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Growth of Norway lobster, *Nephrops norvegicus* (Linnaeus 1758), in the Skagerrak, estimated from tagging experiments and length frequency data

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Parameter values for the von Bertalanffy growth model are estimated for *Nephrops norvegicus* in the Skagerrak on the Swedish west coast using analysis of length frequency distribution from commercial catches and tag-recapture data. The asymptotic lengths (L_∞) for males and females are estimated from size distributions using a modified Powell-Wetherall plot. The tagging experiment was conducted with Floy streamer tag and analysed in a "forced" Gulland-Holt plot to estimate the growth coefficient K for males. The estimates of L_∞ (72.9) and K (0.138) for males differ from those currently used in the ICES assessment for this area (76 and 0.16, respectively), and the results are discussed in relation to sensitivity to reference points from analytical stock assessments and possible implications for management decisions.

Keywords: growth, *Nephrops norvegicus*, tagging.

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Introduction

A major problem in determining age of crustaceans is that these animals possess no detectable annually marked physical structures. In recent years two potential ageing approaches have been developed. First, intermoult period can be characterised by the ratio of the isotopes 228Th/228Ra in the carapace, which is correlated to the age of exoskeleton (Latrouite *et al.*, 1991; Talidec and Reyss, 1993; Verdoit *et al.*, 1999). Second, the accumulation of lipofuscin pigment in the brain is considered to be correlated to age (Sheehy, 1989; Tully, 1993). However, at present these methods are too time consuming and expensive to be applied in regular monitoring programmes. As a consequence assessment methods are based on length data and rely on estimates of growth rate to determine mortality in the population.

Growth in Norway lobster, *Nephrops norvegicus*, is characterised by periodic shedding of its outer shell and growing into a new larger shell. All calcified structures with annual or other periodic marks are lost with the old shell and the age can therefore not be directly determined. The growth of crustaceans thus comprises two different phases, firstly the time interval between moults and secondly, the size increment at moult. The second phase is usually determined by measuring the length of individuals before and after moulting.

Hillis (1979) refers to three methods used to estimate the age of *Nephrops*; (i) the method suggested by Petersen (1891), i.e. the identification of age groups from modes in length frequency distributions; (ii) observation of growth in captivity; (iii) mark-recapture experiments. Bailey and Chapman (1983) applied a combination of these methods to derive growth in two populations of *Nephrops* in Scottish waters. The first method is not applicable to the size distribution in catches of the Swedish West Coast *Nephrops* fishery, as modes cannot be identified either in commercial or in small mesh research vessel catches from the Skagerrak area (Figure 1). The growth rate in lobsters is mainly affected by temperature but also by social interactions (Cobb and Tamm, 1974, 1975), which implies that growth in captivity may not be comparable to that of wild populations (Castro, 1992). However, because recapture rates in tagging experiments are generally low, growth studies of *Nephrops* based on growth in captivity have

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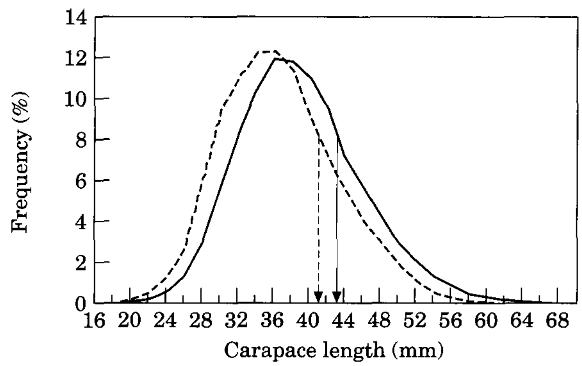

Figure 1. Size distribution of male (continuous line) and female *Nephrops* (broken line) from commercial trawl catches during 1990 and 1992–1998. Arrows indicate size when fully recruited to the fishery (as used in the Powell-Wetherall plot).

been presented recently (Gonzàlez-Gurriarán *et al.*, 1998; Verdoit *et al.*, 1999). In this study we use information from the mark-recapture method, data on length at sexual maturity, and the additional approach by Powell (1979), where length-frequency data are used to derive L_∞ and Z/K.

The seminal paper by von Bertalanffy (1938) assumes that growth rate declines linearly with increased length. This linear assumption has been questioned by, for example, Easton and Misra (1988), who suggested a hyperbolic relationship between premoult and postmoult. Another approach is to keep the linear growth assumption, but allow for a change in slope at the size at sexual maturity (Hiatt, 1948; Sommerton, 1980). The ICES Working Group responsible for *Nephrops* stock assessment applies this approach to female *Nephrops*, whose growth slows after reaching maturity (Bailey and Chapman, 1983).

As growth in weight describes the increase in biomass, knowledge of growth rate is essential for understanding the population dynamics of a *Nephrops* stock. The length based assessment methodology used for *Nephrops* stocks is very sensitive to input growth parameters (Lai and Gallucci, 1988; Bailey and Kunzlik, 1989). So far, the ICES Working Group on Assessment of *Nephrops* Stocks has mostly relied on growth parameters borrowed from neighbouring areas when assessing the stocks (see Table 4). For the Skagerrak-Kattegat *Nephrops* stock assessment, the K value is borrowed from the Scottish west coast (Bailey and Chapman, 1983) and L_∞ is chosen from a size close to the maximum size in length distribution. The uncertainty surrounding these parameter values is judged to be the major cause of the poor assessment quality of this stock (ICES, 1999), and empirical parameter estimates for Skagerrak are of evident interest to the Working Group. The study by Jensen (1965) applied the Petersen method to the Skagerrak *Nephrops* stock, but did not present any growth parameters. Hence, the present study is the first to present growth parameter estimates for the Skagerrak *Nephrops* stock.

The purpose is twofold. Firstly, to describe the growth of *Nephrops* in the Skagerrak by estimating the von Bertalanffy growth parameters. Secondly, to discuss possible management implications by using these parameters in stock assessment.

Material and methods

Estimation of growth parameters

Growth is assumed to follow the von Bertalanffy growth function (von Bertalanffy, 1938):

$$L_t = L_\infty[1 - e^{-K(t - t_0)}] \quad (1)$$

where L_t is length at age t, L_∞ is the asymptotic length, i.e. the mean length that an individual would reach if it grew for an infinite number of years, K (yr^{-1}) is the rate at which L_∞ is approached, and t_0 is the age of the *Nephrops* at zero length if they had always grown in the manner described by the equation.

Analysis of length-frequency data

During the years 1990 and 1992–1998, length-frequency samples from commercial trawl catches, i.e. both landings and discards, were collected on average from three vessel trips per month. Data were collected from about 20 different vessels and >100 000 *Nephrops* were measured. The average length-frequency distributions for males and females are shown in Figure 1. Assuming that Figure 1 shows an equilibrium, which requires constant recruitment and no significant trend in exploitation rates, the Powell-Wetherall method can be applied on the length classes equal to and above the fully recruited length. This method also assumes that the length distribution is not affected by exploitation i.e. it assumes that fast and slow growing individuals within the chosen used size range are equally exploited.

Wetherall (1986) suggests a method, based on Powell (1979), to estimate the asymptotic length (L_∞) and the ratio of Z/K [i.e. the instantaneous rate of total mortality, Z (yr^{-1}) and growth, K (yr^{-1})], using only length frequency distributions. The method is based on the equation of Beverton and Holt (1956):

$$Z = K[(L_\infty - \boldsymbol{L})/(\boldsymbol{L} - L')] \quad (2)$$

which estimates Z in a steady state population with constant exponential mortality and the von Bertalanffy growth function from a mean length sample ($\boldsymbol{L}$) of *Nephrops* above a selected cut-off length L′.

Table 1. Number of tagged, recaptured and its mean lengths for males and females separately for the two tagging periods.

	Number tagged			Number recaptured		
	Males	Females	Total	Males	Females	Total
1987–88	925	286	1211	27	3	30
1991–95	718	267	985	30	9	39
Both periods	1643	553	2106	57	12	69
Mean length (s.d.)	47.2 (7.3)	42.4 (5.8)		50.1 (7.4)	42.8 (3.9)	

It can be shown that for a series of arbitrary cut-off lengths, L_i', and corresponding mean lengths ($\boldsymbol{L}_i$) of all *Nephrops* above L_i' there is a linear relationship:

$$\boldsymbol{L}_i = L_\infty[1/(1+(Z/K))] + L_i'[(Z/K)/(1+(Z/K))] \qquad (3)$$

where i represents length classes larger or equal than the smallest fully recruited length class.

Equation (2) was modified by Pauly (1984) to:

$$\boldsymbol{L}_i - L_i' = \alpha + \beta L_i' \qquad (4)$$

where $\beta = -K/(Z+K)$ or $Z/K = (1+\beta)/-\beta$ and $-\alpha/\beta = L_\infty$.

Here, we use Equation (4), with values on $\boldsymbol{L}_i - L_i'$ from the average *Nephrops* catch curve, to estimate asymptotic carapace length L_∞ (mm) and Z/K. All values are plotted against L_i', in order to judge which points lie on a straight line. α and β are then estimated by linear regression on the selected length class range (Sparre and Venema, 1992).

Analysis of tag-recapture experiment

A total of 1211 and 985 *Nephrops* were tagged with Floy streamer tags FTSL-73 during 1987–1988 and 1991–1995, respectively, as described in Chapman (1982) and Figueiredo (1989). Numbers tagged, numbers and percentages recaptured and mean lengths are reported in Table 1. The streamer tag was inserted through the dorsal musculature between the carapace and abdomen in order to be retained through the moult. The potential loss of tags due to moulting is unknown. During the years 1987–1988, the tagged *Nephrops* were caught on offshore trawl fishing grounds, while those tagged in 1991–1995 were caught on an inshore fishing ground in baited creels deployed both by professional fishers and by staff from the Institute of Marine Research. The carapace length, sex, and gonad stage (females) of each tagged *Nephrops* were recorded. *Nephrops* were tagged onboard the vessel and then immediately returned to the sea. In order to estimate the mortality caused by the tagging procedure, 12 *Nephrops* were tagged and kept in tanks with flow through bottom water in the laboratory at the Institute of Marine Research (unpublished data). Males and females were treated separately in the analysis, as growth rate is known to differ by sex (Chapman, 1980). For individuals above the length at onset of sexual maturity, the von Bertalanffy growth function implies that the growth rate (dL/dt) declines linearly with length. This applies for our sample, where the length at onset of sexual maturity is 28 mm for Skagerrak (Eggert and Ulmestrand, 1999) while the smallest used individual had an initial length of 34 mm. Considering a *Nephrops* of length l_1 that was tagged at time t_1 and recaptured at t_2 with a length of l_2, Gulland and Holt (1959) demonstrated that estimates of K and L_∞ can be obtained by the relationship:

$$(\Delta L/\Delta t) = a + b\boldsymbol{L} \qquad (5)$$

where $\Delta L = l_2 - l_1$, $\Delta t = t_2 - t_1$, $\boldsymbol{L} = l_1 + (\Delta L/2)$. Equation (5) is a reasonable approximation, given that the value of Δt is small compare to the lifespan of the creature (Faben, 1965).

This leads to estimates of K and L_∞ through:

$$K = -b \text{ and } L_\infty = -a/b \qquad (6)$$

The carapace length increments for various time intervals from the tag-recapture data were used to calculate annual increments (ΔL/yr) for each individual (Tables 2 and 3). Parameter estimation with this method may cause serious problems using animals, with periodic growth such as crustaceans. One moult in a short recapture period will result in an unreasonable large annual increment, while individuals with zero growth are likely to be over-represented. To mitigate such effects all individuals with either zero growth or a recapture period of less than one year are excluded in the final analysis. Thus, of the 69 recaptured *Nephrops* (57 males and 12 females), 18 males and 8 females were used in the final analysis. The traditional approach for growth parameter estimates has been to apply the Gulland and Holt plot, but this method simultaneously determines K and L_∞, which may cause problem (Gayanilo and Pauly, 1997). The dependence between K and L_∞ in a Gulland and Holt plot is also clearly shown in Equation (6), where an increase in L_∞ leads to a smaller K. To

Table 2. Length at tagging (L1), length at recapture (L2), number of days from L1 to L2 (Δt) and annual size increment ($\Delta L\ yr^{-1}$) for males. Bold figures are the 18 selected recaptures used in the analysis (Δt larger than one year and ΔL larger than zero).

No.	L1	L2	Δt	$\Delta L\ yr^{-1}$
1	**34.21**	**44.70**	**883**	**4.34**
2	35.09	38.49	279	4.45
3	**37.36**	**40.83**	**378**	**3.35**
4	37.56	37.56	13	0.00
5	38.18	41.89	197	6.87
6	38.18	38.18	240	0.00
7	38.80	38.80	58	0.00
8	38.80	41.27	118	7.65
9	**40.41**	**44.42**	**521**	**2.81**
10	**40.65**	**46.58**	**518**	**4.18**
11	40.83	40.83	95	0.00
12	**41.85**	**45.31**	**376**	**3.36**
13	41.86	41.86	430	0.00
14	41.89	41.89	119	0.00
15	41.89	43.74	37	18.30
16	43.12	43.43	285	0.40
17	43.15	43.15	351	0.00
18	**43.27**	**57.40**	**810**	**6.37**
19	**43.36**	**51.98**	**449**	**7.01**
20	**43.69**	**48.10**	**442**	**3.64**
21	43.87	43.87	94	0.00
22	**44.13**	**48.80**	**393**	**4.34**
23	44.36	45.91	178	3.17
24	**44.41**	**48.61**	**403**	**3.81**
25	45.29	47.45	161	4.91
26	**45.58**	**50.33**	**398**	**4.36**
27	**45.59**	**49.65**	**762**	**1.95**
28	45.60	45.60	367	0.00
29	**46.21**	**46.52**	**414**	**0.27**
30	46.35	46.35	393	0.00
31	48.07	51.16	124	9.10
32	48.07	48.07	235	0.00
33	48.38	48.38	197	0.00
34	49.00	49.61	233	0.97
35	49.00	49.00	244	0.00
36	**50.46**	**53.83**	**461**	**2.67**
37	50.69	56.15	220	9.06
38	51.70	51.70	463	0.00
39	52.32	52.32	434	0.00
40	52.73	52.73	265	0.00
41	52.87	55.28	109	8.08
42	53.40	53.40	100	0.00
43	**53.56**	**58.24**	**454**	**3.77**
44	53.63	53.63	194	0.00
45	54.19	54.19	395	0.00
46	54.25	54.25	321	0.00
47	**54.77**	**59.24**	**449**	**3.64**
48	54.92	54.92	448	0.00
49	55.18	55.18	47	0.00
50	**57.96**	**58.27**	**510**	**0.22**
51	58.29	58.29	94	0.00
52	**59.07**	**63.18**	**420**	**3.57**
53	59.19	60.43	102	4.43
54	61.36	61.97	119	1.90
55	63.83	63.83	57	0.00
56	66.55	66.55	65	0.00
57	66.61	66.61	313	0.00

Table 3. Length at tagging (L1), length at recapture (L2), number of days from L1 to L2 (Δt) and annual size increment ($\Delta L\ yr^{-1}$) for females. Bold figures are the eight selected recaptures used in the analysis (Δt larger than one year and ΔL larger than zero).

No.	L1	L2	Δt	$\Delta L\ yr^{-1}$
1	**34.88**	**37.19**	**458**	**1.84**
2	**36.29**	**44.00**	**1525**	**1.85**
3	**36.61**	**37.73**	**424**	**0.96**
4	**38.16**	**39.12**	**604**	**0.58**
5	**38.68**	**40.60**	**374**	**1.88**
6	41.01	41.01	357	0.00
7	41.05	41.05	14	0.00
8	43.10	44.15	365	1.05
9	**44.73**	**47.91**	**756**	**1.54**
10	45.23	45.55	270	0.43
11	**45.90**	**47.94**	**393**	**1.90**
12	**46.22**	**47.10**	**409**	**0.79**

handle these problems several approaches have been developed (e.g. Faben, 1965; Munro, 1982; Pauly, 1984; Appeldoorn, 1987).

Here, we use the "forced" Gulland and Holt plot (Pauly, 1984), which was estimated using the computer program, FISAT, designed by Gayanilo and Pauly (1997). To estimate K, a fixed value of L_∞, taken from the previous Powell-Wetherall analysis on catch curve, was applied to the tag-recapture data.

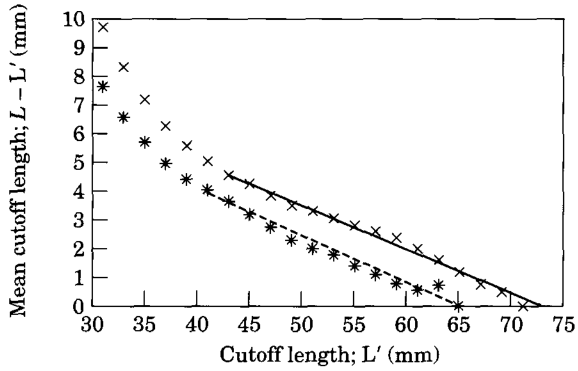

Figure 2. Powell-Whetherall plots from catch curve of male (continuous line) and female *Nephrops* (broken line) from sampling years 1990, 1992–1998.

Results

Estimation of growth parameters

Analysis of length-frequency data

Using the average size distribution (Figure 1), we find that 43 mm carapace length can be considered to be the first fully recruited length group for males. Using the Powell-Wetherall equation for size groups larger then 43 mm leads to estimates of L_∞ equal to 72.9 mm, Z/K equal to 5.50, and an r^2 of 0.988 (Figure 2).

The corresponding analysis of the females, using fully recruited length groups from 41 mm (Figure 1), leads to an L_∞ equal to 64.9 mm, Z/K equal to 5.28, and an r^2 of 0.975 (Figure 2).

Estimation from tag-recapture experiment

The results of the tagging experiment are summarised in Tables 2 and 3. The recapture rates were 3.5% and 2.2% for males and females, respectively. All animals were recaptured only once because they were obtained from commercial landings. The largest value of Δt was less than 2.5 years, which can be considered small compared to the expected lifetime of 15–20 years for *Nephrops* (Sarda, 1995). Hence, the "forced" Gulland and Holt plot applies. The survival rate of the twelve captive tagged specimens was 100%.

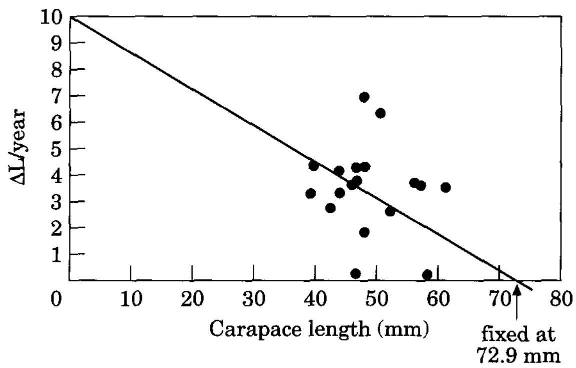

Figure 3. "Forced" Gulland and Holt plot of male *Nephrops* with fixed L_∞ at 72.9 mm carapace length.

Equation (5) and the "forced" Gulland and Holt plot (Figure 3), with a fixed L_∞ of 72.9 mm estimated by the Powell-Wetherall method, gave an estimate of the growth constant K for males of 0.138. Combining the Powell-Wetherall estimate of Z/K, 5.50, and the

Table 4. Growth parameter estimates from this study in comparison with those currently used in the North Sea and neighbouring areas, and references to the source of these estimates (from ICES, 1999).

Area	Males		Mature females		Source
	K (yr^{-1})	L_∞ (mm)	K (yr^{-1})	L_∞ (mm)	
Skagerrak	0.138	72.9	0.056	64	Selected data, this study. Forced G&H
Skagerrak	0.160	76	0.100	65	K adapted from Bailey and Chapman, 1983
Kattegat	0.160	76	0.100	65	K adapted from Bailey and Chapman, 1983
Fladen	0.160	66	0.100	56	Adapted from Bailey and Chapman, 1983
Moray Firth	0.165	62	0.060	56	Bailey and Chapman, 1983
Firth of Forth	0.163	66	0.065	58	Adapted from Bailey and Chapman, 1983
Farn Deeps	0.160	66	0.060	58	Macer (unpubl.) and Bailey and Chapman, 1983
Botney Gut	0.165	62	0.080	60	Adapted from Bailey and Chapman, 1983
North Minch	0.160	70	0.060	60	Adapted from Bailey and Chapman, 1983
South Minch	0.161	68	0.060	59	Adapted from Bailey and Chapman, 1983
Firth of Clyde	0.160	73	0.060	62	Bailey and Chapman, 1983
Irish Sea East	0.160	60	0.100	56	Hillis, 1979
Irish Sea West	0.160	60	0.100	56	Adapted from Bailey and Chapman, 1983

"forced" Gulland and Holt plot estimate of K, 0.138, provides an estimated total mortality, Z, of 0.76.

The corresponding analysis of the females with a fixed L_∞ of 64.9 mm resulted in an estimate of K=0.056. Combining the Powell-Wetherall estimate of Z/K, 5.28, and the "forced" Gulland and Holt plot estimate of K, 0.056, yields an estimated Z of 0.32. This estimate of total mortality for females seems unrealistic low and, given the low number of recaptures, highly uncertain.

Discussion

Size at onset of sexual maturity may differ between areas (Sarda, 1995) but, according to Farmer (1974), it seems to be quite similar between sexes in a geographical area. In this study the size of the smallest recaptured male is similar to the smallest female. The carapace length at which 50% of the females are sexual mature is estimated to be 28 mm and maturity range (25% to 75% maturity) is between 25–32 mm (Eggert and Ulmestrand, 1999). This implies that the smallest recaptures in this study are above the size at 75% maturity for females. We assume that if growth rate changes due to sexual maturity, even for males, this will not affect our growth estimates because our results are based on individuals larger than 32 mm. Hence, the Sommerton (1980) method, taking into account an abrupt change in growth, is not relevant as no intersection point can be expected for our data.

Tag-recapture studies of *Nephrops* growth are few; there are only three previous ones (Hillis, 1971; Chapman, 1982; Figureido, 1989), none of which estimates growth parameters. A major problem is the low recapture rate for tagged *Nephrops*. This study and those previously mentioned, all have recapture rates below 6%. Potential explanations of the low recapture rates are low catchability due to the burrowing behaviour of *Nephrops* and possible underreporting by fishermen. A serious problem is the risk that tagging may affect growth. The Floy streamer tag may cause leakage of blood, which would require extra production of hemocyanin. This, as well as stress, could lead to reduced growth rate. Twelve creel caught specimens were tagged and kept in aquarium for a month. Their survival rate was 100%, which rejects the hypothesis of a large fatal effect from tagging. However, it could not be determined whether growth rate was affected by the tagging procedure. Another source of bias is that the traditional von Bertalanffy model is likely to result in an underestimate of K when growth increment data are analysed (Sainsbury, 1980). The frequency of moulting will also affect growth estimates. A general problem for crustacean growth studies is how to assess the probability of yearly moulting. An individual recaptured after a short time will have a higher probability of zero growth compared to one with a long recapture time. Non-moulting individuals will then be overrepresented, leading to underestimation of K. On the other hand, if all zero growth individuals are excluded, this may cause an overestimated K, as any "true" zero annual growths (but no multiple moults) are excluded from the calculation of the average growth constant K (yr^{-1}).

Table 4 shows the growth parameter estimates from this study for the Skagerrak and those currently used in the North Sea and neighbouring areas. Concerning the females, the Powell-Wetherall estimate of L_∞, based on a large sample, is close to those currently used. The female K deviates substantially from those currently used (40% lower) but, as noted above, the low number of recaptured females indicates that our estimate is of limited value. For males, the Powell-Wetherall estimate of L_∞ is only slightly lower (4%) than those currently used, while our "forced" Gulland and Holt estimate of K is 14% lower. This estimate of K is the average growth rate through a cloud of data points showing a high variation between individuals (Figure 3). Variations in growth rates for *Nephrops* are reported due to sediment structure (e.g. Chapman, 1980; Hillis, 1988) and density-dependent growth (Tuck *et al.*, 1997). The latter study even showed varying growth rates within the same area. Our estimate of Z, 0.76 for males, is close to what is currently derived for the Skagerrak by the ICES Working Group (ICES, 1999). An underlying assumption in using the Powell-Wetherall method is that fast and slow growing individuals in the used size ranges are exploited at the same rate. If fast growing individuals are more easily caught, the L_∞ may be underestimated with the Powell-Wetherall method. For comparable reason, the Powell-Wetherall method was applied on a sample of 1300 *Nephrops* males from an unexploited area (Institute of Marine Research in Lysekil, unpublished data). This sample, coming from outside the trawling area and before the creel fishery was introduced in 1984, gave an L_∞ estimate of 72.5 mm, i.e. very similar to the estimate in this study.

The estimation of t_0 in the von Bertalanffy growth function requires a known length-at-age, which cannot be estimated from catch curve or tag-recapture data. Here, we rely on an aquarium result for a single individual, which reached 20 mm CL in two years. However, a potential error in the the "known" length-at-age will only influence t_0 but not L_∞ and K. Our estimate of age at 20 mm carapace length is also supported by the results from the Irish Sea and the Scottish west coast (Hillis, 1988; Chapman, 1982). In this study, t_0 and the single individual with known age are only used for the purpose to compare the relative difference in length at age between the two growth curves based on our estimations and currently used growth parameters (Figure 4).

Figure 4 shows that our results, compared with the current assumption, imply a slight increase in the average age of a male at the minimum landing size, 40 mm CL, in the Skagerrak/Kattegat.

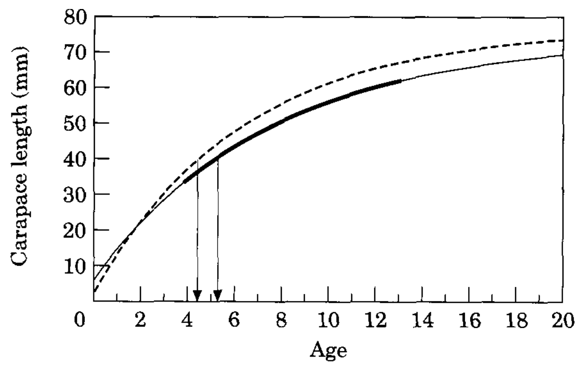

Figure 4. Length-at-age for male *Nephrops* (curves fitted through (20 mm, two years) based on one individual with known age) with currently used growth parameters (L_∞=76 mm carapace length and K=0.16 yr^{-1}, broken line) compared with estimations from this study (L_∞=72.9 mm carapace length and K=0.138 yr^{-1}, continuous line). Arrows show age at minimum landing size (40 mm) for the two growth curves and bold line correspond to size range analysed.

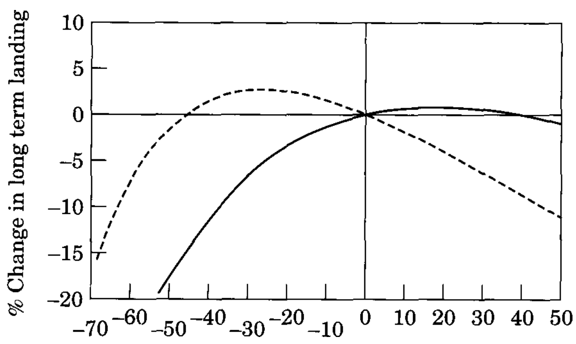

Figure 5. Change in long-term landings against change in fishing effort. From length cohort analysis (Jones, 1979) with currently used growth parameters (L_∞=76 mm carapace length and K=0.16 yr^{-1}, broken line) compared with estimations from this study (L_∞=72.9 mm carapace length and K=0.138 yr^{-1}, continuous line).

Management implications

Lai and Galluci (1988) emphasise that one must be cautious applying length cohort analysis (LCA) based on growth parameters that are uncertain. This is confirmed by our results. Minor separate changes in values of either L_∞ or K lead to drastic changes in the biological reference point (Fmax) derived from a yield per recruit analysis (Jones, 1979). Advice based on Figure 5 could either advocate increased or reduced fishing effort, depending on which growth parameter values are used. It should be noted that policy recommendations based on bioeconomic analysis with standard cost assumptions are not that sensitive to changes in L_∞ and K (cf. Eggert and Ulmestrand, 1999).

In spite of excluding the data with zero growth and recapture times less than a year, the variability in estimated annual growth between individuals with a specific size is still very high. A larger sample size would improve the estimate of the mean growth, but the low recapture rates for tagged *Nephrops* make it difficult to conduct tagging experiments on a scale appropriate for growth studies of *Nephrops*.

As the few ageing methods of crustaceans are in a preliminary stage and not practically applicable to population studies, the low recapture rate in tagging experiments is therefore a major impediment to successful research on population dynamics of *Nephrops*. A methodology to overcome this problem is highly desirable. There is also room for theoretical development of how to handle the problems due to moulting and short recapture time. Further, it is desirable to get data on juveniles and the possibility to follow individual growth through repeated recapturing of individuals. Such contributions could provide valuable additional information to the results in this study.

The results reported here have implications for the assessment and management of *Nephrops* stocks. The putative high variation within *Nephrops* stocks is a major obstacle to get reliable growth estimates from empirical data. However, borrowing population dynamic parameter values from neighbouring areas, which is common practice in absence of empirical data is also questionable. While awaiting more successful methods to estimate *Nephrops* growth, the only valid advice is to be cautious when applying LCA and even more so in making policy recommendations based on the following yield per recruit analysis.

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