/\left[p_{\mathrm{f},i}\mathrm{e}^{Z}+\mathrm{e}^{Z}\mathrm{e}^{D}-p_{\mathrm{f},i}\mathrm{e}^{Z}\mathrm{e}^{D}\right] \\ &= p_{\mathrm{f},i}\mathrm{e}^{Z}/\left[\left(p_{\mathrm{f},i}+e^{D}-p_{\mathrm{f},i}\mathrm{e}^{D}\right)\mathrm{e}^{Z}\right] \\ &= p_{\mathrm{f},i}/\left[\left(p_{\mathrm{f},i}+\mathrm{e}^{D}-p_{\mathrm{f},i}\mathrm{e}^{D}\right)\right] \text{ and } p_{\mathrm{m},i+1}=1-p_{\mathrm{f},i+1} \end{aligned}$$

where Z = instantaneous total mortality experienced by both sexes, D = male-specific additional instantaneous mortality, constant in all age-groups, p = proportion, f = female, m = male, and i = age.

Thus, the proportion at age $i+1$ is a function of the proportion at age i and D only. The proportions in each age are determined based on the (observed or assumed) proportions of the youngest age-group included, and Z need not be constant at different ages.