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The whelk (*Buccinum undatum* L.) in the western Dutch Wadden Sea in the period 1946–1970: Assessment of population characteristics and fishery impact

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ABSTRACT

In the Dutch Wadden Sea a whelk fishery existed from 1900 to 1970. The high post-war catches, following a period without fishery, and the subsequent decrease in catches when fishery was reopened, allowed us to estimate fishery mortality and recruitment. Information on natural mortality and growth, which were required in the estimation procedure, was obtained from previous studies elsewhere. Natural mortality could be calculated from an experiment with marked whelks in the Thames estuary. Age-length relations could be used from French investigations on whelks near the Channel Islands. The size of a potential whelk population could be estimated. Effects of fishery and possible causes of the disappearance of the whelk from the Dutch Wadden Sea are discussed.

1. Introduction

The whelk (*Buccinum undatum* L.) is a neogastropod mollusc that is widely distributed in North Atlantic waters. It lives at depths of at least 3 m and occurs on different substrates. Whelks tolerate salinities down to 20‰. European populations mainly breed during autumn and winter. The whelk is an opportunistic feeder, being a predator as well as a scavenger.

The whelk is fished over its entire range. In the western Dutch Wadden Sea a whelk fishery existed between 1900 and 1970. This fishery culminated in the 1920s when in 1925 and 1926 half a million kg was fished. From the end of March till October the fishery was closed. Contrary to England and France where whelks are fished with pots, special dredges were used. These dredges had a width of 1 m with a bottom of metal wire netting with 10 cm mesh size at the fore end and 8 cm at the lower end, and a top made of rough cotton thread. Three to four dredges were used simultaneously. The majority of whelks caught had a length between 55 and 70 mm and were between 4 and 6 years old (Havinga, 1929). In the 1970s the whelk disappeared from the Dutch waters.

In this paper we explore the causes of disappearance of the whelk in the Western Dutch Wadden Sea. We are specifically interested in whether or not overfishing has been a major cause for the disappearance of the whelk. In order to shed some light on this question, we first try to reconstruct the population dynamical characteristics of the whelk population, including growth, natural mortality, fishing mortality, recruitment, and population size. Next, we will link this information to data on trends in catches and fishing effort. Unfortunately, almost no fishery research has been carried out on the whelk fishery in The Netherlands. The only extensive data we have considered are catches. So we will partly rely on investigations on whelk fisheries which have been carried out elsewhere, e.g. in England (Hancock, 1963), France (Santarelli and Gros, 1985, 1986; Gros and Santarelli, 1986), Ireland (Fahy et al., 1995, 2000), the Channel Island Jersey (Morel and Bossy, 2004) and Sweden (Valentinsson et al., 1999; Valentinsson, 2002).

2. Materials and methods

2.1. Growth

No complete growth curve is available for the Western Wadden Sea. Havinga (1929) only reported that whelks had a length of 16 mm after their first winter and of 30 and 40–45 mm respectively after the second and third winter. After four winters the length could be as much as 55 mm. Santarelli, Véron and Huet (1986) published a much more detailed growth table for whelks occurring east of the Channel Islands. Relations are given between age, height and weight for animals up till nine years old. Lengths for the first four years correspond with those given by Havinga. Data from these French investigators were therefore used, together with their corresponding weights, to estimate a von Bertalanffy length growth curve and a conversion coefficient from cubic length to biomass.

2.2. Natural mortality

Hancock (1963) carried out an experiment with marked whelks in the Thames estuary. In July 1957 marked whelks were released, and

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during the three subsequent years the number of recaptured marked whelks was noted. We used these data to estimate the natural mortality, and applied the estimation method of Paulik (1962, 1963), see also Seber (1973, pp 271–276). This method assumes that both the instantaneous mortality rate and the instantaneous exploitation rate are constant, which is in good agreement with the data provided by Hancock on fishing effort and total catches.

2.3. Recruitment, fishery mortality, and fishery catches and effort

Here we develop a new method to estimate fishery mortality using information on catch rates in a previously unexploited population and compare this to the catch in an exploited population. The situation we have in mind is the observed high catch rate of the whelk in the Dutch Wadden Sea in 1946, the first year after the Second World War. During the German occupation fishing had not been possible for several years (1943–1945). We compare the catch in 1946 to that of 1949 to estimate recruitment and fishery mortality. Fishing effort was very similar in these two years. The method relies on the assumptions that recruitment is constant, growth follows a Bertalanffy growth curve, natural mortality is constant, and in years when fishing occurs fishing mortality is constant. See the Appendix for details.

Catch data and data on fishery effort were obtained from two types of fishery statistics published in the "Jaarcijfers over de visserij [Annual Fishery Statistics]" (Anonymus, 1920–1939, 1940–1941, 1942–1944, 1946–1964, 1965–1970). The first statistic gives the "Extent and outcome of the Wadden Sea Fisheries on the whelk in kg per year". The second statistic gives "A statement showing total quantity and value taken by the different kinds of gear in the coastal waters; dredges and weeks of operation". The latter statistic is lacking from 1965 onwards. From 1938 a minimum size limit of 50 mm is applied in whelk fishery in The Netherlands, because too many small animals were supplied. This implies that catch data before and after 1938 are difficult to compare.

2.4. Population size

Population surveys have not been carried out in the Dutch Wadden Sea. However, an assessment of potential stock size could be made using published whelk densities from other estuaries and fishing areas (Table 1). In these studies estimates were obtained either by fishing with pots or by diving. Kideys (1993) compared four different sampling methods (pot sampling, SCUBA diving, mark-recapture experiments and video) and showed that the estimates obtained by these methods are very similar.

Table 1
Densities of whelks (*Buccinum undatum*) in different estuaries.

Author	Location	Method used	Density
Hancock (1963)	Thames estuary	Fishing with pots	$0.5\ m^{-2}$
Hylleberg (1991), based on the results of Petersen (1911) and Petersen and Boysen Jensen (1911)	Thisted Bredning (Limfjord)	Sampling Diving	$1.23\ m^{-2}$ $0.5–1.5\ m^{-2}$
Legault and Himmelman (1993)	St. Lawrence estuary	Diving ($1771\ m^2$ observed)	$0.417 \pm 0.045\ m^{-2}$
McQuinn, Gendron and Himmelman (1988)	St. Lawrence estuary	Fishing Diving	$0.81\ m^{-2}$ $0.65\ m^{-2}$
Petersen (1918)	Thisted Bredning (Limfjord)	Sampling; $0.1\ m^2$ ($n=15$)	$0.6\ m^{-2}$
	Nissum Bredning (Limfjord)	Sampling; $0.1\ m^2$ ($n=8$)	$0.65\ m^{-2}$
Gros and Santarelli (1986)	Channel Islands	Fishing with pots	$0.37\ m^{-2}$

3. Results

3.1. Growth

Using growth data provided by Santarelli et al. (1986) we obtained estimates for the three growth parameters: the conversion coefficient from cubic length to mass ϕ is 0.114 g cm^{-3}, the ultimate length L_∞ is 10.3 cm, and the Von Bertalanffy growth coefficient γ is 0.191 $year^{-1}$ (Fig 1).

3.2. Natural mortality

Hancock (1963) tagged 4898 animals and recaptured 349, 213 and 74 animals in the first, second, and third year after release, respectively. Maximum likelihood estimation, as presented in Seber (1973, pp. 271–276) resulted in an overall annual instantaneous mortality rate of 0.700. The overall annual instantaneous mortality rate is the sum of an instantaneous natural mortality rate of 0.597 and an instantaneous exploitation rate of 0.104. Hence the annual percentage that survived exploitation equalled 90%, from which 55% survived and 45% died from natural causes. Overall 50% survived each year.

3.3. Fishery mortality and recruitment

Average catches for various periods, both before and after the war and for the Wadden Sea and for Zeeland, are presented in Table 2. The catch per year in the Wadden Sea for the period 1946–1969 is given in Fig 2. The catch peaks in the first year after the end of the German occupation subsequently decrease until the early 1950s when a period of relative stability begins. The last five years (1965–1970) show lower catches.

We used the post-second-world-war 1946 catch (which equalled 140×10^3 kg), and the 1949 catch (which equalled 72×10^3 kg $year^{-1}$) to estimate the annual recruitment and the instantaneous fishery mortality. The renewal rate is estimated at 46.7×10^6 new-born individuals per year, which corresponds to an annual recruitment at the age of 4 of 81.3×10^3 kg. The instantaneous fishery mortality was estimated at 0.815 $year^{-1}$. Our analysis predicts that such fishery mortality has had a major effect on the size distribution of the

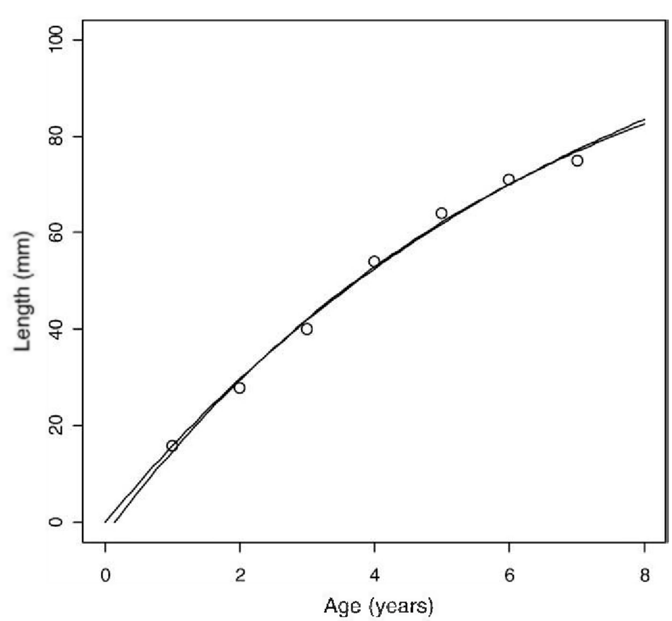

Fig. 1. Length–age data and the fitted von Bertalanffy growth curves (with or without the restriction that length is zero at age zero). Data from Santarelli et al. (1986).

Table 2
Mean yearly catch of the whelk fishery in the Dutch Wadden Sea and Zuiderzee (which disappeared in 1932), and in Zeeland, expressed in kg $\times 10^3$.

Period	Wadden Sea and Zuiderzee	Zeeland
1920–1929	334 ± 124	39 ± 14
1930–1939	217 ± 66	112 ± 27
1950–1959	45 ± 10	42 ± 12
1960–1969	37 ± 15	76 ± 35

population. Older age classes are virtually absent in case fishing occurs every year, compared to the situation without fishing. The situation in the years 1946 (after several years without fishing) and 1949 is in between these two extremes (Fig. 3).

3.4. Fishery effort and catch per unit effort

Although the quantity of whelks caught per year was highest in 1925 and 1926, no data for fishery effort are available for this period, not even the number of boats involved. In the period 1932–1938 only the number of boats fishing on whelks is known, no other data on fishery effort are available. The mean catch per boat per year decreased gradually from about 3300 kg in 1932 to 1200 kg in 1938.

For the period 1946–1963 data for fishery effort are available in the form of the number of dredges used and the number of weeks per year that they were used. Multiplying these two factors provides a measure indicating fishery effort. From 1946 onwards the effort decreases continuously till 1955, after which it remains at a rather constant low level. The catch per unit effort is initially rather low, but shows a large increase after the early 1950s (Fig. 4).

3.5. Population size

The mean density of whelk populations in estuaries and coastal waters that are more or less comparable with the Wadden Sea, was estimated at $0.69 \pm 0.28\ m^{-2}$ (Table 1). The surface area of the Western Dutch Wadden Sea deeper than 3 m equals $306 \times 10^6\ m^2$ (Dekker 1989). Total potential whelk population can thus be estimated at 211×10^6 with a standard error of 86×10^6 animals. A crude estimate of the total biomass of whelks larger than 5 cm is in the range of $2280–5400 \times 10^3$ kg.

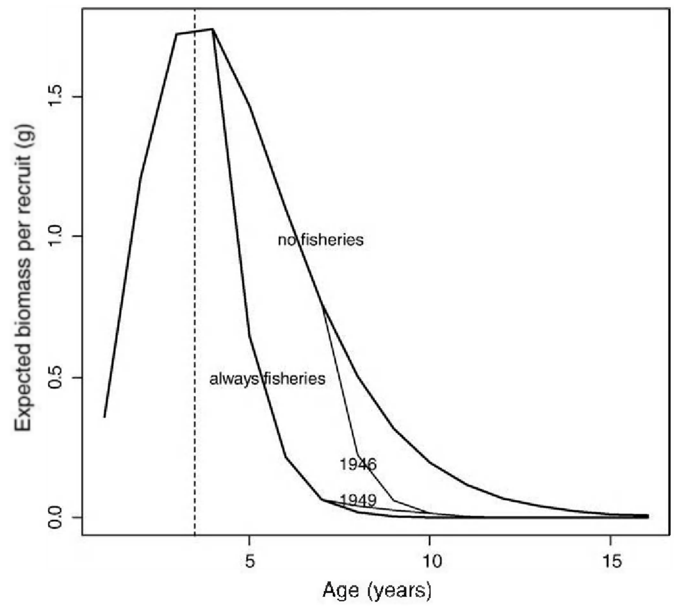

Fig. 3. Expected biomass versus age. The two thick lines represent (from right to left) an unexploited population and a population exploited from the age of 4 onwards. The thin lines give the 1946 and the 1949 situation.

4. Discussion

4.1. Growth, natural mortality, recruitment and population size

Whelks show only limited movements and they disperse slowly (Hancock, 1963; Himmelman and Hamel, 1993). This enables mark-recapture experiments, because even after several years marked animals can be recaptured. The estimated natural mortality rate of about 0.6, using data from the mark-recapture experiments of Hancock (1963) is considerably higher than those obtained by other investigators. Santarelli and Gros (1986) assumed, on the basis of literature data of two other gastropod species from Australia and the west coast of the US, a natural mortality of 20 or 30% in the seas east of the Channel Islands. Fahy et al. (2000) assumed a natural mortality of 20% in the coastal

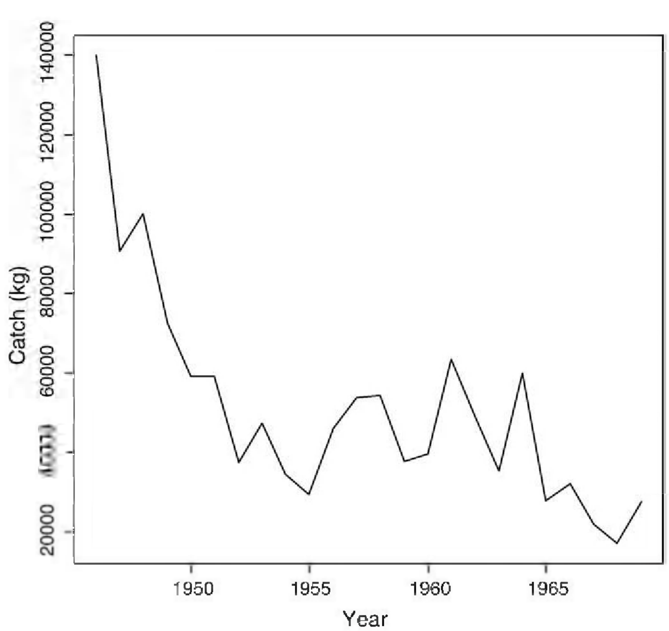

Fig. 2. Catch of whelks (in kg) in the western Dutch Wadden Sea from 1946 to 1969.

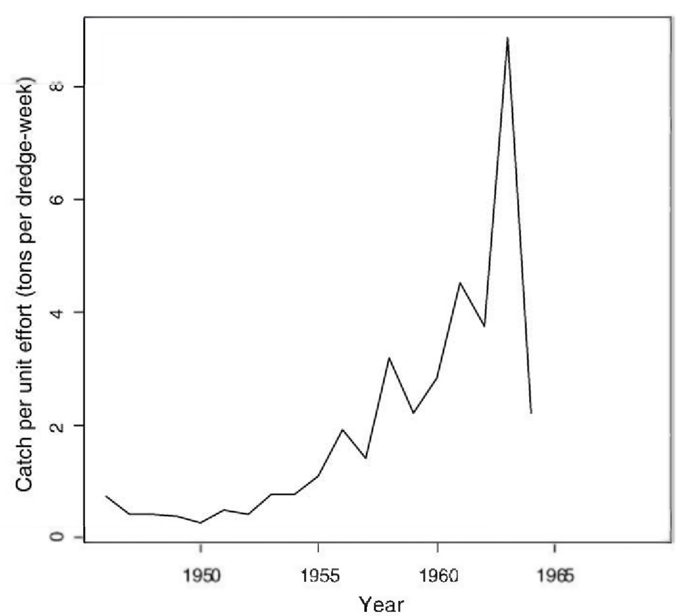

Fig. 4. Catch per unit effort in whelk fishery in the western Dutch Wadden Sea from 1946 to 1964, expressed as tons per number of dredges used multiplied with the number of weeks in which the dredge was in use.

waters of South-East Ireland. Compared with our experimentally based estimate, these assumptions are probably too low.

We assumed that recruitment was constant during the war and the post-war period. Given the limited data available, this was merely a necessity in order to estimate fishery mortality, than that this assumption was based on rigid data. The high catches in the pre-war period were compared to the low catches in the post-war period point, however, to a much more complicated situation. Overfishing in the 1930s, as indicated by the decreasing catch per unit effort in this period may have resulted in a population decrease, but most likely other factors than fishery will also have contributed to the decrease of the whelk population in the Western Dutch Wadden Sea. These factors are related to the closure of the Zuiderzee in 1932. First of all, area reduction may have contributed considerably to the decline in whelk catches. Reclamation started already at the end of the 1920s, when the region south of Wieringen was reclaimed. Second, as a result of the closure, the channels leading to the former Zuiderzee became silted and unsuitable for whelks and oysters alike. Oyster beds disappeared completely from the western Dutch Wadden Sea. It is known that many whelks are found near or on oyster beds (Fig 5). In Zeeland, for example, the whelk catch has always been a subsidiary to the oyster harvest. The decline in the whelk catches in the western Wadden Sea after the 1930s and which did not occur in Zeeland, could thus be related to the disappearance of the oyster beds.

Our analysis pointed to a post-war stock of approximately hundred ton whelks, which is low compared to the potential population size of several thousand tons, as assessed on the basis of comparable areas. This implies that the post-war stock was already in a phase of severe decline.

4.2. Fisheries

In the period 1932–1938, the mean catch per boat per year decreased gradually from about 3300 kg in 1932 to 1200 kg in 1938.

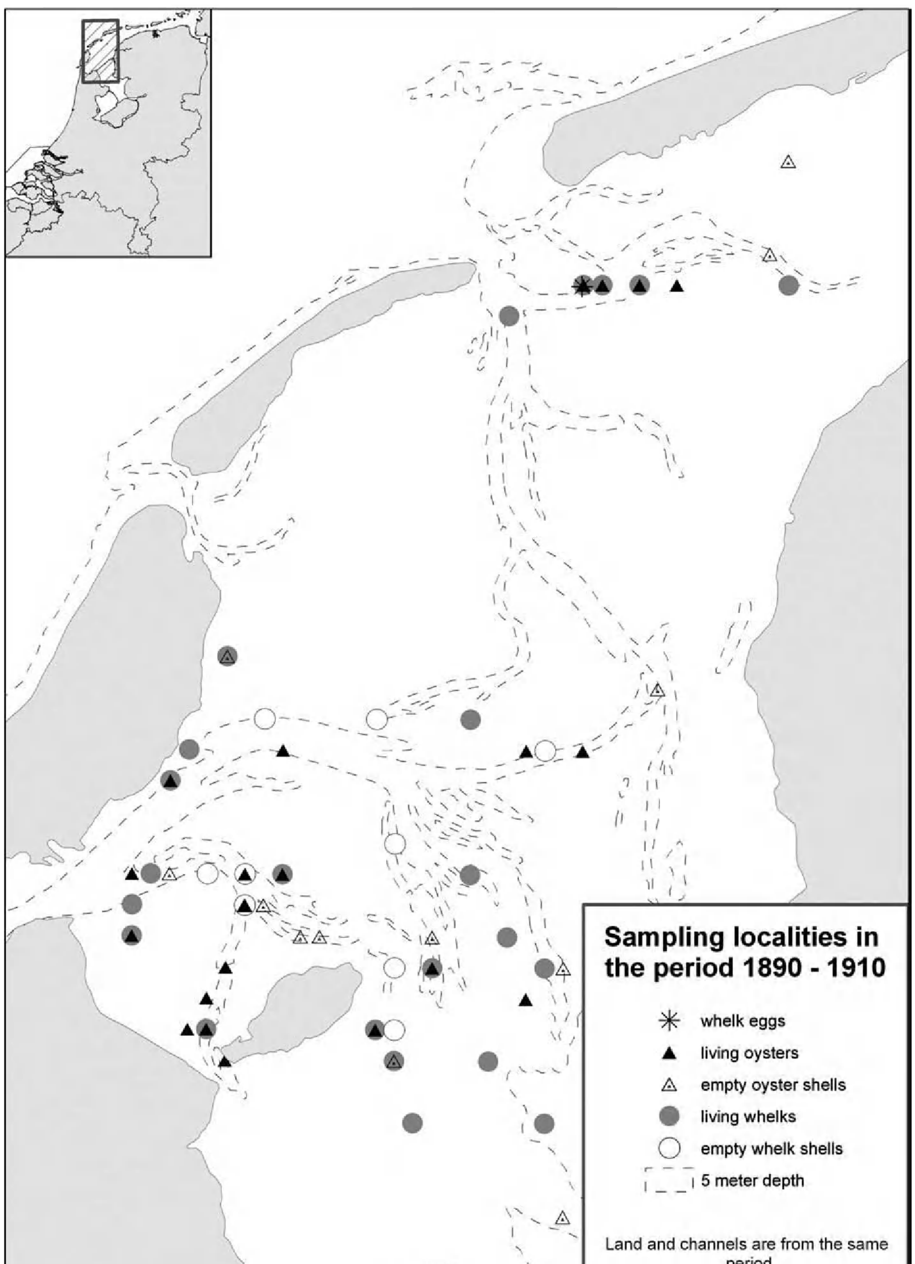

Fig. 5. The occurrence of whelks and oysters in the western Wadden Sea in the period 1890–1910, presented on a recent map.

This reduction in the catch per unit effort points to overfishing. For this reason, the authorities introduced, from 1938 onwards, a minimum size limit of 50 mm in the whelk fishery in The Netherlands. For the period 1946–1963 much better data for fishery effort are available in the form of the number of dredges used and the number of weeks of use per year. From 1947 to 1955 the catch per unit effort remained at a rather constant and low level, but from 1956 onwards a large increase in catch per unit effort is observed until 1963. This is a surprising result and one explanation might be that the way fishery effort is calculated, that is in multiplying the number of dredges used by the number of weeks the dredges are in use, is of rather limited value. Most likely the motor power of the ships involved has been increased during this period, and ignoring motor power may give a wrong impression of the fishery effort. Unfortunately, no information is available for motor power of vessels fishing on whelks. However, national statistics are available for categories of fishing vessels. Mean HP for fishing vessels greater than 7 BRT increased between 1950 and 1955 with 20% and between 1956 and 1964 with 194%. For vessels smaller than 7 BRT, mean HP increased by 10% between 1950 and 1955, and by 60% between 1956 and 1964. Both categories of vessels showed a strong increase in motor power after 1955. From 1965 to 1969 the catch is lower compared with the earlier periods, but over these years no data on fishery effort are available.

5. Conclusions

Overfishing in the pre-war period in combination with the loss of area and the disappearance of the oysters initiated the decline of the whelk. Despite intensive fishing mortality during the post-war period 1947–1963, there are no strong indications of overfishing in terms of a decreasing catch per unit effort, and fishery probably stopped definitely in 1969 for economical reasons. Most likely other factors such as the use of tributyltin antifouling paints since the 1970s may explain the later complete extinction of the whelk in the Wadden Sea (Cadée et al., 1995).

Acknowledgement

The authors thank Jenny Cremer (Imares, Texel) for the preparation of the map.

Appendix A. Estimating fishery mortality and recruitment rate in the whelk

Fishery biologists usually distinguish between natural mortality and fishery mortality. Here we present a new method on how to estimate fishery mortality using very limited information on catch rates; i.e. information is available on the total catch in a previously unexploited population and on the catch in an exploited population. The situation we have in mind is the observed high catch rate of the whelk in the Dutch Wadden Sea after the Second World War, during which fishing had not been possible for several years. We assume that growth and naturality mortality are known and that the population is stationary, i.e. recruitment or renewal rate B is constant. For illustrative purposes first we start with the idealized situation where fishery mortality affects all ages (A). After this we continue with a more realistic case, where older age classes only are subject to fisheries (B).

(A). Assume that the instantaneous mortality rate λ is constant, which means that the life span X is exponentially distributed, and that the expected mass of living individuals equals the expected mass at death (Van Straalen, 1985). Assume further that growth is of the Von Bertalanffy type. Van der Meer et al. (2001) showed that the expected mass at death W is then equal to

$$E(W) = \phi L_\infty^3 \left(\frac{6\gamma^3}{(\gamma+\lambda)(2\gamma+\lambda)(3\gamma+\lambda)} \right),$$

where ϕ is a condition parameter relating cubic shell length to mass, L_∞ the asymptotic length, and γ the Von Bertalanffy growth parameter. The population biomass equals $B \cdot E(W)/\lambda$.

Assume that the instantaneous mortality rate is the sum of an instantaneous natural mortality λ_m and an instantaneous fishery mortality λ_f. This means that the catch rate can be written as $B \cdot E(W) \cdot \lambda_f/(\lambda_m + \lambda_f)$. Consider now the situation where a population without fisheries (population biomass equals $B \cdot E(W)/\lambda_m$), is suddenly exposed to fisheries, with instantaneous fishing mortality λ_f. The initial catch rate will then equal to $B \cdot \phi L_\infty^3 \left(\frac{6\gamma^3}{(\gamma+\lambda_m)(2\gamma+\lambda_m)(3\gamma+\lambda_m)} \right) \cdot \lambda_f / \lambda_m$. In the long run, the catch rate will settle at $B \cdot \phi L_\infty^3 \left(\frac{6\gamma^3}{(\gamma+\lambda_m+\lambda_f)(2\gamma+\lambda_m+\lambda_f)(3\gamma+\lambda_m+\lambda_f)} \right) \cdot \lambda_f / (\lambda_m + \lambda_f)$.

These two catch rate equations contain only two unknowns, the instantaneous fishery mortality rate λ_f and the recruitment rate B, which can thus be easily obtained. For example, the fishery mortality rate λ_f follows from the ratio between these two catch rates, which equals:

$$\frac{(\gamma+\lambda_m+\lambda_f)(2\gamma+\lambda_m+\lambda_f)(3\gamma+\lambda_m+\lambda_f)}{(\gamma+\lambda_m)(2\gamma+\lambda_m)(3\gamma+\lambda_m)} \frac{(\lambda_m+\lambda_f)}{\lambda_m}.$$

(B). Some of the assumptions made above are too rigid (e.g. that of equal fishery mortality for all age classes and that of a stationary population that is already in equilibrium at the end of the war after a three year fishery mortuarium) and we will proceed with a more specific treatment. We first consider an exploited population, consisting of annual cohorts. Only individuals that have reached the age of 4 are fished. Furthermore fishery occurs in annual pulses, immediately after each birth day. Hence when it is fished for the first time, the abundance of age cohort 4 equals

$$N_4 = B \exp(-\lambda_m \cdot 4).$$

Its individual biomass is

$$G_4 = \phi L_\infty^3 (1 - \exp(-\gamma \cdot 4))^3,$$

and its contribution to the catch equals

$$C_4 = (1-q) \cdot B \exp(-\lambda_m \cdot 4) \cdot \phi L_\infty^3 (1 - \exp(-\gamma \cdot 4))^3,$$

where the fraction that survives fishing q can also be expressed as $q = \exp(-\lambda_f)$. Similarly the contribution of age class 5 equals

$$C_4 = (1 - \exp(-\lambda_f)) \cdot B \exp(-\lambda_m \cdot 5 - \lambda_f \cdot 1) \cdot \phi L_\infty^3 (1 - \exp(-\gamma \cdot 5))^3,$$

and the total annual catch equals

$$C = \sum_{i=4}^{\infty} (1 - \exp(-\lambda_f)) \cdot B \exp(-\lambda_m \cdot i - \lambda_f \cdot (i-4)) \cdot \phi L_\infty^3 (1 - \exp(-\gamma \cdot i))^3$$
$$= (1 - \exp(-\lambda_f)) B \phi L_\infty^3 \sum_{i=4}^{\infty} \exp(-\lambda_m \cdot i - \lambda_f \cdot (i-4)) \cdot (1 - \exp(-\gamma \cdot i))^3.$$

For a population that has not been exploited for several years (as the post-war whelk population) this latter equation should be replaced by

$$C_j = (1 - \exp(-\lambda_f)) B \phi L_\infty^3 \sum_{i=4}^{\infty} \exp(-\lambda_m \cdot i - \lambda_f \cdot z_{ij}) \cdot (1 - \exp(-\gamma \cdot i))^3,$$

where z_{ij} reflects the fishery history of age class i in year j and gives the number of years that each specific cohort at a specific age has been fished previously. See Table A1 for the case of the whelk fisheries in the Dutch Wadden Sea.

Table A1
Fishery histories.

	1	2	3	4	5	6	7	8	9	10	11	12	13	…	30
46	45	44	43	42	41	40	39	38	37	36	35	34	33	…	16
	0	0	0	0	0	0	0	1	2	3	4	5	6		23
					(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)		(26)
47	46	45	44	43	42	41	40	39	38	37	36	35	34	…	17
	0	0	0	0	1	1	1	1	2	3	4	5	6		23
						(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)		(26)
48	47	46	45	44	43	42	41	40	39	38	37	36	35	…	18
	0	0	0	0	1	2	2	2	2	3	4	5	6		23
							(3)	(4)	(5)	(6)	(7)	(8)	(9)		(26)
49	48	47	46	45	44	43	42	41	40	39	38	37	36	…	19
	0	0	0	0	1	2	3	3	3	3	4	5	6		23
								(4)	(5)	(6)	(7)	(8)	(9)		(26)
50	49	48	47	46	45	44	43	42	41	40	39	38	37	…	20
	0	0	0	0	1	2	3	4	4	4	4	5	6		23
									(5)	(6)	(7)	(8)	(9)		(26)
51	50	49	48	47	46	45	44	43	42	41	40	39	38	…	21
	0	0	0	0	1	2	3	4	5	5	5	5	6		23
										(6)	(7)	(8)	(9)		(26)
52	51	50	49	48	47	46	45	44	43	42	41	40	39	…	22
	0	0	0	0	1	2	3	4	5	6	6	6	6		23
											(7)	(8)	(9)		(26)

Rows refer to the year of fishing (1946–1952), columns to the age class (1 year old to 30 years old).
Upper figure gives the year of birth, lower figure the number of previous years in which fishing took place. Between brackets is the number of years in which fishing took place if fishing would have continued during the years 1943–1945. For example, just before the 1946 fishing, age class 8, which was born in 1938 has experienced only one fishing year, that is in 1942. Before 1942 they were too small (in 1939, 1940 and 1941) and from 1943 to 1945 no fishing took place.

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