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## Fishing and jellyfish eradicate fish 180 years ago

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### Abstract:

Sustainable fish populations require both healthy ecosystems in which they can live and grow, and protection from overfishing. A rare historical example from the first half of the 19<sup>th</sup> century allowed us to describe the chronology of how the vulnerability of a herring (*Clupea harengus*) population to ecosystem variability was increased by effects of fishing on the population and food web interactions within the ecosystem. Both the population and fishery collapsed when several years of increasing exploitation were followed by an extreme climatic-hydrographic perturbation in 1825 that affected herring survival and changed food web structure (jellyfish bloom). Estimated levels of fishing mortality in years leading up to the collapse of Limfjord herring were 3-5 fold higher than natural mortality rates and similar to those which later led to collapses of 3 major herring populations in the north Atlantic (North Sea Norwegian spring-spawning herring, Georges Bank). These high exploitation rates suggest that fishing was a key factor which increased the vulnerability of the Limfjord herring to collapse. Changes in trophic interactions in the Limfjord after 1825 were therefore facilitated by fishing, which had reduced the abundance of jellyfish food competitors (herring) to low levels, and consequently expanded a niche in the ecosystem for other zooplanktivores with opportunistic lifehistories. Lowering the risks of future collapses of fish populations and of trophic re-organisations to less desirable configurations, including gelatinous dominance of foodwebs, requires low exploitation rates that buffer against environmental variability and measures to support well-functioning and structured ecosystems.

Keywords: herring, exploitation, fishing, jellyfish, sustainability, ecosystems, regime shift

## Introduction:

Evidence from several recent studies shows that fish populations lose their buffering capacity against ecosystem changes as the full impact of fishing on exploited populations progresses and accumulates over time. First, fishing directly reduces the number of eggs produced by removing spawners. This fact alone can increase vulnerability to environmental fluctuations. For example an increase in the frequency of years with more predators of, or lower food supply for, larvae during years when egg production rates are already low (due to exploitation of adults) could result in fewer larvae and juveniles surviving to become new adults, and therefore a faster decline in population size, than if egg production rates were higher (Cushing 1995).

Second, fishing can eliminate local, and sometimes genetically distinct populations, which are adapted to specific abiotic (e. g., salinity or temperature conditions) or biotic (e. g. predator behaviours) characteristics of the ecosystems in which they live (Hiddink et al. 2008); their loss represents an erosion of intraspecific biodiversity (Hiddink et al. 2008) and could result in altered structures and functioning of food webs. Third, fishing compresses the age and size composition and maturation rates of adults remaining in the sea – populations consist typically of smaller and younger individuals, which mature at a lower size or age (Jørgensen et al. 2007). Young individuals often have reproductive characteristics which give them lower probability of producing surviving offspring (i. e., narrower ranges of spawning times and locations; lower quality and quantity of eggs (Marshall et al. 2003)). Hence populations of small young adults tend to produce lower quality eggs, and in a narrower time/space window which has lower probability of coinciding with oceanographic conditions which lead to high survival; buffering capacity provided by a diverse age/size structure of adults against a series of years with bad survival conditions is lost (Anderson et al. 2008). High levels of fishing mortality therefore interact with environmental variability to increase the vulnerability of populations to collapse (Brander 2005; Ottersen et al. 2006).

In this account of marine ecological history, we use detailed historical records to document the chronology of how fishing and an extreme climatic event interacted in a coastal food web and led to eradication of a major commercial herring fishery and new trophic interactions already in the 1820s. Our analyses and interpretations are based on time series of landings and fishing effort, and written reports of both the natural history of the Limfjord estuary, Denmark (Figure 1) in 1700-1800s and the socio-cultural context of the fishery (Poulsen et al. 2007). These data and observations were recovered during original archival research of historical fisheries in Denmark (Poulsen et al. 2007). The sources of data included customs and tax records, bailiff's reports and sketches (Figure 2), natural scientists' reports, Parliamentary documents and petitions to the king.

### *Historical fisheries in the Limfjord*

The herring fishery in the Limfjord was an important and highly regulated source of income for the Danish monarchy and private fishermen since at least the 1500s (Johansen 1929; Rasmussen 1968; Poulsen et al. 2007). The fishery was sustainable for several centuries until the early 1820s when there was a large increase in fishing effort and fishermen implemented new fishing practices. These included increases in the number of participants, increases in the sizes of nets, expansion of fishing activities to previously unexploited spawning areas in the Limfjord, and the dragging of large seines over herring eggs incubating on the fjord bottom (Figure 2, 3). Moreover onsite inspections by natural historians documented that fishers captured not only adult herring, but millions of juvenile herring as bycatch (Poulsen et al. 2007). The new fishing practices directly impacted nearly all key

lifehistory stages of the species (adults, juveniles, and even eggs) at the same time, a phenomenon to our knowledge never previously documented for any other fish population in the world. Contemporary ecologists recognized the likelihood that these fishing methods were unsustainable and urged for changes in fishing regulations (Poulsen et al. 2007).

We investigated this possibility using an age-structured, stochastic analytical model of herring population dynamics forced by different levels of realistic fishing mortality and herring lifehistory (e. g., growth, survival, maturation and reproduction rates; see Table 1 and Appendix for details of the modeling approach). We first estimated the pre-exploitation spawner biomass to be ca. 22,500 t from considerations based on population dynamics, catch data, and abundance-area relationships (Figure 4; (Iles & Sinclair 1982)). We then estimated population development assuming different levels of fishing mortality on different ages (sizes) of herring to see which rates were sustainable and which ones would lead to cause collapse. The model showed that the population could be sustainably exploited for decades (annual yields 1000-2000 t), using a fishing practice in which all juveniles (ages < 2) were protected from capture and if adults were exposed to fishing mortalities (F) which did not exceed natural mortality rates (Figure 5; Appendix: Figure A1). Such a strategy would reduce the initial population biomass by about 50% yet remain relatively stable subsequently (Figure A1). Indeed, this fishing practice reflects the long-term catch pattern seen in the Limfjord: average annual yield was ca. 2000 t in the 120 years before the early 1800s (Poulsen et al. 2007).

However the fishing effort in the Limfjord did not remain at this low and sustainable level. As described above, total effort increased and technology and gear deployment strategy changed. Linking the impacts of such changes quantitatively to fishing mortality rates is difficult (Hilborn & Walters 1992; Marchal et al. 2007) and is not possible for the 1800s Limfjord herring fishery: for example, details of fishing practices by the entire or even a large proportion of the fisher community are not documented nor were there independent research fisheries being conducted at the time using standardized fishing methods which could be used for population monitoring. However, given the increase in landings in the late 1810s-early 1820s, it is likely that fishing mortalities did increase, and were increasing the risk that the population would decline or even collapse.

In particular, one of the Limfjord fishermen (Peder Kold) at the time used the same gear and deployed it in the same area during 1817-1832, which covers the years leading up to and following the collapse. This fisherman also wrote his annual landings and number of nets (a measure of fishing effort) in records which have survived to the present day (Poulsen et al. 2007). Kold's catches and effort data therefore can be used to derive a time series of catch per unit effort (CPUE), which is directly comparable across years because the technology did not change. These data are therefore equivalent to a relative index of abundance. The CPUE and the total landings by all fishermen in the Limfjord both declined rapidly at the same time (Figure 1), while available effort indicators showed increases (Figure 3b, c). These changes suggest that the cause of the decline in total landings and CPUE was due to a major decline of herring abundance in the Limfjord.

In order to estimate approximate levels of F that contributed to the collapse, we used our population model to investigate levels of F which would lead to decline and collapse, and compared these levels of F with those which led to mid-late 20<sup>th</sup> century declines in other herring populations throughout the Atlantic Ocean. The model showed that if adult F was increased to 3 or especially 5 times the natural mortality rate of adults, then the declines of biomass were larger and there was a higher risk of population collapse (Figure 5; Appendix: Figure A1, A2). Such high levels of F

relative to M are typical in heavily exploited herring populations, and led to collapses of three of the largest herring populations in the world (Norwegian spring-spawning herring, Georges Bank herring and North Sea herring (Fiksen & Slotte 2002; Melvin & Stephenson 2007; ICES 2008a). Given these analytical results and modern knowledge of the levels of fishing mortality which cause herring populations to collapse (see above), we believe that fishing mortality rates increased by similar (or larger) amounts in the Limfjord in the early decades of the 1800s and that this increase probably would have led to population collapse, even in a stable and productive ecosystem.

*Ecological calamity: disaster for some, opportunity for others*

Unfortunately for the herring in 19<sup>th</sup> century Limfjord, a devastating perturbation (regime shift: (Carpenter et al. 2008)) to the ecosystem occurred. In 1825, a massive winter storm permanently broke the Agger Tange isthmus, which separated the western end of the Limfjord from the North Sea. Before 1825, herring and saltwater could only enter through a narrow, shallow opening at the estuary's eastern end; salinity here probably averaged 12-15 practical salinity units (PSU), whereas it was only 5-6 PSU in the western end (Johansen 1929). The inflow of saltwater in 1825 and in subsequent years increased salinity throughout the fjord to 20-25 PSU (Johansen 1929). Marine species from the North Sea invaded and flourished, as did existing resident species which were previously stressed by low salinity, including jellyfish (Figure 1). In contrast, populations of freshwater species, such as whitefish, *Coregonus lavaretus*, collapsed in 1826 as a direct consequence of physiological stresses following the rise in salinity (Poulsen et al. 2007).

One group of species which was a major beneficiary of the breach was jellyfish. Already in 1827, Limfjord eel (*Anguilla anguilla*) fishermen complained that jellyfish were so abundant in summer that they could not drag their seines through the water (Poulsen et al. 2007). Although we will likely never know for sure which jellyfish species were present, *Aurelia aurita* Linnaeus has been present in waters near Denmark for centuries, including on rare occasions in the Limfjord (Johansen 1929), as northern European waters are believed to be its native habitat (Purcell 2005). This species can still be very abundant during summer in the Limfjord (Hansson et al. 2005; Møller & Riisgård 2007) and other waters near Denmark (Lynam et al. 2005; Barz et al. 2006).

Jellyfish, including *A. aurita*, can be voracious consumers of zooplankton and fish larvae and eggs (Hansson et al. 2005; Purcell et al. 2007). Outbreaks of *A. aurita* are associated with declines in survival rates of young herring and even entire herring populations in nature (Lynam et al. 2005; Purcell et al. 2007). Recent studies of the trophic control of *A. aurita* on fish eggs and larvae in the Limfjord demonstrated that abundances were inversely related during 2003-2005 (Hansson et al. 2005; Møller & Riisgård 2007), and that *A. aurita* abundance in summer both in Limfjord and in other estuaries (e. g., eastern Baltic Sea) depends partly on inflow-related salinity variations (Barz et al. 2006; Møller & Riisgård 2007). Reproduction rate in a related species, *A. labiata*, responds positively as salinity increases (Purcell et al. 2007). Since Limfjord herring in the 1820s spawned in the late spring (Johansen 1929), larvae would have emerged and been developing as juveniles during summer in an ecosystem thick with gelatinous predators and competitors for their zooplankton food. This environment would have reduced growth and survival potential of the young herring (Cushing 1995; Lynam et al. 2005; Purcell et al. 2007). As a result, within two more years, in 1829, the herring population and fishery started to decline and eventually collapsed by the mid-1830s (Figure 1). For example, landings and catch rates (Poulsen et al. 2007) each differed significantly before and after 1829 (t-tests for landings and catch rates:  $P < 0.0001$ ). The herring

fishery later recovered in the early 1900s, partly based on seasonal immigrants from the North Sea (Johansen 1929; Poulsen et al. 2007).

Herring fishing, via food web effects, also would have made the 1820s Limfjord ecosystem more vulnerable to trophic re-organisation and subsequent dominance by an alternative zooplanktivore. Given contemporary knowledge of how zooplanktivores control zooplankton populations in marine food webs (Frank et al. 2005; Daskalov et al. 2007; Casini et al. 2009), we assume that removal by fishing of the dominant zooplanktivore (herring) would have reduced their predatory impact on the zooplankton community. Zooplankton populations would have increased in response to relaxed predatory control. As a result, the small resident and invading jellyfish populations experienced an ecosystem whose major competitor for prey was declining due to fishing; ingestion and growth rates of jellyfish would have been high (Hansson et al. 2005; Møller & Riisgård 2007). The successful invasion and subsequent high survival rate of jellyfish in the system was therefore partly promoted by herring exploitation prior to the environmental change. Jellyfish remained problematic for Limfjord fisheries until at least 1856 when legislation on the topic was discussed in the Danish Parliament (Rigsdagstidende 1856). Other gelatinous zooplanktivores and fish egg predators have led to more recent collapses of other fish populations and ecosystem reorganisations (Daskalov et al. 2007; Purcell et al. 2007). (Additional details of interactions between fishing, fish, zooplankton and jellyfish are available in the Appendix.)

High rates of herring exploitation probably also compressed the age/size structure of the population while it was declining. This phenomenon is common in many heavily exploited populations, although we do not know for sure whether it happened in this particular instance. Indeed, herring recruitment in another population (Norwegian spring-spawners) is higher when there are more age classes among the spawning population (Lambert 1990). If fishing reduced the age/size structure of the Limfjord population, the natural variability in spawning time and location may have become smaller. The smaller time-space reproduction window associated with compressed age/size structure would have reduced potential overlap with suitable ecosystem conditions for survival of larvae and young juveniles, including periods of the year when jellyfish predators and competitors were relatively rare.

The sudden increase in salinity itself may also have contributed directly to the decline of Limfjord herring. Although as a species, herring reproduces successfully across a wide range of salinities (Bekkevold et al. 2005), the decreasing salinity gradient from the North Sea through the Danish straits into the Baltic Sea is accompanied by significant genetic structuring of local present-day populations (Bekkevold et al. 2005). This salinity gradient has led to local physiological adaptations of reproductive traits (e. g., activation of spermatozoa and egg buoyancy (Nissling & Westin 1997)) and to local genetic population differentiation (Nielsen et al. 2003) in another marine species (cod, *Gadus morhua*). It is possible that Limfjord herring in the 1820s may also have been adapted to low salinity for reproduction and that the climatic event and fishing may therefore have collapsed a locally adapted population.

The influence of the inflow-related change in herring productivity on herring population dynamics can be assessed quantitatively using our analytical model. We assumed that the main mechanism of change was via a jellyfish-induced decrease in survival rates of herring larvae and juveniles younger than 1-year (i. e., 0-group herring). This change was simulated by assuming that spawners produced a lower fraction of surviving offspring than under the pre-inflow conditions. Such shifts in productivity of fish populations are common (deYoung et al. 2004; Carpenter et al. 2008; Casini et

al. 2009); here we assume that recruit production per spawner decreased by 75% relative to pre-inflow levels. In absence of fishing, this decline reduced biomass by a similar amount (ca. 75%) within 8-10 years (Figure 5). However when combined with F, the declines occur to lower levels thereby increasing risk of local extinction (Figure 5, Appendix: Figure A1). In particular, if F is assumed to increase from 1M to initially 3M and then 5M in the years leading up to the inflow (i. e., replicating approximately the increase in fishing effort documented qualitatively in historical accounts), then the population is essentially extirpated within a few years of the increase in F and the inflow event (Figure 5D, E). This pattern of F and its impact on herring biomass is similar to what happened in the Limfjord. Although we cannot quantify with certainty the true rate of decline in productivity associated with the inflow, the principle demonstrated here is useful: a combination of two extreme situations (productivity change; high fishing) presents higher risk of collapse than either acting alone.

### *Expansion of other marine species*

In contrast to herring, some other marine species that were previously rare in the Limfjord increased in abundance and eventually supported commercial fisheries despite the rise in jellyfish biomass. These species included some flatfish (plaice, *Pleuronectes platessa* and flounder *Platichthys flesus*; (Johansen 1929)). Both species spawn earlier near Denmark (respectively January-April and February-May (Muus & Nielsen 1999)) than herring (April – July (Johansen 1929; Hansson et al. 2005; Møller & Riisgård 2007)), so flatfish eggs and larvae would have had less predatory and competitive overlap with jellyfish, which reach maximum biomass in summer in Limfjord (Hansson et al. 2005; Møller & Riisgård 2007). Moreover, metamorphosed flatfish settle on the bottom and switch to a diet of benthic species whereas herring juveniles remain pelagic and continue to feed on zooplankton; both attributes of flatfish lifehistory (earlier spawning; benthic juvenile stage) reduce jellyfish-related food competition and predation, and would have promoted successful colonization. Following the break of the isthmus, these species had 10-20 years to build populations before becoming targets of major fisheries; the abundance of flatfish motivated the 1848 invention of the Danish seine in the Limfjord (Poulsen et al. 2007). Species-specific differences in lifehistory, diets and habitats therefore allowed some species to flourish after 1825 despite the presence of jellyfish.

### *Management implications and Conclusions:*

Our report of the processes by which fishing, hydrography and jellyfish synergistically contributed to the collapse of a fish population is to our knowledge the earliest yet reported, and our documentation of how jellyfish interfered with commercial fishing operations is one of the earliest in the literature (see e. g., (Purcell et al. 2007; Boero et al. 2008)). In particular, our conclusions regarding the role of fishing differ from those made by an earlier diagnosis of the causes of this collapse: “It is however improbable that the great decline in the yield of the herring fishery which began in 1829 and continued for the rest of the century was due to “over-fishing” since this decline took place suddenly and was for a long time of permanent nature” (Johansen 1929). Given hindsight and analytical modeling results (Figure 5; Appendix: Figures A1, A2) based on advances in understanding of mechanisms by which fishing and environmental variability interact to affect fish populations, we believe the earlier conclusion underestimated the role of fishing. According to our calculations, fishing mortality rates in the Limfjord in years preceding the collapse were similar to those which were major contributors to collapses of much larger herring populations in the north Atlantic. Continuation of those high rates probably would have led to a similar collapse in the Limfjord, even if the climatically-induced ecosystem perturbation had not occurred.

The chronology and succession of ecological processes (fishing, a high-impact climate event, invasion of a species, altered trophic interactions) which led to the collapse of Limfjord herring and jellyfish dominance offers several insights for managers of fisheries and ecosystems. First, environmental changes, which lead to major changes in abiotic conditions or trophic interactions, can quickly push fish populations to collapse, especially when they are already heavily exploited and if they are adapted to local environmental conditions. Second, combinations of multiple stressors, including fishing, can hasten impending ecological breakdowns that individual impacts could eventually cause on their own (Jackson et al. 2001; Lotze et al. 2006). Third, stakeholders (e. g., fishery/ecosystem managers, scientists, fishing industry) need to ensure that exploited populations have sufficient reproductive capacity and population age/size structure to increase their robustness to natural and man-induced ecological changes. Maintaining sustainable fish populations, and avoiding the rise of gelatinous-dominated ecosystems (Jackson et al. 2001; Daskalov et al. 2007; Purcell et al. 2007), will require lower exploitation rates than in recent decades as well as measures to support well-functioning and structured ecosystems.

### **Acknowledgements:**

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Table 1. Settings for model simulations of a hypothetical herring population in the Limfjord, northern Denmark during a 42 year period. Fishing mortalities are multiples of natural mortality (see table S1 for values). The high and low productivity regimes are those associated with the pre- and post-inflow event which occurred in 1825. We assumed that recruitment per spawner was reduced by 75% in the low regime. Initial population size and age composition was derived from the long-term mean maximum abundance and composition above the level of SSB which was assumed to limit recruitment. See text and Appendix for details.

Scenario	Population productivity regime	Adult F	Juvenile F
1	high	0	0
2	high	1	0
3	high	3	0
4	high	5	0
5	high	1	0.1
6	high	3	0.1
7	high	5	0.1
8	Low	0	0
9	Low	1	0
10	Low	3	0
11	low	5	0
12	high	1 during years 0-14; 3 during years 15-20; 5 during years 21-41	0
13	High during years 0-24; low during years 25-41	1 during years 0-14; 3 during years 15-20; 5 during years 21-41	0
14	High during years 0-24; low during years 25-41	1 during years 0-14; 3 during years 15-20; 5 during years 21-41	0.1



Figure captions:

Figure 1. Top panel: Landings and catch rates for herring in the Limfjord, Denmark (Poulsen et al. 2007). Inset shows map of Limfjord with Agger Tang isthmus (triangle pointing right) and Sebblerå (location of herring traps shown in Figure 2; triangle pointing to left). Lower panel: Chronology of ecological events leading to the collapse of the herring population and fishery in Limfjord, Denmark during the 1820s-1840s. The red line shows semi-quantitatively the change in abundance and landings.

Figure 2. Map from 1741 showing locations of several hundred herring traps near Sebblerå, Limfjord (Figure 1), as drawn by district bailiff C. Testrup. Each trap is ca. 80 m long. The sketch in the lower right corner shows a herring trap and staging rack system for drying herring. Maps like this one drawn by district bailiffs were often used in court judgements of fishery disputes (Rasmussen 1968). Note that fishing effort (number of traps, boats, participants) all subsequently increased after this map was drawn and in the years leading up to the collapse of the fishery in the late 1820s (see text and Figure 3). Map reproduced with permission of the Royal Library of Denmark.

Figure 3. Development of fishing effort in the Limfjord fisheries prior to and after the collapse of the herring population (Poulsen et al. 2007). A. Number of fishers participating in the herring, whitefish and flatfish (mainly flounder and plaice) fisheries. B. Mean number of pound- and gill-nets ( $\pm$  standard error, s. e.) deployed in the Limfjord during different time periods. C. Mean number of beach seines ( $\pm$  s. e.) deployed on herring spawning beds and other sites in the Limfjord during different time periods. Number of observations (years) is shown above bars.

Figure 4. The relationship between larval retention area and spawner biomass for herring populations in the north Atlantic Ocean. Data represented by the four solid circles are from Iles and Sinclair (1982) and correspond to populations at Ile Verte (Quebec, Canada), southwestern Nova Scotia (Canada), Georges Bank (Canada/USA) and the Norwegian spring-spawners. The dashed line and its 95% prediction limits (solid lines) is a fitted regression line estimated by ourselves ( $\log\text{SSB} = 1.614 \cdot \log\text{Area} - 0.552$  ( $R^2_{\text{adj.}} = 0.95$ ;  $P = 0.02$ ;  $N = 4$ )). Note that the spawner biomasses for these four areas represent populations subjected to a moderate fishing intensity (Iles & Sinclair 1982). The open circles represent spawner biomass predictions made by assuming the retention area for Limfjord herring is 500 or 1500 km<sup>2</sup> (note that the lower estimate is beyond the range of original data; its associated prediction may be less certain). For comparison, an independent spawner biomass estimate (triangle) for the Limfjord is shown which was derived from Limfjord catch and cpue data and assumed population dynamics. See text and Appendix for details.

Figure 5. Hindcasted population development trajectories for herring in the Limfjord assuming different levels of exploitation and herring productivity affecting offspring survival. Solid and dashed lines: median, 5th and 95<sup>th</sup> percentiles of spawner biomass from probability distributions derived from 200 simulations per year incorporating stochasticity in recruitment and initial numbers at age. A. No fishing mortality and constant ecosystem productivity (scenario 1, Table 1); B. Adult  $F = 1M$  and constant ecosystem productivity (scenario 2); C. Adult  $F = 1M$  and reduced herring productivity starting in year 25 (scenario 9); D. Adult  $F = 1M$  during year 0-14, 3F during year 15-20 and 5F during year 21-41, with constant ecosystem productivity (scenario 12). E. Adult  $F = 1M$

during year 0-14, 3F during year 15-20 and 5F during year 21-41, with reduced herring productivity starting in year 25 (scenario 13). In panels D and E the trajectory of adult F is shown on right axis and with the symbolled line. Juvenile fishing mortality was assumed zero in all simulations. See Appendix for modelling details and results of other combinations of F and productivity.

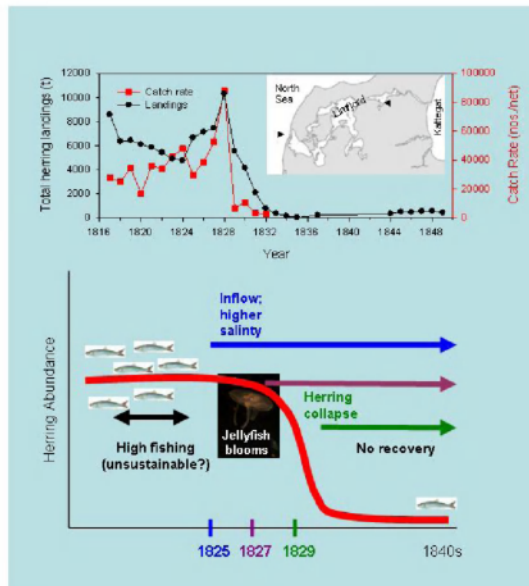


Figure 1



Figure 2

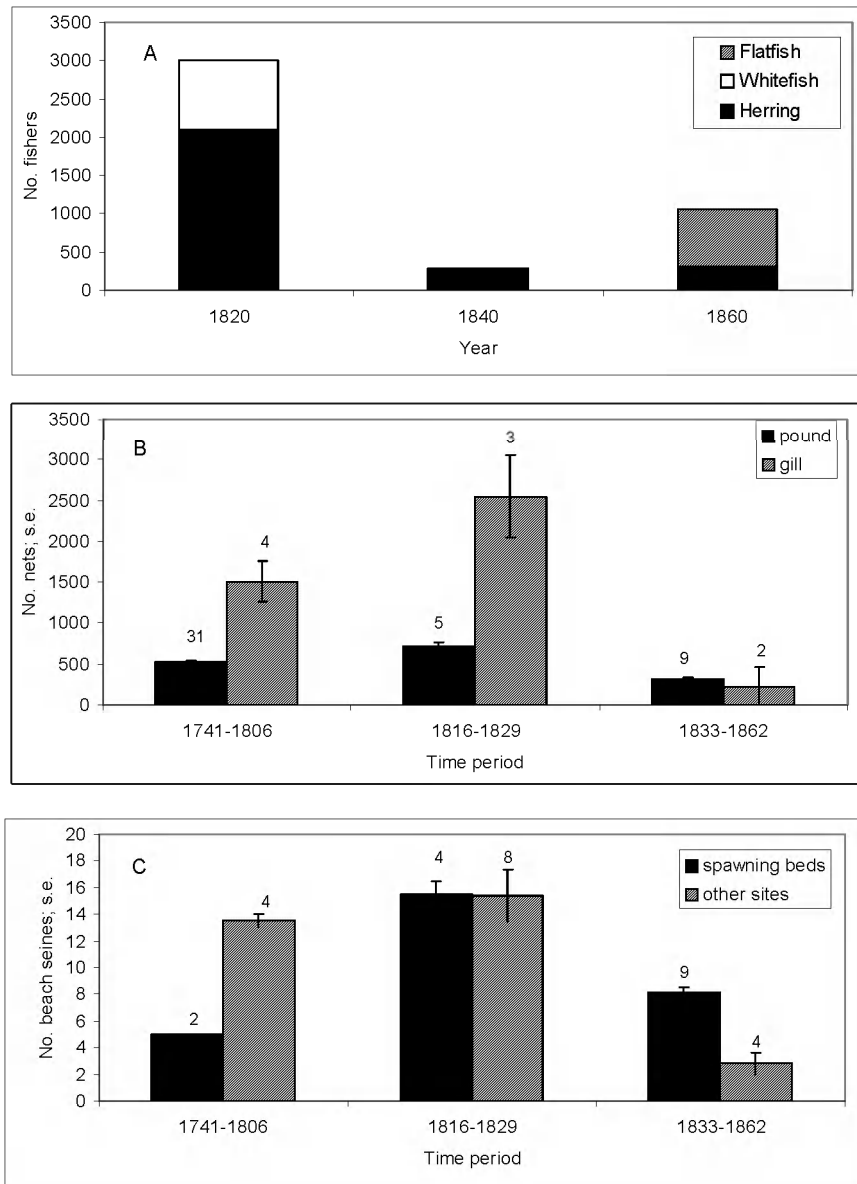


Figure 3

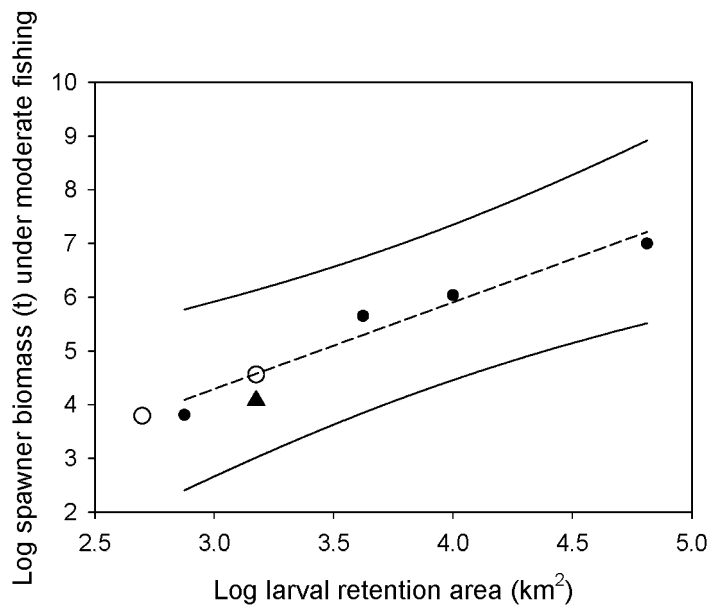


Figure 4

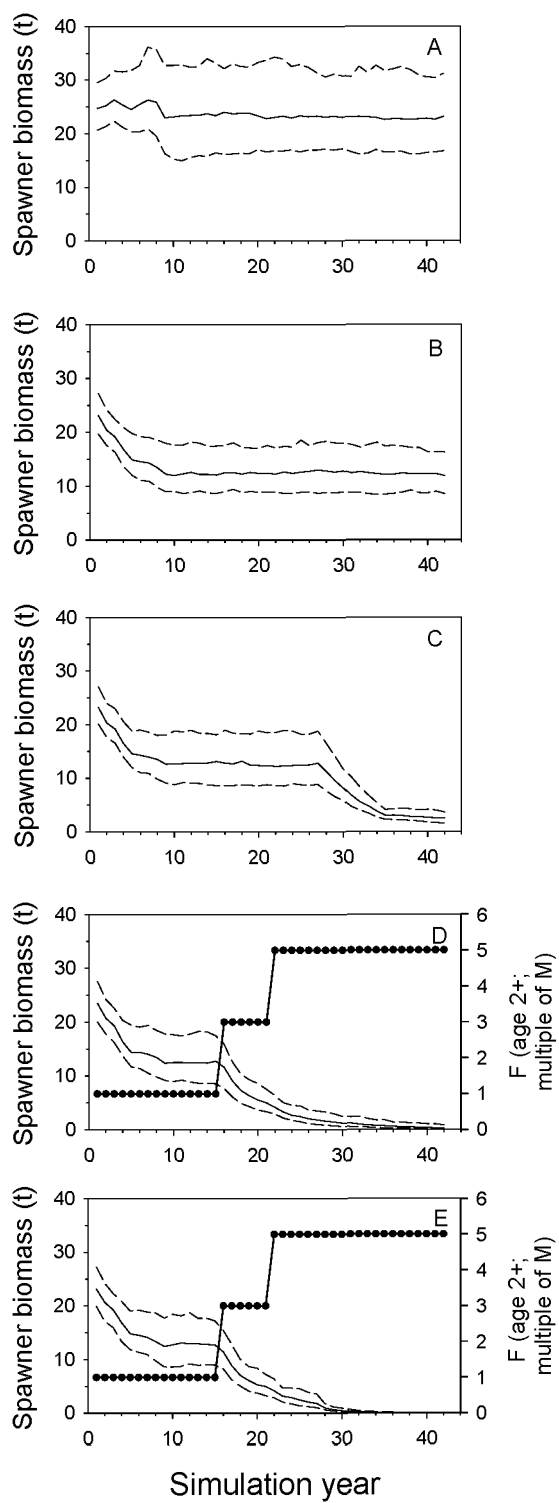


Figure 5

## **Fishing and jellyfish eradicate fish 180 years ago**

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### **Appendix (Appendix text, table and figure captions)**

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Population modelling:

i) Model description:

The model we used for investigating effects of fishing and productivity changes on Limfjord herring population dynamics is structured by age, and projects numbers and biomass forwards in time in user-defined time increments. For this analysis, we used annual time steps for a period of 42 years (e. g., 1800-1841). The model is stochastic and allows uncertainty in numbers at age and production of new herring. Inputs are key biological and lifehistory information for herring (ICES 2008a) such as numbers, weights, maturity, and natural mortality (M). Growth, maturation and natural mortality were assumed constant in projections because functional relationships describing their variability are unknown (ICES 2008b). Outputs are probabilistic estimates of numbers-at-age, biomass and fishery yields for future time periods.

We used the model to understand general principles of the likely relative importance of fishing and ecosystem productivity on herring population dynamics in the Limfjord. As true population abundance estimates of Limfjord herring exist neither for the time period of our study, nor for the present, we cannot conduct a precise reconstruction of the dynamics of this population. However by developing a realistic biological model, we can simulate probable scenarios of how a fish population would react when confronted with fishery and ecosystem drivers. The outputs can help identify likely causes of the decline of the population.

Our model is initialized with starting population size on January 1 of a given year and is driven forwards by applying natural and fishing mortality on age-specific basis to the population. We assume that the initial population at time zero was in an unexploited state and therefore at maximum carrying capacity. Production of new herring is specified by a spawner biomass-recruitment model (explained below). Numbers at start of the following year are estimated based on numbers of survivors, given the starting numbers and their uncertainty. Adult biomass is estimated annually from numbers of fish, their probability of being mature and their weights. Spawner biomass is estimated at spawning time, which for Limfjord herring is in spring (Johansen 1929); we assumed that 33% of annual natural and fishing mortality occurred before spawning.



The model requires population-specific biological data for Limfjord herring. However these data are not available for Limfjord herring either in the past or at present. Instead we used biological and productivity data from a nearby herring population (North Sea), for which such information is available (ICES 2008a; ICES 2008b). Application of North Sea data is reasonable because many Limfjord herring migrated to neighboring areas including the North Sea (Johansen 1929) and therefore would have experienced ecosystem conditions (e. g., temperatures, prey and predator communities) similar to North Sea herring during much of their lives before returning annually to the Limfjord to spawn. A second benefit of using the North Sea data is that the population dynamics of this population are reasonably well described over the full range of population sizes, including those at low population sizes due to a population collapse in the 1970s. Hence our model uses growth, natural mortality and maturity data from the North Sea herring population (ICES 2008a), as well as its underlying population replacement relationship (spawner biomass-recruitment relationship). This relationship is a segmented function and also known as the hockey stick model (ICES 2008b). The specific data we used were those used in North Sea herring population projection models (ICES 2008b).

Overall population size for Limfjord herring is not known for any time period, but is assumed to be much smaller than for the North Sea, partly because of the large difference in habitat areas. North Sea population numbers and the spawner biomass-recruitment relationship, which generates new herring, cannot therefore be directly applied to the Limfjord. We downscaled North Sea population estimates and the spawner biomass-recruitment relationship to those which we hypothesize were probably typical for the Limfjord. The downscaling was based on various considerations. First, we inspected the historical catch data for Limfjord (Poulsen et al. 2007), which shows that the area supported annual catches of ca. 2000 t for many decades. This pattern suggests that the spawner biomass during the time of fishing may have been several fold larger (e. g., 10,000-20,000 t), and that the unexploited biomass (i. e., before fishing started) was even larger. Secondly, a population supporting a relatively constant level of catches for a long period further suggests that fishing mortality rates were relatively low (e. g., not much higher than natural mortality rates).

Given a Limfjord spawner biomass of ca. 10,000-20,000 t and the maximum spawner biomass of North Sea herring (ca. 1.5-2 million t; (ICES 2008a)), the Limfjord spawner biomass was probably 0.5-1% of the North Sea population. Preliminary calculations showed that downscaling the North Sea population to 0.5% gave results which approximated likely dynamics in Limfjord (i. e., fishing mortality rates similar to natural mortality rates applied to an initially unexploited Limfjord herring population of size 22,500 t yielded landings of ca. 1000-2000 t/year; see below). Hence a hypothetical Limfjord herring population was constructed whose spawner biomass and recruitment were 0.005 x North Sea values during 1960-2007, and whose spawner biomass-recruit relationship was similarly downscaled (i. e., the breakpoint used by ICES' North Sea herring experts in 2008 for the North Sea spawner biomass-recruitment relationship, 800,000 t, was also reduced by the same fraction to 4000 t).

We also estimated spawner biomass using different ecological considerations. The basis for this alternative estimate is a log-log correspondance between larval retention area and spawning stock biomass for moderately exploited herring populations in the north Atlantic Ocean (Iles & Sinclair 1982; Sinclair 1988). The pattern was detected by Iles and Sinclair from analysis of physical oceanographic processes which lead to structuring of individual herring populations. In brief, herring larvae are retained in areas defined by an interaction between physical oceanographic processes (e. g., tidal mixing, estuarine circulation) and larval behaviour (e. g., vertical migration).

The relationship between log area and log spawner biomass under moderate fishing mortality can be quantified from data in Iles and Sinclair (1982; their Figure 5) as  $\log \text{SSB} = 1.614 * \log \text{Area} - 0.552$  ( $R^2_{\text{adj.}} = 0.95$ ;  $P = 0.02$ ;  $N = 4$ ; Figure 4).

We used this relationship to predict the spawner biomass for Limfjord herring by assuming that all herring larvae produced by adults in the Limfjord remained in the fjord at least until metamorphosis to the juvenile stage; hence the theoretical maximum retention area was the entire area of the fjord, which is  $1500 \text{ km}^2$ . It is however not clear whether larvae would have been distributed in the whole Limfjord: because of the west-east salinity gradient which prevailed until 1825, spawning was limited to only the eastern one-third of the fjord (Johansen 1929; Rasmussen 1968), so the appropriate retention area would have been  $500\text{-}1500 \text{ km}^2$ . Predicted spawner biomasses under moderate fishing mortality for input areas of  $500$  and  $1500 \text{ km}^2$  therefore range from  $6200\text{-}36,500 \text{ t}$ .

Our alternative estimate of  $22,500 \text{ t}$  under a no-fishing scenario (corresponding to  $12,000 \text{ t}$  under a moderate fishing scenario in which fishing mortality rate is identical to natural mortality rate; see Results and Figure 5b) is close to, and lies within the 95% prediction intervals of, these predictions (Figure 4). This comparison suggests that the population dynamics and lifehistory assumed for Limfjord herring are fair approximations and consistent with the way herring populations in other parts of the north Atlantic are regulated under moderate fishing intensity.

We assume therefore that an initial spawner biomass of  $22,500 \text{ t}$  is a reasonable estimate of the unfished spawner biomass for use in simulations of population dynamics. These assumptions allowed us to quantitatively assess how various combinations of fishing (exploitation) and ecosystem productivity affected Limfjord herring dynamics.

## ii) Incorporation of biological uncertainty:

Model inputs are uncertain so we included stochasticity in our simulations. For initial numbers-at-ages 1 and older (1+), we assumed a coefficient of variation (CV) of 0.30 (ICES 2008a; ICES 2008b). Numbers-at-age were then estimated from a random lognormal distribution based on observed numbers-at-age and their variability. Annual numbers of recruits (age 0) were estimated using the hockey-stick stock-recruitment relationship with breakpoint at  $\text{SSB} = \text{SSB}_{\text{low}}$  (ICES 2008b), defined as  $4000 \text{ t}$ .

Uncertainty in recruitment was simulated by sampling randomly from a log-gaussian distribution fitted to historical time series of recruitment.

For the hockey stick model, if simulated  $\text{SSB}_i > \text{SSB}_{\text{low}}$ , then

$$R_i \sim LN(\overline{\ln R}, \sigma_{\ln R}^2)$$

where

$R_i$  = expected recruitment in projected year  $i$ ,

$\overline{\ln R}$  = mean of  $\ln R$  (19.047),

$\sigma_{\ln R}^2$  is the variance of  $\ln R$  (= 0.314).

If  $\text{SSB}_i < \text{SSB}_{\text{low}}$ , then recruitment and its variance were estimated as:

$$\frac{SSB_{low}}{SSB_i} * R_i \sim LN(\ln R, \sigma_{\ln R}^2)$$

In the low productivity regime, mean of  $\ln R$  when  $SSB_i > SSB_{low}$  was reduced by 75% (17.661)

The model is implemented in a spreadsheet. Stock development for each set of inputs (see below for specification) were repeated 200 times using the random variation associated with initial population numbers-at-age and the spawner biomass – recruitment relationship. Uncertainty of population trajectories, and the risk that the population would become extinct (here defined as  $SSB_{ext} \leq 1$  t), were based on distributional percentiles (5, 10, 25, 50, 75, 90, 95) from model outputs based on the 200 simulations.

### iii) Scenarios:

We conducted scenarios which investigated how a population would react to levels of  $F$  and productivity change that the Limfjord herring probably experienced. Simulations considered these factors both individually and in combination. Initial population size (22,500 t) and age composition was based on the estimated carry capacity for the population based on the downscaled North Sea abundance. We conducted simulations starting with this size and composition to simulate how imposition of the various levels of  $F$  affected population trends.

All scenario settings are summarized in Table 1 of the main text. The first set of simulations evaluated the population response to variations in  $F$ , assuming constant ecosystem productivity. We assumed that  $F$  was equal to 0, 1, 3 and 5 times the level of natural mortality, except that we assumed juvenile fishing mortality was zero (i. e.,  $F = 0$  for ages 0 and 1). The levels of  $F$  on adults were chosen because inspection of the time series of  $F$ ,  $SSB$  and recruitment for North Sea herring shows that  $F$  preceding and during the period of collapse of this population was at these levels and even higher for some age-groups.

The second set of simulations imposed a regime shift in herring productivity to simulate the proposed consequences of the 1825 inflow event. The shift in productivity was accomplished by reducing the maximum expected geometric mean recruitment when  $SSB > 4000$  t from the pre-inflow situation (187 million) by 75% to 47 million starting in year 25. Hence, in these simulations, all years from 25 onwards in which  $SSB > 4000$  t had geometric mean recruitment = 47 million. If  $SSB < 4000$  t then recruitment was estimated from the sloping part of the hockey stick model. The choice of 75% reduction is arbitrary although within the range of decline in recruitment per spawner biomass seen in some other populations following regime shifts (Jarre-Teichmann et al. 2000; Collie et al. 2004; deYoung et al. 2004).

Additional simulations considered changes both in fishing pressure and ecosystem productivity. Scenarios assumed the same range of  $F$  as above (i. e.,  $F = 0, 1, 3$  and 5 multiples of  $M$ , but with zero juvenile fishing mortality) throughout the 42-year projection period, and included the reduction in productivity starting in year 25. We conducted a further simulation to represent the increase in  $F$  over time in the years leading up to the inflow event, as has been documented for the Limfjord (Poulsen et al. 2007). This scenario used the following temporal development of  $F$  on adults:  $F = 1M$  during year 0-14,  $F = 3M$  during year 15-20 and  $F = 5M$  during year 21-41.

## Results:

When the population was not exploited and under stable ecosystem productivity conditions, the biomass fluctuated at a level of ca. 25,000 t. Imposition of adult F at three multiples of M resulted in rapid declines within 8-10 years to lower levels which were relatively stable during the remainder of the simulation period (Fig. A1). Exploitation at levels of 5 M resulted in severe declines to near extinction ( $SSB < 5$  t) also within ca. 10 years. Simulated populations declined to lower levels when juvenile fishing mortality was permitted at a rate of 10% of natural mortality rate (i. e., F on ages  $< 2 = 0.1M$ ; Fig. A2).

If a regime shift occurred which affected recruit production per spawner, then the population declined further (Fig. A1). The productivity – related decline is directly proportional to the assumed change in recruit survival. Simulations using both increases in F and reductions in recruit per spawner showed declines to lowest levels. In particular, assumptions of transient increases in F similar to those which likely occurred in the real Limfjord herring fishery, and combined with a decline in productivity (similar to that likely induced by the 1825 salinity inflow and subsequent jellyfish blooms) led to a herring collapse over similar time scales as the observed decline of the herring fishery and population in the Limfjord (Fig. 4 of main manuscript).

The modelled dynamics depend on the choice of inputs, and in particular, the combination of initial spawner biomass and fishing mortalities. However, two independent estimates of spawner biomass were similar. Consequently, the availability of two similar spawner biomass estimates shrinks the scope of possible fishing mortalities immensely and suggests that the trends are reasonable approximations of the true dynamics.

## Interactions between jellyfish, zooplankton, fish and fishing in marine ecosystems:

Jellyfish have functional roles in marine ecosystems as predators of zooplankton, including fish eggs and larvae (Hansson et al. 2005; Suchman & Brodeur 2005; Purcell et al. 2007; Møller & Riisgård 2007; Boero et al. 2008). Their interaction with fish can therefore be as a competitor of zooplanktivorous lifehistory stages (e. g., larvae and young juveniles) and as a predator. In some systems populations of jellyfish increase to levels which control population dynamics of their prey (Hansson et al. 2005; Daskalov et al. 2007).

On the other hand, jellyfish may offer small juvenile fish a refuge from predation. Juveniles of some gadoid species swim among jellyfish tentacles (Brodeur 1998; Lynam & Brierley 2007). These latter effects might explain positive correlations between survival of whiting juveniles and jellyfish abundance in the North Sea (Lynam & Brierley 2007), even though the same jellyfish species inhibits survival of North Sea herring (Lynam et al. 2005).

The mechanisms which lead to jellyfish population increases are complex and believed to be combinations of abiotic (e. g., temperature, salinity, light) and biotic (food and predator abundances) factors (Mills 2001; Purcell et al. 2001; Aksnes 2007; Purcell et al. 2007; Boero et al. 2008). In the Black Sea, an invasive jellyfish species reached high abundances following a complex sequence of events involving heavy exploitation of local zooplanktivorous fish populations (anchovy, horse mackerel), eutrophication (which had stimulated the food web) and climatic conditions, which in different years favoured survival and production of *Mnemiopsis leidyi* more than in the zooplanktivorous fish species (Daskalov 2002; Aksnes 2007; Daskalov et al. 2007; Oguz

et al. 2008). In the Benguela upwelling system, a similar switch in the dominance of zooplankton occurred after fishing had reduced the abundance of local zooplanktivores such as sardine and anchovy from 17 million t to 1 million t (Lynam & Brierley 2007). Prior to the decrease, jellyfish were rare, but afterwards their abundance and spatial extent expanded (biomasses reaching 12 million t). Abundances in the 1990s reached levels which impaired commercial fishing operations (Lynam & Brierley 2007).

Recent increases in jellyfish abundances in other systems (e. g., Bering Sea, North Sea, Limfjord) have also been reported but the causes are not yet clear (Brodeur et al. 2002; Lynam et al. 2005; Møller & Riisgård 2007). Recently, a new jellyfish species (*Mnemiopsis leidyi*) has been introduced to the North and Baltic Seas (Haslob et al. 2007; Huwer et al. 2008; Viitasalo et al. 2009). The ecological consequences of this introduction are still being investigated as the population establishes itself.

Fishing may have direct and indirect roles on zooplankton abundances (i. e., cascading effects on marine food webs). On the Scotian Shelf (eastern Canada), a (mainly) fishing-induced decline in predators of zooplanktivorous fish species such as herring allowed the zooplanktivorous fish populations to increase 8-10-fold (Frank et al. 2005). As a consequence of the increase in food demand associated with the increased zooplanktivorous fish biomass, biomass of zooplankton in this system declined by ca. 50%.

Another example of cascading effects is available from the central Baltic Sea (Casini et al. 2008; Möllmann et al. 2008; Casini et al. 2009). The main predator of zooplanktivorous fish species (herring and sprat *Sprattus sprattus*) in this system is cod, whose abundance has declined due to high fishing and poor environmental conditions for reproduction and recruitment (Köster et al. 2005). When the cod biomass declined, sprat biomass increased 2-3 fold. As a result of the increase in sprat biomass, overall predation pressure on the zooplankton community increased and zooplankton biomass fell by ca. 50% (Casini et al. 2008).

Given these recent documentations of interactions between fishing, fish, zooplankton and jellyfish, we can offer a hypothesis for the ecological events in the Limfjord after the 1825 inflow. We hypothesize that the increased salinity and fishing-induced reduction in herring biomass combined to create conditions (i. e., a niche) which would have promoted expansion of a new marine zooplanktivore. Such a niche was probably filled by the initial low population of *A. aurita* in the Limfjord and by invading individuals of this (and possibly other unidentified) species from outside. Our historical evidence supports many aspects of this hypothesis, including the increase of jellyfish populations after the inflow and the decline of the herring population.

Table A1. Input biological values used for population modelling of herring in the Limfjord, northern Denmark. Numbers data represent an initially unexploited population at estimated long-term maximum carrying capacity based on a downscaling of herring population size from the North Sea and using estimated uncertainties from stock assessment and the stock-recruitment relationship. The coefficient of variation of the numbers-at-age was 0.6 for age 0 and 0.3 for other ages and was used in population simulations. The downscaling factor was 0.005. Fishing mortalities used in simulations are multiples of natural mortality,  $M$ , and depend on scenario. Data sources: ICES 2008a, ICES 2008b. See details in text and Appendix.

Age	Numbers	Weight (kg)	Prob. mature	Natural mortality	Fishing mortality
0	187071228	0.006	0	1	0 or proportional to $M$
1	76716427	0.051	0	1	0 or proportional to $M$
2	57937176	0.128	0.71	0.3	proportional to $M$
3	24004810	0.161	0.92	0.2	proportional to $M$
4	13247955	0.180	0.96	0.1	proportional to $M$
5	7342747	0.216	1	0.1	proportional to $M$
6	17182528	0.236	1	0.1	proportional to $M$
7	17353053	0.196	1	0.1	proportional to $M$
8	7822581	0.255	1	0.1	proportional to $M$
9	10718704	0.264	1	0.1	proportional to $M$

### Appendix figure captions:

Figure A1. Hindcasted population development trajectories for a hypothetical herring population in the Limfjord assuming different levels of exploitation and herring productivity affecting offspring survival. Solid and dashed lines: median, 5th and 95<sup>th</sup> percentiles of spawner biomass from probability distributions derived from 200 simulations per year incorporating stochasticity in recruitment and initial numbers at age. Fishing mortality was 0, 1M (M = natural mortality), 3M and 5M respectively with constant population productivity (panels A-D) or a decrease in population productivity starting in year 25 by 75% (panels E-H). See Appendix for modelling details.

Figure A2. Hindcasted population development trajectories for a hypothetical herring population in the Limfjord assuming different levels of exploitation and herring productivity affecting offspring survival. Solid and dashed lines: median, 5th and 95<sup>th</sup> percentiles of spawner biomass from probability distributions derived from 200 simulations per year incorporating stochasticity in recruitment and initial numbers at age. Panels A-D: Adult (age groups 2 and older) fishing mortality was 0, 1M (M = natural mortality), 3M and 5M respectively. Panels E-H Same as panels A-D, except that fishing mortality on juveniles (ages 0 and 1) was assumed to be 0.1M. All panels show simulations with constant population productivity.

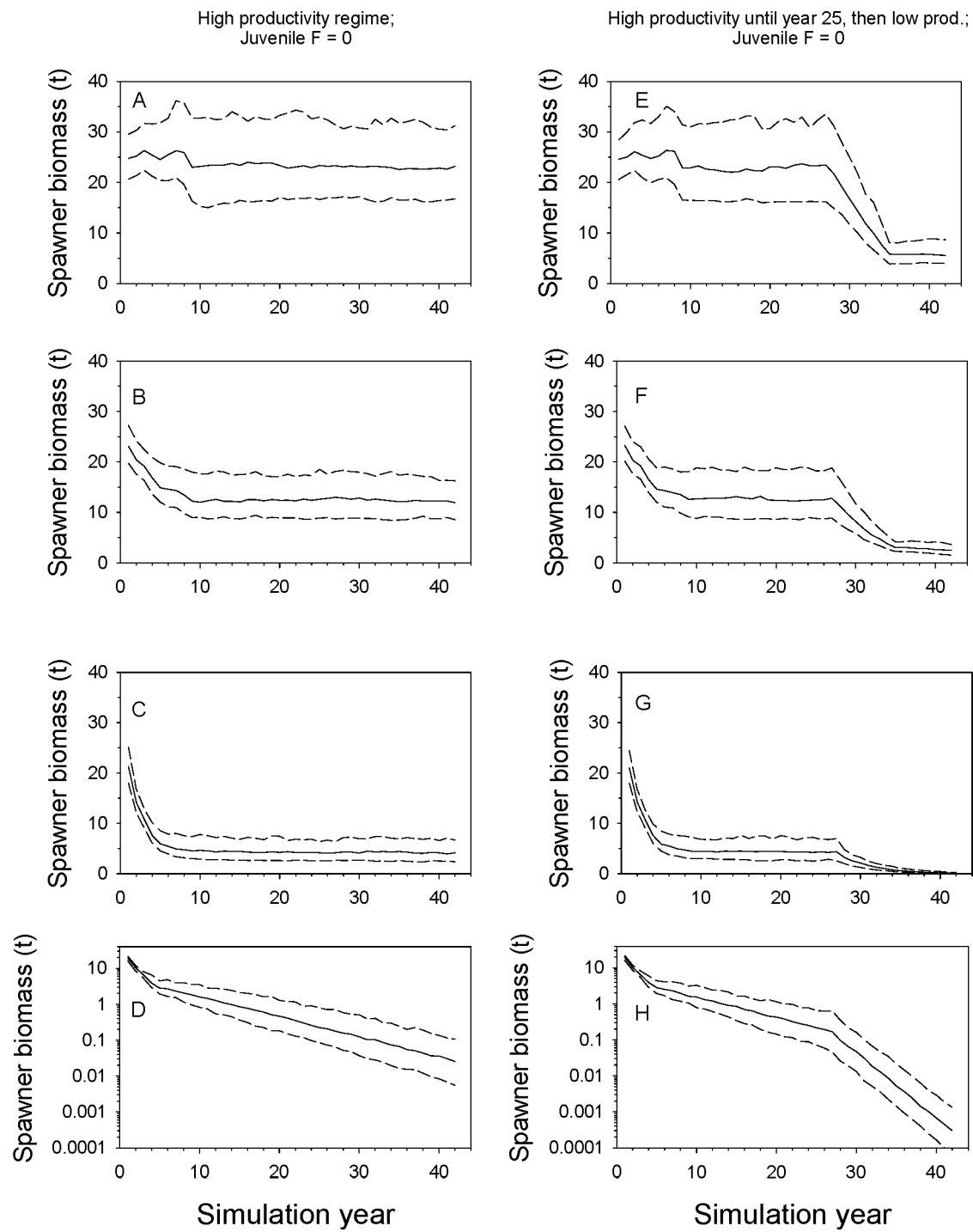


Figure S1



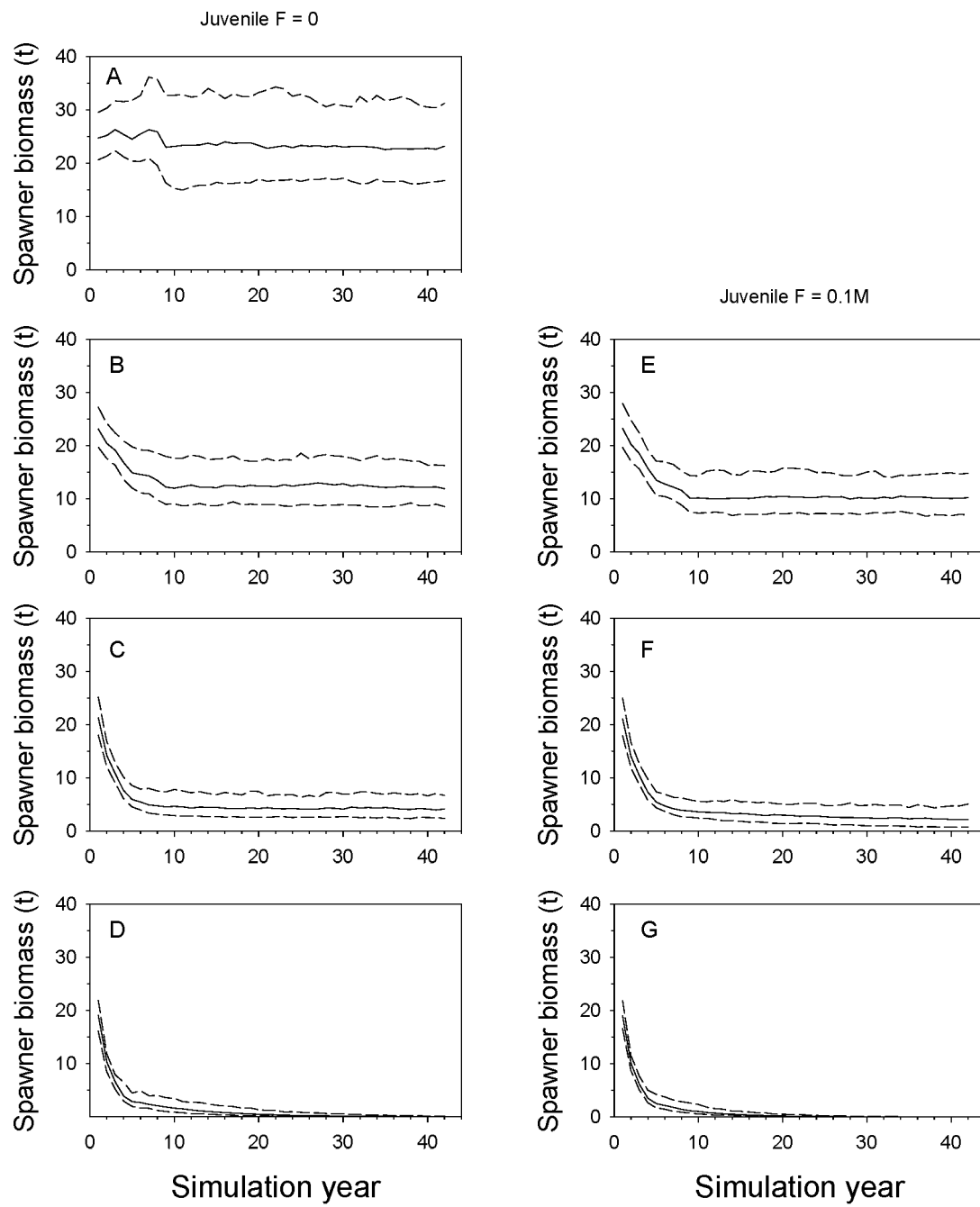


Figure S2

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