Body size dimorphism of sea-reared Atlantic salmon (*Salmo salar* L.): implications for the management of sexual maturation and harvest quality

Leclercq E.[1], Taylor J.F.[1], Hunter D.[2], Migaud H.[1]*

1. Institute of Aquaculture, University of Stirling, Stirling, Scotland, UK.

2. Marine Harvest Scotland Ltd., Blar Mhor Ind Est, Fort William, Scotland, UK.

Accepted for publication in *Aquaculture* published by Elsevier. Published version available at: http://dx.doi.org/10.1016/j.aquaculture.2010.01.029

*Correspondence: E-mail: hm7@stir.ac.uk (H. Migaud)

Tel: 00-44-01786 467886

Fax: 00-44-01768 472133

Abstract

Body size dimorphism between immature and early sexually recruited cohorts of farmed Scottish Atlantic salmon were investigated with the view to optimize the practical management of early maturation over the second-year at sea. Mixed-sex smolts from a single strain and freshwater source were stocked into four discrete commercial sites and sampled at harvest from June to December 2007, 15 to 22 months post-sea transfer. Individuals were sexed and their maturity status determined based on gonado-somatic-index (GSI) and oocyte leading stage. Whole body weight (BW), fork length (FL) and Fulton condition factor (K) were measured and flesh quality analyzed. The immature mixed-sex population and each gender analyzed separately had an isometric weight-length relationship (WLR) but exhibited seasonal variations in K. Body size of immature Atlantic salmon were consistently sexually dimorphic with males exhibiting a higher BW (+13.4%) and FL (+5.9%) but a lower K (-5.0%) than females. Individuals at an early stage of sexual maturation had a significantly higher BW (+35.2%) and K (+20.6%) than the immature cohort in June and July. During this period BW, FL and K together or BW alone were strong and standard indicators of early maturity in our discrete sites. Body size dimorphism described in this study show that sex-ratio is an important parameter of farmed Atlantic salmon populations which is likely to vary following weight-grading and that population composition (sex-ratio and maturation rate) affects the seasonality in K typically observed at harvest. Importantly, the commitment of Atlantic salmon into maturation in spring can be rapidly and accurately estimated in a number of discrete populations by using simple weight-length morphological indicators characterized in a single rearing unit. Following maturation rate estimation, weight-grading implemented according to the predicted stock morphological structure could be used to selectively harvest a high proportion of maturing individuals at a stage where their flesh quality

remains optimal. This could be applied as a powerful and practical on-site maturation management tool in the salmon industry as well as in other commercially important fish species.

Keywords: Atlantic salmon, dimorphism, sexual maturation, prediction, weight-grading, stock management

Introduction

Sexually mature Atlantic salmon (*Salmo salar*) have a reduced flesh quality and distinctive skin colouration based on which they are downgraded and lost for human consumption (Michie, 2001). Besides their poor commercial value once harvested, salmonids undergoing maturation can be immunodepressed leading to increased disease susceptibility and mortality rate during on-growing (Bruno, 1989; Salte et al., 1995; Traxler et al., 1997; St-Hilaire et al., 1998; Currie and Woo, 2007). Feeding and growth patterns of maturing Atlantic salmon are also altered being enhanced at an early stage of sexual development (up to summer in Scotland) then reduced during gonadogenesis from late summer onward (Aksnes et al., 1986; Kadri et al., 1997a and b). These successive anabolic and catabolic windows inherent to reproduction are likely to compromise feeding performances of the cohabiting immature cohort due to increased competition and then run the risk of feed-waste from biomass overfeeding. Overall, health, welfare, growth and feeding performances of the whole stock are at risk where significant rates of sexual maturation occur. This is particularly true during the second year at sea when the reproductive window, which extends over the second-half of the year, typically coincides with high water temperature, maximum standing biomass and feeding rate. In order to address this bottleneck, the on-growing salmon industry routinely applies artificial continuous light (LL) from the winter to summer solstice during the second-year at sea. This photoperiod regime is recognized as the most effective (Hansen et al., 1992; Taranger et al., 1998; Endal et al., 2000) and is overall most successful as a commercial management practice. However, sporadic events of high maturation rates are still experienced, hence the need for a complementary strategy toward the comprehensive prevention of maturation at harvest.

Poorly studied as a potential management tool, the altered growth pattern of sexually recruited individuals is concomitant with body size dimorphism between maturity cohorts. In this respect Kadri et al. (1997a) found that, in one sea-winter salmon, relative condition factor and fork-length (FL) but not whole body weight (BW) were good indicators of sexual initiation in advance of gonadogenesis, a period when skin colour and flesh quality remains optimal (Aksnes, 1986, Kadri et al., 1997b). Nonetheless, these predictors were specific to each population/site assessed and did not lead to practical recommendations. Similarly, weight-grading of the stock is routinely performed at sea and is now recognized as playing a part in minimizing maturation rate at harvest, i.e. by segregating best performers for early harvest ahead of their maturation window. However, grading schemes presently applied aim primarily at managing stock variability, density and harvest quality and hence remain empiric and inconsistent for the management of sexual maturity. Furthermore the Scottish salmon industry is nowadays highly concentrated with, in 2007, 93% of the total annual harvest (130,000t) produced by 10 companies, 70% of which in 55 sea-sites producing over 1,000t a year (Fisheries Research Services, 2008). While this scale of production does not often permit "visual grilse grading" as traditionally performed, it allows stocking large-scale site with a single freshwater population but also different sites with populations from the same strain and a close freshwater history. During further on-growing a high number of related but discrete populations within different pens or site might accordingly exhibit standard size dimorphism between maturity cohorts. If consistent they could, once characterized in a representative rearing unit, be applied to other ones for rapid and non-invasive estimation of their maturation rates followed by the selective harvest of a high proportion of maturing individuals by simple weight-grading. Such a management strategy

would optimize the output of superior quality biomass while isolating the immature cohort from maturating individuals but its feasibility remains poorly assessed.

In association with the dimorphism in growth, differences in Fulton condition factor (K) between maturity cohorts were reported in Atlantic salmon (Aksnes et al., 1986; Rowe et al. Thorpe, 1990; Peterson and Harmon, 2005). This parameter is primarily a shape indicator (Froese, 2006) that correlates positively with "visual fatness score", i.e. rounded appearance, and filleting yield in Atlantic salmon and Atlantic cod (*Gadus morhua*, Einen et al., 1998, 1999; Margeirsson et al., 2007). In this respect K alone can dictate different quality grades at processing and is regularly assessed during on-growing to achieve quality targets. Importantly K is also a recognized indicator of nutritional status in Atlantic salmon where it correlates positively with dietary energy fed (Young et al., 2006) and total flesh lipid at the parr stage (Herbinger and Friars, 1991). In teleosts, the accepted form of weight-length relationships (WLR): $BW=aFL^b$, where BW and FL are body size variables and a and b are parameters of the relationship (Froese, 2006), also expresses variations in K over a population size range. Overall constant in populations with an isometric WLR (b=3), heavier individuals have a higher K in populations exhibiting a positive allometric relationship (b>3) and inversely a smaller K in populations with a negative allometric WLR (b<3). With surprisingly few data on Atlantic salmon WLR, this species has like most other teleosts a recognized isometric growth type (Wootton, 1990; Froese and Pauly, 2009) suggesting that a constant shape, K, could be achieved for any given length at sea. Nonetheless, a seasonality in K has been reported in farmed stocks that could arise from a seasonal pattern in weight-length development while K appears to be also affected by light-manipulation (Oppedal et al., 1999, 2003; Johnston et al., 2003; Nordgarden et al., 2003; Young et al., 2006). In the

industry, a detrimental spring and early summer drop in K is usually considered as the result of sub-optimal feeding but may also be exacerbated by other management practices.

The main objective of this study was to investigate body size dimorphism between immature and sexually recruited fish in four discrete sea-water populations with the view to optimize the practical management of early maturation during on-growing.

1. Materials and methods

1.1. Fish stock and rearing conditions

Atlantic salmon smolts from the same genetic strain and freshwater origin were transferred to sea as S0+ post-smolts from the 30 January 2006 to the 9 March 2006 with an average weight of 95±3g (n=2,242,060; 22 sea transfers). Individuals were reared in square pens (24mx24m sides, 10m to 12m depth) in four different commercial sea sites (Sites A, B, C and D) located on the same Scottish loch system (Loch Linnhe: Lat: 56º39'19'', Long: -5º19'56'') up to harvest size. Over the second-year at sea, stocks were fed two commercial diets (Site A, B and C: 35% protein, 32% lipids and 16.5% carbohydrates; Site D: 34% protein, 37% lipids, and 13.5% carbohydrates; Skretting, Invergordon, UK) according to manufacturer recommendations based on monthly sample weight adjusted daily to estimated biomass and observed feeding response (Average daily feeding rate over the production cycles = 0.71% body weight.day^{-1}). Temperature, salinity at 6m depth and water turbidity by means of Secchi disk were measured daily throughout the production cycle. The light-manipulation strategy was common among sites with LL applied using submerged metal-halide lighting units (400W/unit, 4 units/cage, Pisces 400, BGB Engineering, Grantham, UK) from early January 2007 to mid-June 2007 only in pens to be harvested from August onward, i.e. over the reproduction window. Also consistent among

sites was the top-crop harvest strategy consisting in segregating best performing individuals during on-growing and harvesting individual pens with the highest standing BW. This was achieved through biomass weight-grading performed for each pen between October 2006 and February 2007. The harvest season extended from April 2007 to December 2007 in which each site had more than 50% of the biomass harvested between September and December. The total harvested biomass (10,116.5t) was 3708.5t, 3016.6t, 1747.0t and 1644.4t in site A, B, C and D respectively.

1.2. Data sampling and analysis

For each site, a cross sectional monthly sampling was performed on harvest batches at the processing plant from June to December 2007. Up to three distinctive skin colour categories were subjectively observed: silver, intermediary (Green-back and white belly) and nuptial. Their prevalence was determined by a minimum of 600 observations from at least three counting sessions over the batch-processing period (Data not shown). At each sampling points, a minimum of 25 individuals/sex/skin colour were randomly sexed. Among them, 25 to 30 individuals/sex/skin colour class were measured for BW (±0.1g), FL (±0.1cm) and gonad weight (GW) (±0.01g). K was calculated as $K=(BWx100)/FL^3$ and gonado-somatic-index (GSI) as GSI(%)=(GWx100)/BW. This sampling strategy allowed optimal characterization of gender and maturity cohorts. Males were classified as immature or sexually recruited based on their bimodal GSI frequency distribution in the population (Kadri et al., 1997a) with a threshold value of GSI=0.20%. Female ovary samples were preserved in Bouin`s fixative for 24h before being processed for histological observation and classified according to their leading oocyte stage (Taranger et al., 1999). They are referred to as immature up to the oil drop stage, as (early)

maturing or initiating at the primary and secondary yolk stages indicating the onset of and commitment toward sexual maturation and as mature or sexually advanced when the tertiary yolk stage was reached. The left-hand side flesh Scottish quality cut of 10 females/skin colour class/sampling point was stored at -20°C until analysis of flesh colour by means of subjective colour card rating and tristimulus colorimeter, and of total carotenoid and total lipid content using near infrared reflectance according to standard industrial practices (Robb, 2001; Fjellanger et al., 2001).

1.3. Statistical analysis

The accepted form of WLR in fish: $BW=aFL^b$, where BW and FL are body size variables and a and b are parameters of the relationship is presented for illustration and was transformed into its logarithmic equivalent: log(BW)=log(a)+b*log(FL) for analysis by least-square regression based on individuals pooled per 1cm fork length (Froese, 2006) using Microsoft Excel software. Using b-parameter from WLR analysis at each sampling point, mean-b±SE was also determined as this parameter was suggested to better represent the actual WLR of a species (Froese, 2006). It may also be a better indicator of the shape of individuals relative to one another achieved on average in individual harvest batches. Significant variations from the isometry (slope=3) were determined using a Student t-test (α=0.05) (Arslan et al., 2004). Harvest batch sex-ratio was calculated by performing a weighted average of gender proportion in each skin colour category. Significant variation of the sex-ratio from 1:1 was determined using a chi-square goodness of fit test. Body size dimorphisms in BW, FL and K between genders at an immature stage and between cohorts of sexual development were calculated at each sampling point and averaged according to Saillant et al. (2001). Direction of size dimorphisms (isometry, negative or positive allometry) in datasets

was determined using log-transformed data by plotting the male or maturing mean body-size parameter against the corresponding female or immature values at each sampling point and testing the Reduced Major Axis (RMA) regression slope. This was determined using Past software against the isometry (slope=1; t-test, α=0.05) with a slope not significantly different to 1 indicating a dimorphism proportionally constant among the sampling points (Dale et al.; 2007). The effects of gender or maturity status and time on morphological (BW and K) and flesh quality parameters (Total lipid and total carotenoid) were assessed on individual sites by applying a General Linear Model (GLM) with a significance level of 5% using Minitab v.15. Prior to analyses, datasets were checked for normality using the Kolmogorov-Smirnov test and for homogeneity of variance using Bartlett's test. Log or square root transformations were applied when required and proportions were arcsin-transformed. Normality and homogeneity of variance were confirmed by observation of residual plots. Where statistical differences occurred, a Tukey's post-hoc multiple comparisons test was applied (Zar, 1999). Discriminant analyses were performed on June and July samples pooled per site to determine the correct prediction rate of gender or maturity status in each site with either individual's BW, FL and K together or BW alone as predicting parameters using SPSS v.15.0 (modified from Kadri et al., 1997a). Only three sites were analyzed for prediction of maturity status due to the reduced number of individuals initiating sexual development in site D. For prediction of gender and maturity status, analyses were performed using each site's own dataset with the correct prediction rate being provided directly by the software. Prediction of maturity status was also performed on each site using the two other discrete site datasets to assess if body size dimorphism between maturity cohorts characterized in one site could be used as an indicator of maturation in an other discrete site. The predicted maturity status of each individual, output of the discriminant analysis, was then

compared to its actual maturity status determined from GSI and histological analysis to establish the rate of correct prediction in each analysis. In a similar fashion, discriminant analyses were also performed to determine the power of GSI in predicting the vitellogenic status of females with a GSI below 1%. Based on Wilks-lambda multivariate test the predicting models were always a good fit for the data ($P<0.01$).

2. Results

Among the four sites and over the rearing cycle, temperature profiles were identical with an average water temperature of 10.7±0.1°C. Average Secchi depth varied from 4.8±0.1m (Site A) to 6.8±0.1m (Site C) and strong differences in salinity profiles were observed with constant full strength seawater in sites C and D (33.9ppm to 34.9ppm) and variable salinity in sites A and B (20.1±0.3ppm and 27.0±0.2ppm respectively).

2.1. Immature population

2.1.1. Weight-Length Relationship (WLR) analysis and population sex-ratio

Over the sampling period the sex-ratio significantly varied from the expected balanced 1:1 ratio in 13 out of the 23 sampling points assessed. From June to August inclusive the proportion of males was significantly higher than the proportion of females in 6 out of 11 harvest batches sampled whilst females never were. Conversely in harvest batches from September onward (n=12), females were dominant in 5 harvest batches and males only in 2 (Table 1a). Morphological parameters of the immature cohort sampled over a 7-month period in the four sites were as follow: n=2235, BW=5013±22g (p_5-p_{95}=3528g-6860g), FL=76.9±0.1cm (p_5-p_{95}=69.3-85.5cm), K=1.09±0.02 (p_5-p_{95}=0.93-1.26) where p values indicate the percentiles. The

WLRs of the mixed-sex population as a whole and of each gender analyzed separately were isometric over the study period (Fig. 1a and 1b with parameters of the WLRs). A strong positive allometric relationship was nonetheless observed when plotting average BW and FL of individual harvest batches (Fig. 1a). This was consistent with the increase of both BW and K over the harvest season in the immature male, female and mixed-sex cohorts within each site. There was indeed a significant effect of time on BW and K of the immature cohorts in all sites (GLM, P<0,001) (Table 1b, 1c, 2a and 2b). Both parameters were significantly lower in June and July. Mean b-parameters for each individual site or all sites pooled were always significantly lower than 3 except in site D (all sites=2.70±0.04; site A=2.70±0.09, B=2.70±0.10, C=2.67±0.09 and D=2.76±0.11) but never significantly different to the isometry when considering genders separately (Male: all site=2.86±0.05; site A=2.84±0.11, B=2.86±0.09, C=2.93±0.11 and D=2.79±0.09; Female: all sites=2.88±0.07; site A=2.94±0.09, B=2.79±0.20, C=2.81±0.13, D=2.97±0.23).

2.1.2. Sexual size dimorphism (SSD) and discriminant analysis

There was an overall significant effect of sex on BW, K and FL of the immature cohort in each individual site (GLM, P<0,001) with males showing a significantly higher BW in 14 out of 23 harvest batches and a significantly lower K in 11 out of 23 harvest batches (Table 1b and 1c). Sexual size dimorphisms were observed at each sampling points (Fig. 2a,b,c) and were proportionally constant as shown by the RMA regression slopes which were never significantly different to the isometry (t-test, α=0.05, P=0.4899; P=0.2630; P=0.1253 for respectively BW, FL and K). Based on sampling point means (n=23), immature males (n=1131) compared to females (n=1104) were 13.4% heavier (BW_{Male}=5232±140g; BW_{Female}=4592±119g) and 6.1% longer

(FL_{Male}=78.9±0.6cm; FL_{Female}=74.3±0.5cm) while females had a 5.0% higher K (K_{Male}=1.06±0.01; K_{Female}=1.11±0.01). From discriminant analyses using as predictors BW, FL and K of individuals from the site under analysis, 74.8% (Site C) to 78.9% (Site B) of the site`s population were correctly classified within their gender cohort. These rates of correct prediction were in all cases significantly higher than 50% which could have been achieved by chance alone. Using BW as a sole predictive factor, correct prediction of gender ranged from 57.1% (Site C) to 68.2% (Site D), significantly more than 50% in all but site C (Table 3).

2.2. Dimorphism between maturity cohorts

2.2.1. Dimorphism over the study period

Fish undergoing sexual maturation in June and July were always at an early stage of sexual development based on GSI and oocyte leading stage (GSI_{Male}=0.51±0.02%; GSI_{Female}=1.37±0.11% at the primary or secondary yolk stage). During this period, a total of 502 immature (Male=244; female=258) and 150 sexually recruited (Male=78; Female=72) individuals were sampled from a total of seven harvest batches and four sites. At each sampling point, maturing fish were 25.7% to 56.1% heavier (significant differences observed in 5 out of 7 harvest batches) than immature siblings and displayed a significantly higher K in all harvest batches (19.0% to 29.0%) (Table 2a and 2b). No differences in FL between maturity cohorts were observed. Based on sampling point means, individuals that initiated sexual development were 37.9% heavier ($BW_{Recruited}$=5777±224g; $BW_{Immature}$=4188±94g), 4.0% longer ($FL_{Recruited}$=76.7±1.0cm, $FL_{Immature}$=73.8±0.6cm) and had a 22.6% higher K ($K_{Recruited}$=1.28±0.02; $K_{Immature}$=1.04±0.01). Body size dimorphisms between maturity cohorts in June and July are illustrated by the WLR of the 652 individuals sampled over this period and classified according

to their maturity status (Fig. 3a). As the maturation cycle progressed, maturing fish lost their body size advantage. They remained significantly heavier in August in site B only and had a higher K in site C. From September onward, maturing fish were at an advanced stage of sexual maturation (GSI_{Male}=3.67±0.06%; GSI_{Female}=20.30±0.28% always at the tertiary yolk stage) and significantly lighter than immature fish (in 10 out of 12 harvest batches) with also a significantly lower K (in 6 out of 12 harvest batches) (Table 2a and 2b). With regard to flesh quality, no significant differences between maturity cohorts were observed in July for subjective colour rating, tristimulus colour composition (data not shown), total carotenoid and total lipid (Table 2c and 2d, GLM, α=0.05). The effects of sexual maturation on flesh quality were then detected from August onward with a significantly lower total flesh lipid, measured in two sites in August, followed by a significantly lower total flesh carotenoid observed in one site in September. From October onward, both those parameters were significantly reduced in fish reaching full maturity. Further analyses were therefore performed on the June and July period only that corresponds to the anabolic window of early sexual development prior to flesh quality deterioration as confirmed above.

2.2.2. Discriminant analysis between immature and early recruited cohorts

Over the June-July period, discriminant analyses were performed to predict individual maturity status based on their body size parameters. Results are presented in table 4 and illustrated by a specific example (Fig. 3b). When performed on each individual site using its own data set and three external morphological predictors (BW, FL and K), correct prediction of maturity status averaged 92.2±1.3% of the sites` population and 87.6±4.1% of their recruited cohort (Table 4a). Using the discriminant functions from different discrete sites, on average 89.5±1.2% of each site

population was correctly classified including 85.7±4.5% of maturing individuals. In those last analysis, 81.9±4.0% of individuals predicted as maturing were truly maturing while 5.9±1.7% of individuals predicted as immature where in fact maturing as determined from GSI and histological analysis. Compared to a true maturation rate averaging 31.2±4.0% in our four site datasets, the predicted maturation rate averaged 33.2±3.9% with an error on individual sites of -5.1% (Site A) +6.1% (Site B) and +5.0% (Site C). Analyses were also performed using BW as the sole discriminating factor between maturity cohorts allowing determination of an optimal BW threshold between maturity cohorts (Table 4b). Using each site's own dataset the maturity status of on average 84.1±1.6% of the populations and 76.5±2.0% of the recruited cohorts was correctly predicted. Using discrete site datasets the maturity status of on average 80.1±2.5% of the populations and 71.8±7.1% of the recruited cohorts was correctly classified. Compared to the analyses based on three morphological predictors, using BW alone reduced the accuracy of the prediction in the different site populations by an average of 9.4% (based on site's own dataset) and 13.9% (based on discrete site datasets). Furthermore, an average of 34.7±7.7% of the populations including 71.8±7.1% of truly recruited fish were over the optimal BW threshold between maturity cohorts characterized from a discrete site. Conversely 28.2±9.5% of truly recruited fish were below this BW threshold leading to an actual maturation rate of 11.9±1.7% in this cohort predicted as immature, compared to 5.9±1.7% using BW, FL and K for prediction and 31.2±4.0% in the initial population. The potential for cohort segregation using the optimal BW threshold characterized from another discrete population is illustrated on fig. 4. In a similar fashion, we applied discriminant analysis in the female population with a GSI below 1% and harvested in June and July to assess the power of BW, FL, K in conjunction with GSI in predicting their vitellogenic status. Applying discrete sites datasets, the vitellogenic status of on

average 97.7±1.2% of the populations (female with GSI<1%) and 83.6±10.4% of the corresponding recruited females were correctly classified using GSI as sole predictor. No significant improvement arose from adding BW, FL and K as predicting factors (Data not shown).

3. Discussion

3.1. Sexual Size Dimorphism (SSD) at the immature stage

Sexual size dimorphism (SSD) was reported in various teleosts at the post-juvenile stage but often without indications of individual maturity status (Saillant et al., 2001; Young, 2005; Hanson et al., 2008). Species identified as exhibiting SSD specifically at the immature stage are comparatively scarce and include sea bass (*Dicentrarchus labrax,* Saillant et al., 2001), European eel (*Anguilla anguilla*, Degani et al., 2003) and yellow perch (*Perca flavescens*, Shewmon et al., 2007). Atlantic salmon is usually considered monomorphic prior to sexual maturation (Kadri et al., 1997a) but our data unexpectedly unveiled a significant SSD at the immature stage in this key aquacultural species. Surveyed 15 to 22 months post-sea transfer in different populations of siblings, immature males consistently achieved at each sampling point a higher body mass (+13.4%) and length but exhibited a lower K than immature females. If confirmed, SSD in immature Atlantic salmon is an important species characteristic. Occuring SSD are partly responsible for variations in individual performances in mixed-sex teleost stocks, a critical factor under experimental conditions with negative implications under commercial management (Fontaine et al., 1993). The overall apparent reduced feed intake in larger individuals in three sites surveyed, as shown by the negative allometry in mean-b parameter (Arslan et al., 2004), was not observed in any gender considered separately and therefore was primarily due to SSD.

Importantly, described SSD highlights that growth performances are affected by the stock sex-ratio such that genders should be addressed separately in experimental studies. Sex-ratio is an important population parameter and is likely to be skewed following weight-grading in sexually dimorphic populations. This was shown in sea bass (Papadaki et al., 2005) and in this study by the power of BW to discriminate between genders in association with the seasonality in sex-ratio observed at harvest. Significant dimorphism most probably occurs at the time of weight-grading leading to a higher proportion of males in the best performing cohorts harvested earlier in the season. If occurring at the freshwater stage, SSD could likewise lead to skewed sex-ratio in graded smolt populations with consequences on subsequent performances at sea. Finally, our data highlight a potential advantage for male-monosex stocks toward a shorter production cycle or a higher individual weight at harvest but also a reduced size variability. Nonetheless male weight advantage was on average below 15% and counterbalanced by their lower K in this study, which could result in their higher downgrading rate at processing. Furthermore, such monosex stocks would yield an increased risk of pre-harvest maturation since different studies have reported a higher rate of early maturation in males (Kråkenes et al., 1991; Oppedal et al., 2003). Taken together, SSD should be further assessed in different populations of immature Atlantic salmon to determine if it is a characteristic of the species with global implications. Further investigations are also required to describe its time of onset but also its origin which could be alimentary and metabolic (feed level, intake and utilization) and/or if it may be linked to a sex-specific maturation strategy ahead of actual sexual recruitment as addressed in other species (Fontaine et al., 1997; Imsland et al., 1997).

3.2. WLR and K seasonality of the immature cohort

Regardless of existing or potential dimorphisms, gender/maturity cohorts are seldom distinguished in teleost growth studies. An isometric growth type is common in the adult stanza of teleosts fish (Wootton, 1990) and was recently reported in Atlantic cod (Árnason, 2007), brown trout (*Salmo trutta*, Arslan et al., 2004), golden grey mullet (*Liza aurata*, Ilkyaz et al., 2006) and various breams (Mehanna, 2007; Chilari et al., 2006; Türkmen and Akyurt, 2003). However, actual field data on Atlantic salmon WLR could not be obtained from the literature. Sampled from four distinct sea-sites over a seven months period, WLR of the mixed-sex, single strain immature population and of each sex analyzed separately was isometric but K had a tendency to increase over the harvest season. This shows that immature individuals displayed a constant shape over the harvest period but not over time, their growth in weight being overall proportionally superior to their growth in length from spring to winter under an increasing temperature. This is consistent with previous studies in which K seasonality was linked to a lower growth in weight than in length in periods of low water temperature (Oppedal et al., 1999; 2003; 2006). Photoperiod was also shown to affect growth pattern with stocks exposed to LL exhibiting a higher rate of muscle fibre recruitment and ultimately an improved K (Johnston et al., 2003; Oppedal et al., 2006). In our survey, immature fish harvested in June and July and showing the lowest K at harvest (Table 2b) were not exposed to LL unlike stocks harvested from August onwards. The commercial practice of applying LL only to stocks to be harvested over the reproductive season, i.e. during second half of the year when water temperature is higher, is likely to further accentuate K seasonality inherent to the seasonal pattern of weight-length development. Finally, K will also vary with the composition of the harvest batch, i.e. sex-ratio and maturation rate, due to size dimorphism between cohorts. With males exhibiting a lower K than females, mean-K of the stock would increase with the decreasing rate of males along the

harvest season in weight-graded populations. Beside, the proportion of early maturing fish would positively affect mean-K of the stock in June and July when they exhibited a strong advantage in K as reported in this study (+20.6%) and previously (Aksnes, 1986; Kadri et al., 1997a). Overall, this analysis highlights that a population or species with an isometric WLR can also exhibit seasonal variarions in K and that the apparent condition of the stock is in practice also affected by its composition (sex-ratio and maturation rate) and probably history of LL exposure, both of which vary with harvest time under typical commercial management. Such factors should also be considered before strict conclusion on feeding performances.

3.3. Implications of size dimorphism between maturity cohort

It is well recognized in Atlantic salmon that some threshold of size and/or body condition must be surpassed during the spring window for sexual maturation to proceed (Thorpe, 1986, 1989). In the current study, sexually recruited individuals had in June and July a strong advantage in BW and K but not FL over the immature cohort. Although they already initiated sexual development, our data shows that a higher growth in weight but not in length, hence a higher K, is likely critical for recruitment into maturation in spring over the second year at sea. Following recruitment, a surge in appetite and growth characterize individuals initiating sexual development during the so-called anabolic window and lead to significant discrepancies in weight-length parameters between maturity cohorts (Aksnes et al., 1986; Kadri et al., 1996). While relative condition factor and FL have previously been identified as strong but population specific predictors of early sexual maturation (Kadri et al., 1997a), our survey yielded BW, K and FL as standard predictors among different rearing units. Importantly, stocks from each site were from the same strain, reared together at the freshwater stage and transferred to sea within

the same period. At sea, they experienced the same overall feeding management and temperature profiles but strong variations in water clarity and salinity (strong to moderate). Such differences in salinity profiles could have led to growth discrepancies between sites due to the energetic cost of osmoregulation (Boeuf and Payan, 2001). However, temperature was shown to be the main factor influencing Atlantic salmon growth with no effect of strong to moderate salinity (Duston, 1994; Usher et al., 1991; Handeland et al., 1998). Furthermore, different growth patterns are observed in smolts transferred to sea at different times of the year (Duncan et al., 1998). In our survey, the proximity of the life-cycle history and the common genetic origin was undoubtedly critical in the occurrence of standard morphological attributes among our discrete sites which constituted in that sense a cluster of rearing units.

Those results highlight the possibility to implement a practical maturation management strategy during the anabolic window of the reproduction cycle. Within identified rearing clusters, characterization of size dimorphism between maturity cohorts can be restricted to a "model" population then directly extended to discrete units to estimate their maturation rate on-site by simple weight-length assessment of the stock, an approach that correctly identified over 85% of recruited individuals in this study. It must be acknowledged that using the body size dimorphism characterized in the specific rearing unit increases the accuracy of the predicted maturation rate. This might prove worthwhile particularly with the possibility to estimate maturity status of sacrificed females based on their GSI only, as shown by the common GSI threshold between non-vitellogenic and vitellogenic ovaries in our discrete populations. Following maturation rate estimation, simple weight-grading has the potential if required to mechanically segregate a high proportion of maturing fish. As shown in the case illustrated in fig. 4, top-grade harvest based on the optimal cut-off weight determined in a discrete site would have segregated 80% of the

recruited individuals in 38% of the whole stock. However, nearly 90% of maturing fish were among the heaviest half of the stock highlighting that, in practice, lowering the statistically optimal cut-off weight could increase the selective harvest of maturing fish. Thanks to its restricted reliance on invasive sampling, this maturation detection-segregation strategy can be readily implemented by the Atlantic salmon industry with twofold advantages. Primarily an increased output of quality biomass by harvesting early maturities when yielding superior quality characteristics but also an improved growth, feeding and welfare of the immature stock left for further on-growing. However, the feasibility and economic interest of selective harvest of maturity will likely be significant over some threshold of maturation rate hence the importance of its prior estimation. The widespread implementation of this detection-segregation strategy for managing sexual maturation at sea requires confirmation that significant body size dimorphisms occur in different strains farmed under a variety of conditions along with a better knowledge of the genetic (e.g. strain, families, generations), environmental and husbandry parameters resulting in standard size dimorphism between discrete populations. A more thorough set of morphometric indicators could also increase the accuracy of maturation rate estimation since body depth at the point where anal fin arises was shown to be a significant predictor of early maturation in Scottish Atlantic salmon (Kadri et al., 1997a). Importantly, the window of opportunity for implementation of this management strategy was identified as June and July and closed from August onward but could occur earlier in the spring. Finally, biomass scanning technologies (e.g. Vaki, Storvik) could greatly facilitate the monitoring of maturation onset in salmon stocks by assessing a high number of morphological predictors in a more representative sampling size *in situ*. Likewise, stock grading based on a number of external morphological parameters could

improve the selective harvest of the maturing cohort in comparison to simple weight-grading but no equipment is presently available to do so.

The negative impact of sexual maturation on product marketability and growth is common among most commercially important species (Kjesbu et al., 1991; Bromage et al., 2001; Felip et al., 2001; Almansa et al., 2001; Grigorakis, 2007; Roth et al., 2007) while age at first maturity varies according to sex in various teleosts such as sea bass (Felip et al., 2008). In this later species, repetitive weight-grading of mixed-sex population allowed segregating a fast-growing, 96.5% female, population for experimental purpose (Papadaki et al., 2005). Mechanical segregation of genders and sex-specific harvest could minimize maturation during sea bass on-growing to optimize biomass output and facilitate the production of various market size. Similarly in turbot (*Scophthalmus maximus*), it was recommended to segregate non-maturing fish by size grading but also to develop methods for the production of all-female stocks to optimize growth performances (Imsland et al., 1997). Dimorphism-based management strategies are likely to prove beneficial in various aquacultural species and modeling of weight-length dimorphism among rearing units to facilitate their commercial implementations.

Acknowledgements

The authors would like to thank BBSRC for funding an Industrial CASE Award studentship (BBS/S/M/2006/13133) in association with Marine Harvest UK as well as staff who provided help and access on commercial sea-sites and at the process plant.

References

Aknes, A., Gjerde, B., Roald, S.O., 1986. Biological, chemical and organoleptic changes during maturation of farmed Atlantic salmon, *Salmo salar*. Aquaculture 53, 7-20.

Almansa, E., Martin, M.V., Cejas, J.R., Badia, P., Jerez, S., Lorenzo, A., 2001. Lipid and fatty acid composition of female gilthead seabream during their reproductive cycle: effects of a diet lacking n-3 HUFA. J. Fish Biol. 59, 267-286.

Árnason, T., 2007. The effect of temperature on growth of the Atlantic cod (*Gadus morhua*). University of Akureyri, Msc thesis 1-20.

Arslan, M., Yildirim, A., Bektas, S., 2004. Length-weight relationship of brown trout, *Salmo trutta* L., inhabiting kan stream, Çoruh basin, north-eastern Turkey. Turkish J. Fish. Aquat. Sci. 4, 45-48.

Boeuf, G., Payan, P., 2001. How should salinity influences fish growth? Comp. Biochem. Phys. 130C, 411-423.

Bromage, N., Porter, M., Randal,C., 2001. The environmental regulation of maturation in farmed finfish with special reference to the role of photoperiod and melatonin. Aquaculture 197, 63-98.

Bruno, D.W., 1989. Fungal infections of farmed salmon and trout. Aquaculture Information 5, 1-5.

Chilari, A., Petrakis, G., Tsamis, E., 2006. Aspects of the biology of blackspot seabream (*Pagellus bogaraveo*) in the Ionian sea, Greece. Fish. Res. 77, 84-91.

Currie, J., Woo, P., 2007. Susceptibility of sexually mature rainbow trout, *Oncorhynchus mykiss* to experimental cryptobiosis caused by *Cryptobia salmositica*. Parasitol. Res. 101, 1057-1067.

Dale, J., Dunn, P.O., Figuerola, J., Lislevand, T., Székely, T., Whittingham, L.A., 2007. Sexual selection explains Rensch's rule of allometry for sexual size dimorphism. Proc. R. Soc. Lond., Ser. B: Biol. Sci. 274, 2971-2979.

Degani, G., Tzchori, I., Yom-Din, S., Goldberg, D., Jackson, K., 2003. Growth differences and growth hormone expression in male and female European eels [*Anguilla anguilla* (L.)]. Gen. Comp. Endocrinol. 134, 88-93.

Duncan, N.J., Auchinachie, N., Robertson, D., Murray, R., Bromage, N., 1998. Growth, maturation and survival of out-of-season 0+ and 1+ Atlantic salmon (*Salmo salar*) smolts. Aquaculture 168, 325-339.

Duston, J. 1994. Effect of salinity on survival and growth of Atlantic salmon (*Salmo salar*) parr and smolts. Aquaculture 121, 115-124.

Einen, O., Waagan, B., Thomassen, M.S., 1998. Starvation prior to slaughter in Atlantic salmon (*Salmo salar*). I. Effects on weight loss, body shape, slaughter- and fillet-yield, proximate and fatty acid composition. Aquaculture 166, 85-104.

Einen, O., Mørrøre, T., Bencze Røra, A.M., Thomassen, M.S., 1999. Feed ration prior to slaughter : a potential tool for managing product quality of Atlantic salmon (*Salmo salar*). Aquaculture 178, 149-169.

Endal, H.P., Taranger, G.L., Stefansson, S.O., Hansen, T., 2000. Effects of continuous additional light on growth and sexual maturity in Atlantic salmon, *Salmo salar*, reared in sea cages. Aquaculture 191, 337-349.

Felip, A., Piferrer, F., Zanuy, S., Carrillo, M., 2001. Comparative growth performance of diploid and triploid European sea bass over the first four spawning seasons. J. Fish Biol. 58, 76-88.

Felip. A., Zanuy, S., Muriach, B., Miguel, J., Reverter-Cerdá, J.M., Carrillo, M., 2008. Reduction of sexual maturation in male *Dicentrarchus labrax* by continuous light both before and during gametogénesis. Aquaculture 275, 347-355.

Fjellanger, K., Obach, A., Rosenlund, G., 2001. Proximate analysis of fish with emphasis on fat In: S.C. Kestin and P.D. Warriss (Editors). Farmed fish quality, Blackwell Science, Oxford, pp. 307-317.

Fontaine, P., Gardeur, J.N., Kestemont, P., Georges, A. 1997. Influence of feeding level on growth, intraspecific weight variability and sexual growth dimorphism of Eurasian perch *Perca fluviatilis* L. reared in a recirculation system. Aquaculture 157, 1-9.

Froese, R., 2006. Cube law, condition factor and weight–length relationships: history, meta-analysis and recommendations. Journal of Appl. Ichtyol. 22, 241-253.

Froese, R. and D. Pauly. Editors. 2009. Fishbase. http://www.fishbase.org/PopDyn/LWRelationshipList.php?ID=236&GenusName=Salmo&SpeciesName=salar&fc=76. Date accessed: 24/06/09.

Grigorakis, K., 2007. Compositional and organoleptic quality of farmed and wild gilthead sea bream (*Sparus aurata*) and sea bass (*Dicentrarchus labrax*) and factors affecting it: A review. Aquaculture 272, 55-75.

Handeland, S.O., Berge, Å, Björnsson, B.Th., Stefansson, S.O., 1998. Effects of temperature and salinity on osmoregulation and growth of Atlantic salmon (*Salmo salar* L.) smolts in seawater. Aquaculture 168, 239-302.

Hansen, T., Stefansson, S.O., Taranger, G.L., 1992. Growth and sexual maturation in Atlantic salmon, *Salmo salar* L., reared in sea cages at two different light regimes. Aquacult. Fish. Manage. 23, 275–280.

Hanson, K.C., Gravel, M.A., Graham, A., Shoji, A., Cooke, S. J., 2008. Sexual variation in fisheries research and management: when does sex matter? Rev. Fish. Sci. 16, 421-436.

Herbinger, C.M., Friars, G.W., 1991. Correlation between condition factor and total lipid content in Atlantic salmon, *Salmo salar* L., parr. Aquacult. Res. 22, 527-529.

Ilkyaz, A.T., Firat, K., Saka, S., Kinacigil, H.T., 2006. Age, growth, and sex ratio of golden grey mullet, *Liza aurata* (Risso, 1810) in homa lagoon (Üzmir Bay, Aegean Sea). Turkish J. Fish. Aquat. Sci. 30, 279-284.

Imslad, A.K., Folkvord, A., Grung, G.L., Stefansson, S.O., Taranger, G.L., 1997. Sexual dimorphism in growth and maturation of turbot, *Scophthalmus maximus* (Rafinesque, 1810). Aquacult. Res. 28, 101-114.

Johnston, I.A., Manthri, S., Smart, A., Campbell, P., Nickell, D., Alderson, R., 2003. Plasticity of muscle fibre number in seawater stages of Atlantic salmon in response to photoperiod manipulation. J. Exp. Biol. 206, 3425-3435.

Kadri, S., Mitchell, D., Metcalfe, J.D., Huntingford, F.A., Thorpe, J.E., 1996. Differential patterns of feeding and resource accumulation in maturing and immature Atlantic salmon, *Salmo salar*. Aquaculture 142, 245-257.

Kadri, S., Metcalfe, N.B., Huntingford, F.A., Thorpe, J.E., Mitchell, D.F., 1997a. Early morphological predictors of maturity in one-sea-winter Atlantic salmon. Aquacult. Int. 5, 41-50.

Kadri, S., Thorpe, J.E., Metcalfe, N.B., 1997b. Anorexia in one-sea winter Atlantic salmon (*Salmo salar*) during summer, associated with sexual maturation. Aquaculture 151, 405-409.

Kjesbu, O., Klungsøyr, J., Kryvi, H., Witthames, P.R., Greer-Walker, M., 1991. Fecundity, atresia, and egg size of captive Atlantic cod (*Gadus morhua*) in relation to proximate body composition. Can. J. Fish. Aquat. Sci. 8, 2333-2343.

Kråkenes, R., Hansen, T., Stefansson, S.O., Taranger, G.L., 1991. Continuous light increases growth rate of Atlantic salmon (*Salmo salar* L.) postsmolts in sea cages. Aquaculture 95, 281-287.

Margeirsson, S., Jonsson, G.R., Arason, S., Thorkelsson, G., 2007. Influencing factors on yield, gaping, bruises and nematodes in cod (*Gadus morhua*) fillets. J. Food Eng. 80, 503-508.

Mehanna, S.F., 2007. A preliminary assessment and management of gilthead bream *Sparus aurata* in the port Said fishery, the southeastern mediterranean, Egypt. Turkish J. Fish. Aquat. Sci. 7, 123-130.

Michie, I., 2001. Causes of downgrading in the salmon industry In: S.C. Kestin and P.D. Warriss (Editors). Farmed fish quality, Blackwell Science, Oxford, pp. 129-136.

Nordgarden, U., Oppedal, F., Taranger, G. L., Hemre, G.I., Hansen, T., 2003. Seasonally changing metabolism in Atlantic salmon (*Salmo salar* L.) I - Growth and feed conversion ratio. Aquacult. Nutr. 9, 287-293.

Oppedal, F., Taranger, G.L., Juell, J.E., Hansen, T., 1999. Growth, osmoregulation and sexual maturation of underyearling Atlantic salmon smolt *Salmo salar* L. exposed to different intensities of continuous light in sea cages. Aquacult. Res. 30, 491-499.

Oppedal, F., Taranger, G.L., Hansen, T., 2003. Growth performance and sexual maturation in diploid and triploid Atlantic salmon (*Salmo salar* L.) in seawater tanks exposed to continuous light or simulated natural photoperiod. Aquaculture 215, 145-162.

Oppedal, F., Berg, A., Olsen, R.E., Taranger, G.L., Hansen, T., 2006. Photoperiod in seawater influence seasonal growth and chemical composition in autumn sea-transferred Atlantic salmon (*Salmo salar* L.) given two vaccines. Aquaculture 254, 396-410.

Papadaki, M., Piferrer, F., Zanuy, S., Maingot, E., Divanach, P., Mylonas, C., 2005. Growth, sex differentiation and gonad and plasma levels of sex steroids in male- and female-dominant populations of *Dicentrarchus labrax* obtained through repeated size grading. J. Fish. Bio. 66, 938-956.

Peterson, R.H., Harmon, P.R., 2005. Changes in condition factor and gonadosomatic index in maturing and non-maturing Atlantic salmon (*Salmo salar* L.) in Bay of Fundy sea cages, and the effectiveness of photoperiod manipulation in reducing early maturation. Aquacult. Res. 36, 882–889.

Robb, D.H.F., 2001. Measurement of flesh colour In: S.C. Kestin and P.D. Warriss (Editors). Farmed Fish Quality, Blackwell Science, Oxford, pp. 298-306.

Roth, B., Jenssen, D.M., Jonassen, T.M., Foss, A., Imsland, A., 2007. Change in flesh quality associated with early maturation of Atlantic halibut (*Hippoglossus hippoglossus*). Aquacult. Res. 38, 757-763.

Rowe, D.K., Thorpe, J.E., Shanks, A.M., 1991. Role of fat stores in the maturation of male Atlantic salmon (*Salmo salar*) parr. Can. J. Fish. Aquat. Sci. 48, 405-413.

Saillant, E., Fostier, A., Menu, B., Haffray, P., Chatain, B., 2001. Sexual growth dimorphism in sea bass *Dicentrarchus labrax*. Aquaculture 202, 371-387.

Salte, R., Norberg, K., Ódegaard, O.R., 1995. Evidence of ongoing coagulation and fibrinolysis in early-maturing Atlantic salmon, *Salmo salar* L.. J. Fish Dis. 18, 623-626.

Shewmon, L., Godwin, J., Murashige, R., Daniels, H., Losordo, T., 2007. Environmental manipulation of growth and sexual maturation in yellow perch, *Perca flavescens*. J. World Aquacult. Soc. 38, 383-394.

St-Hilaire, S., Ribble, C., Whitaker, D.J., Kent, M., 1998. Prevalence of Kudoa thyrsites in sexually mature and immature pen-reared Atlantic salmon (*Salmo salar*) in British Columbia, Canada. Aquaculture 162, 69-77.

Taranger, G.L., Haux, C., Stefansson, S.O., Björnsson, B.T., Walther, B.T., Hansen, T., 1998. Abrupt changes in photoperiod affect age at maturity, timing of ovulation and plasma testosterone and oestradiol-17ß profiles in Atlantic salmon, *Salmo salar*. Aquaculture 162, 85-98.

Taranger, G.L., Haux, C., Hansen, T., Stefansson, S.O., Björnsson, B.T., Walter, B.T., Kryvi, H., 1999. Mechanisms underlying photoperiodic effects on age at sexual maturity in Atlantic salmon, *Salmo salar*. Aquaculture 177, 47-60.

Thorpe, J.E., 1986. Age at first maturity in Atlantic salmon, *Salmo salar*: freshwater period influences and conflicts with smolting. Can. Spec. Publ. Fish. Aquat. Sci. 89, 7-14.

Thorpe, J.E., 1989. Developmental variation in salmonid populations. J. Fish Biol. 35, 295-303.

Traxler, G.S., Roome, J.R., Lauda, K.A., LaPatra, S., 1997. Appearance of infectious haematopoietic necrosis virus (IHNV) and neutralizing antibodies in sockeye salmon *Oncorhynchus nerka* during their migration and maturation period. Dis. Aquat. Org. 28, 31-38.

Türkmen, M., Akyurt, I., 2003. Growth characteristics, sex inversion and mortality rates of stripped sea bream, *Lithognathus mormyrus* L., in Iskenderun Bay. Turkish J. Fish. Aquat. Sci. 27, 323-329.

Usher, M.L., Talbot, C., Eddy, F.B., 1991. Effect of transfer to seawater on growth and feeding in Atlantic salmon smolts (*Salmo salar* L.). Aquaculture 94, 309-326.

Wootton, R.J., 1990. Ecology of Teleost Fishes, second ed. Chapman and Hall, London.

Young, K.A., 2005. Life-history variation and allometry for sexual size dimorphism in Pacific salmon and trout. Proc. R. Soc. Lond., Ser. B: Biol. Sci. 272, 167-172.

Young, A., Morris, P.C., Huntingford, F.A., Sinnott, R., 2006. Replacing fish oil with pre-extruded carbohydrate in diets for atlantic salmon, *Salmo salar*, during their entire marine grow-out phase: Effects on growth, composition and colour. Aquaculture 253, 531-546.

Zar, J.H., 1999. Biostatistical Analysis, fourth ed. Prentice-Hall International, New Jersey.

Table 1. (a) Number of individuals sexed and proportion of male within each harvest batch for each of the four sites studied. Significant difference to the expected balanced sex-ratio (1:1) was determined by a chi-square test for goodness of fit (α=0.05) and shown in bold when significantly skewed toward an excess of Male (+) or Female (-). (b) Average whole body weight (BW) and (c) Fulton condition factor (K) of immature males and immature females within each harvest batch for each of the four sites studied. Values are expressed as mean±SE with n=30 fish/sex/month/site. Significant differences between genders within each harvest batch are shown in bold. Significant differences between month within each gender cohort are shown by different superscript letters (GLM, α=0.05).

Site	Month	June	July	August	September	October	November	December
	(a) N Ind. (% Male)							
A		**106 (71.7+)**	197 (49.3)	161 (53.9)	**235 (62.5+)**	**187 (41.8-)**	**242 (63.3+)**	239 (48.4)
B		62 (51.6)	**145 (58.9+)**	**163 (62.6+)**	**187 (39.2-)**	169 (46.2)	175 (42.6)	173 (56.0)
C			**168 (63.6+)**	**194 (58.0+)**		187 (44.4)	**226 (38.4-)**	
D		63 (52.4)	122 (49.4)	**136 (60.1+)**	**113 (37.9-)**		**211 (38.4-)**	
	(b) BW (g)							
A	Male	**4498±169^{a}**	4399±120^{a}	4603±77^{a}	**5928±116^{cd}**	**5437±151^{bc}**	**5368±130^{b}**	**6196±134^{d}**
	Female	**3644±91^{a}**	3934±106^{ab}	4340±84^{b}	**5115±86^{c}**	**4834±101^{bc}**	**4429±92^{b}**	**5289±104^{c}**
B	Male	4446±97^{a}	4365±99^{a}	5283±92^{b}	**6202±91^{c}**	**6313±184^{c}**	5633±164^{bc}	5971±185^{c}
	Female	4001±77^{a}	4116±67^{a}	4817±68^{b}	**5156±99^{bc}**	**5509±119^{c}**	5027±116^{bc}	5318±110^{bc}
C	Male		**4883±108^{a}**	5452±114^{ab}		**5791±157^{b}**	**5620±149^{b}**	
	Female		**3934±106^{a}**	4882±91^{b}		**5023±113^{b}**	**4918±125^{b}**	
D	Male	**4035±89^{a}**	**4797±80^{bc}**	**5156±96^{c}**	4645±117^{b}		**5315±138^{c}**	
	Female	**3446±97^{a}**	**4214±60^{b}**	**4557±89^{bc}**	4325±98^{b}		**4785±108^{c}**	
	(c) K							
A	Male	1.04±0.01^{ab}	1.01±0.01^{a}	**1.05±0.01^{ab}**	**1.08±0.01^{bc}**	**1.09±0.01^{bc}**	**1.02±0.01^{a}**	**1.13±0.01^{c}**
	Female	1.06±0.01^{ab}	1.05±0.01^{a}	**1.14±0.01^{c}**	**1.14±0.01^{c}**	**1.15±0.01^{c}**	**1.07±0.01^{a}**	**1.19±0.01^{c}**
B	Male	1.08±0.02^{b}	**1.00±0.01^{a}**	**1.08±0.01^{b}**	1.12±0.01^{b}	**1.09±0.01^{b}**	**1.10±0.02^{b}**	**1.11±0.02^{b}**
	Female	1.14±0.01^{ab}	**1.09±0.01^{a}**	**1.15±0.01^{ab}**	1.15±0.01^{ab}	**1.15±0.01^{ab}**	**1.20±0.01^{b}**	**1.19±0.02^{b}**
C	Male		1.02±0.01^{a}	1.03±0.01^{a}		1.08±0.01^{b}	**1.04±0.01^{ab}**	
	Female		1.05±0.01^{a}	1.07±0.01^{a}		1.12±0.01^{b}	**1.10±0.02^{ab}**	
D	Male	0.99±0.01^{a}	1.00±0.01^{a}	1.04±0.01^{ab}	1.08±0.01^{bc}		1.10±0.01^{c}	
	Female	1.01±0.02^{a}	1.05±0.01^{a}	1.06±0.01^{a}	1.12±0.01^{b}		1.14±0.01^{b}	

Table 2. (a) Average whole body weight (BW), (b) Fulton condition factor (K), (c) total lipid and (d) total carotenoid of immature (Immat.) and sexually maturing (Mat.) fish within each harvest batch for each of the four sites studied. Values are expressed as mean±SE with (a) n=50-60 fish/maturity cohort/month/site (except in June for all sites and site D throughout where n=10-15 maturing fish/site/month) (c) and (d) n=10 female/site/month/maturity cohort. Significant differences between maturity cohorts within each harvest batch are shown in bold. Significant differences between month within each maturity cohorts are shown by different superscript letters (GLM, α=0.05). Maturing fish in June and July only were at an early stage of development and are underlined.

Site	Month	June	July	August	September	October	November	December
	(a) BW (g)							
A	Immat.	4086±113^{a}	**4139±84^{a}**	4480±58^{ab}	**5535±82de**	**5127±94^{cd}**	4919±92^{bc}	**5802±98^{e}**
	Mat.	5191±264^{abcd}	**5534±177^{a}**	4099±218^{cd}	**4745±142^{bc}**	**3883±149de**	5013±154^{ab}	**3271±86^{e}**
B	Immat.	4223±68^{a}	**4232±60^{a}**	**5054±61^{b}**	**5702±83^{cd}**	**5890±113^{d}**	**5268±100^{bc}**	**5684±119^{cd}**
	Mat.	5610±530^{ab}	**5944±194^{a}**	**6186±267^{a}**	**4145±206^{b}**	**4304±199^{b}**	**3812±145^{b}**	**3873±139^{b}**
C	Immat.		**4409±93^{a}**	5202±81^{b}		**5411±103^{b}**	**5282±103^{b}**	
	Mat.		**5543±168^{a}**	5499±174^{a}		**4159±158^{b}**	**4109±116^{b}**	
D	Immat.	**3730±77^{a}**	**4498±57^{b}**	4886±4^{c}	4468±76^{b}		**5080±94^{c}**	
	Mat.	**5594±617^{a}**	**7025±275^{a}**		3410±269^{b}		**3844±100^{b}**	
	(b) K							
A	Immat.	**1.05±0.01^{ab}**	**1.03±0.01^{a}**	1.09±0.01^{b}	**1.11±0.01^{bc}**	**1.12±0.01^{bcd}**	**1.04±0.01^{a}**	**1.16±0.01^{d}**
	Mat.	**1.25±0.07^{ab}**	**1.23±0.02^{a}**	1.08±0.03^{b}	**1.05±0.01^{bc}**	**1.03±0.02^{bcd}**	**0.98±0.01^{d}**	**1.06±0.02^{bc}**
B	Immat.	**1.11±0.01^{b}**	**1.05±0.01^{a}**	1.12±0.01^{b}	1.13±0.01^{b}	1.12±0.01^{b}	**1.16±0.01^{b}**	**1.14±0.01^{b}**
	Mat.	**1.39±0.04^{a}**	**1.28±0.01^{a}**	1.11±0.01^{b}	1.07±0.02^{b}	1.09±0.02^{b}	**1.08±0.02^{b}**	**1.09±0.02^{b}**
C	Immat.		**1.04±0.01^{a}**	**1.04±0.01^{a}**		1.10±0.01^{b}	1.07±0.01^{ab}	
	Mat.		**1.26±0.01^{a}**	**1.17±0.02^{b}**		1.07±0.01^{c}	1.06±0.02^{c}	
D	Immat.	**1.00±0.01^{a}**	**1.02±0.01^{ab}**	1.05±0.01^{b}	1.10±0.01^{c}		1.11±0.01^{c}	
	Mat.	**1.29±0.03**	**1.25±0.02**		1.05±0.07		1.11±0.02	
	(c) Total Lipid (g.100g^{-1} flesh)							
A	Immat.	16.1±0.8	16.6±0.8	**16.1±0.5**	**15.4±0.4**	**16.6±0.5**	**15.7±1.0**	**16.2±0.7**
	Mat.		17.9±0.6^{a}	**10.3±6.3^{b}**	**11.0±0.8^{b}**	**10.0±0.8^{b}**	**10.0±1.2^{b}**	**7.8±0.6^{b}**
B	Immat.	15.1±0.7^{ab}	12.1±0.5^{a}	**14.4±0.5^{ab}**	**15.8±0.9^{b}**	**15.4±0.9^{ab}**	**15.3±0.9^{ab}**	**15.4±0.8^{ab}**
	Mat.		14.5±0.8^{a}	**10.1±0.5^{b}**	**6.9±1.2^{b}**	**7.8±0.9^{b}**	**6.8±0.6^{b}**	**7.4±0.5^{b}**

C	Immat.		12.0±0.9^{a}	16.1±0.6^{b}		**15.4±0.7^{ab}**	**15.9±1.0^{b}**	
	Mat.		15.3±0.9^{a}	13.3±0.6^{a}		**7.2±0.7^{b}**	**8.0±0.9^{b}**	
D	Immat.	14.7±0.9^{ab}	11.6±0.4^{a}	14.2±0.6^{ab}	15.1±0.7^{b}		**14.5±1.1^{ab}**	
	Mat.		14.3±0.5^{a}	10.8±1.3^{a}	12.2±1.0^{a}		**6.9±0.7^{b}**	
	(d) Total Carotenoid (mg.kg^{-1} flesh)							
A	Immat.	6.6±0.2^{a}	7.0±0.2^{abc}	7.6±0.3^{bc}	7.8±0.2^{c}	**7.7±0.2^{c}**	**7.3±0.7^{abc}**	**6.6±0.3^{ab}**
	Mat.		6.8±0.2^{a}	6.33±0.6^{ab}	6.6±0.4^{ab}	**5.5±0.5^{ab}**	**5.1±0.5^{b}**	**2.3±0.4^{c}**
B	Immat.	7.3±0.3^{ab}	7.4±0.2^{ab}	7.6±0.2^{ab}	**8.0±0.2^{a}**	**7.4±0.2^{ab}**	**7.0±0.2^{ab}**	**6.9±0.2^{b}**
	Mat.		8.2±0.2^{a}	7.3±0.3^{ab}	**6.5±0.3^{bc}**	**5.9±0.4^{c}**	**4.2±0.3^{d}**	**2.4±0.2^{e}**
C	Immat.		7.1±0.3	8.0±0.2		**6.9±0.1**	**7.0±0.3**	
	Mat.		7.3±0.3^{a}	7.7±0.2^{a}		**5.0±0.4^{b}**	**3.6±0.3^{c}**	
D	Immat.	7.9±0.2	7.5±0.2	7.9±0.1	7.7±0.1		**7.3±0.2**	
	Mat.		7.8±0.3^{a}	7.2±0.1^{a}	7.3±0.2^{a}		**4.9±0.3^{b}**	

Table 3. Proportion of correct classification of individuals into their gender cohort based on each site own dataset, June and July sampled pooled, using as predictors whole body weight (BW), fork length (FL) and Fulton condition factor (K) or BW alone. Significant differences from 50% of correct prediction, which could have been expected by chance alone, were determined by using a chi-square test for goodness of fit ($\alpha = 0.05$) and are shown in bold.

Site	n Ind.	Predictors: BW, FL and K			Predictor: BW		
		Correct prediction (%)	χ^2	P-value	Correct prediction (%)	χ^2	P-value
A	177	**77.4**	30.03	0.000	**64.4**	8.29	0.004
B	180	**78.9**	33.40	0.000	**63.9**	7.73	0.005
C	119	**74.8**	24.60	0.000	57.1	2.02	0.156
D	176	**75.6**	26.21	0.000	**68.2**	13.25	0.000

Table 4. Results (mean ± SE) from discriminant analysis performed on site A, B and C on June and July datasets pooled (except site C where no harvest occurred in June) using (a) BW, FL and K as predictors and (b) BW as the sole predictor. For each set of predictor used, analyses were done using the site own dataset and the two discrete site datasets for which the actual composition of the cohorts predicted as immature and maturing is presented.

Site	A	B	C	Average
Initial population				
Immature (n)	124	135	73	111±19
Maturing (n)	53	45	46	48±3
Maturation rate (%)	29.9	25.0	38.7	31.2±4.0
(a) PREDICTORS: BW, FL, K				
• **Correct prediction from own site dataset (%)**				
Immature	91.9	96.3	93.2	93.8±1.3
Maturing	84.9	82.2	95.7	87.6±4.1
Population	89.8	92.8	94.1	92.2±1.3
• **Correct prediction from discrete site datasets (%)**				
Immature	96.0±0.8	87.8±6.3	89.1±1.4	91.0±2.3
Maturing	73.6±0.0	87.8±5.6	95.7±4.4	85.7±4.5
Population	89.3±0.6	87.8±3.4	91.6±0.8	89.5±1.2
Predicted maturation rate	24.9±0.6	31.1±6.1	43.7±2.5	33.2±3.9
Error on maturation rate	-5.1	+6.1	+5.0	+2.0±3.6
• **Composition of the cohort predicted as maturing using discrete site datasets (%)**				
Maturing	88.7±2.0	72.5±9.8	84.7±1.0	81.9±4.0
Immature	11.3±2.0	27.5±9.8	15.3±1.0	18.1±4.0
• **Composition of the cohort predicted as immature using discrete site datasets (%)**				
Immature	89.5±0.1	95.7±1.6	97.1±2.9	94.1±1.7
Maturing	10.5±0.1	4.3±1.6	2.9±2.9	5.9±1.7
(b) PREDICTOR: BW				
• **Correct prediction from own site dataset (%)**				
Immature	85.5	91.1	84.9	87.2±2.0
Maturing	73.6	75.6	80.4	76.5±2.0
Population	81.9	87.2	83.2	84.1±1.6
• **Correct prediction from discrete site datasets (%)**				
Immature	92.0±3.25	91.5±6.3	62.4±3.5	81.9±6.5
Maturing	58.5±11.3	66.7±8.9	90.2±1.1	71.8±7.1
Population	82.0±1.15	85.3±2.5	73.1±1.7	80.1±2.5
Predicted maturation rate	23.2±5.7	23.1±6.9	58.0±2.5	34.7±7.7
Error on maturation rate	-6.8	-1.9	+19.3	+3.5±8.0
• **Composition of the cohort predicted as maturing using discrete site datasets (%)**				
Maturing	76.6±4.1	76.3±13.4	60.2±1.0	71.0±5.0
Immature	23.4±4.1	23.7±13.4	39.7±1.0	29.0±5.0
• **Composition of the cohort predicted as immature using discrete site datasets (%)**				
Immature	84.1±3.2	89.3±1.9	97.1±2.9	88.1±1.7
Maturing	15.9±3.2	10.7±1.9	2.9±2.9	11.9±1.7

List of Figures Caption

Figure 1. (a) WLR and least-square regression line of immature population based on individuals pooled per 1cm length class ($y=0.0172x^{2.893}$, CI-b=2.76-3.02, $r^2=0.984$, n=36, isometric relationship with P-value=0.105) and using mean-FL and mean-BW at each sampling point (genders average) ($y=0.0005x^{3.7268}$, CI-b=3.23-4.22, $r^2=0.921$, positive allometry with P-value=0.006). The dashed grey line represents isometrics WLRs of given condition factor (Italic) (b) WLR of the immature females (N=1104) and immature males (N=1131) cohorts with regression line based on individual pooled per 1cm length class (Males: $y=0.0229x^{2.827}$, CI-b=2.62-3.03, $r^2=0.962$, isometric relationship with P-value=0.097; Females: $y=0.0104x^{3.0135}$, CI-b=2.904-3.123, $r^2=0.993$, isometric relationship with P-value=0.801).

Figure 2. Relationship at each sampling point (grey dotes) between mean immature male and mean immature female (a) BW (b) FL and (c) K given with their RMA regression line (long spotted grey line). The plain black line is the isometry of equality between genders, the black dot and short spotted black line indicates the harvest batches average. Coefficients of the RMA regression slope were never significantly different to the isometry (a) a=1.05±0.07; CI-a=0.92-1.26; $r^2=0.955$; (b) a=1.08±0.07; CI-a=0.95-1.29; $r^2=0.951$; (c) 0.85±0.09; CI-a=0.70-1.06; $r^2=0.867$.

Figure 3. (a) WLR of immature (n=502) and recruited (n=150) individuals sampled in June and July, all sites pooled, with their respective least-square regression line. (b) WLR of immature (n=124) and recruited (n=53) individuals sampled from site A in June and July and presented as result of the discriminant analysis using a discrete site dataset (Site B) with BW, FL and K as predictors. For comparison, the black dashed line represents the optimal segregating BW between maturity cohorts using BW as sole predictor. Any individuals above the BW threshold

were predicted as maturing and any individuals below were predicted as immature. The dashed grey line represents isometric WLRs of given condition factor (Italic).

Figure 4. Cumulative weight-structure diagram of the population addressed in Fig.3.b. (Site A, June and July sample pooled), classified per maturity status and presented with the optimal segregating BW determined using a discrete site dataset (Site B) and BW as sole predicting factor.

Figure 1.

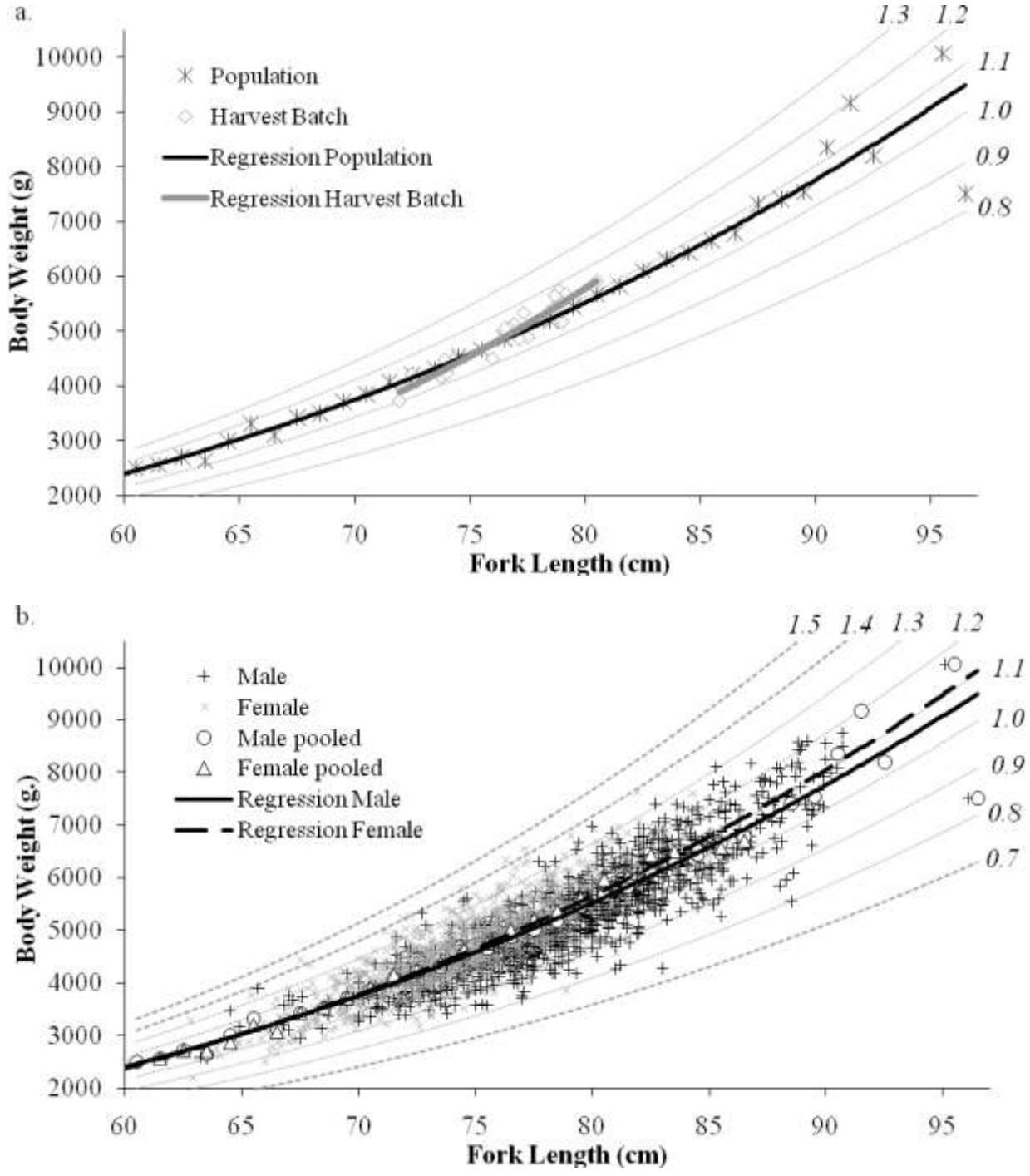

a.
Population
Harvest Batch
Regression Population
Regression Harvest Batch
1.3
1.2
1.1
1.0
0.9
0.8
Body Weight (g)
Fork Length (cm)
b.
Male
Female
Male pooled
Female pooled
Regression Male
Regression Female
1.5
1.4
1.3
1.2
1.1
1.0
0.9
0.8
0.7
Body Weight (g.)
Fork Length (cm)

Figure 2.

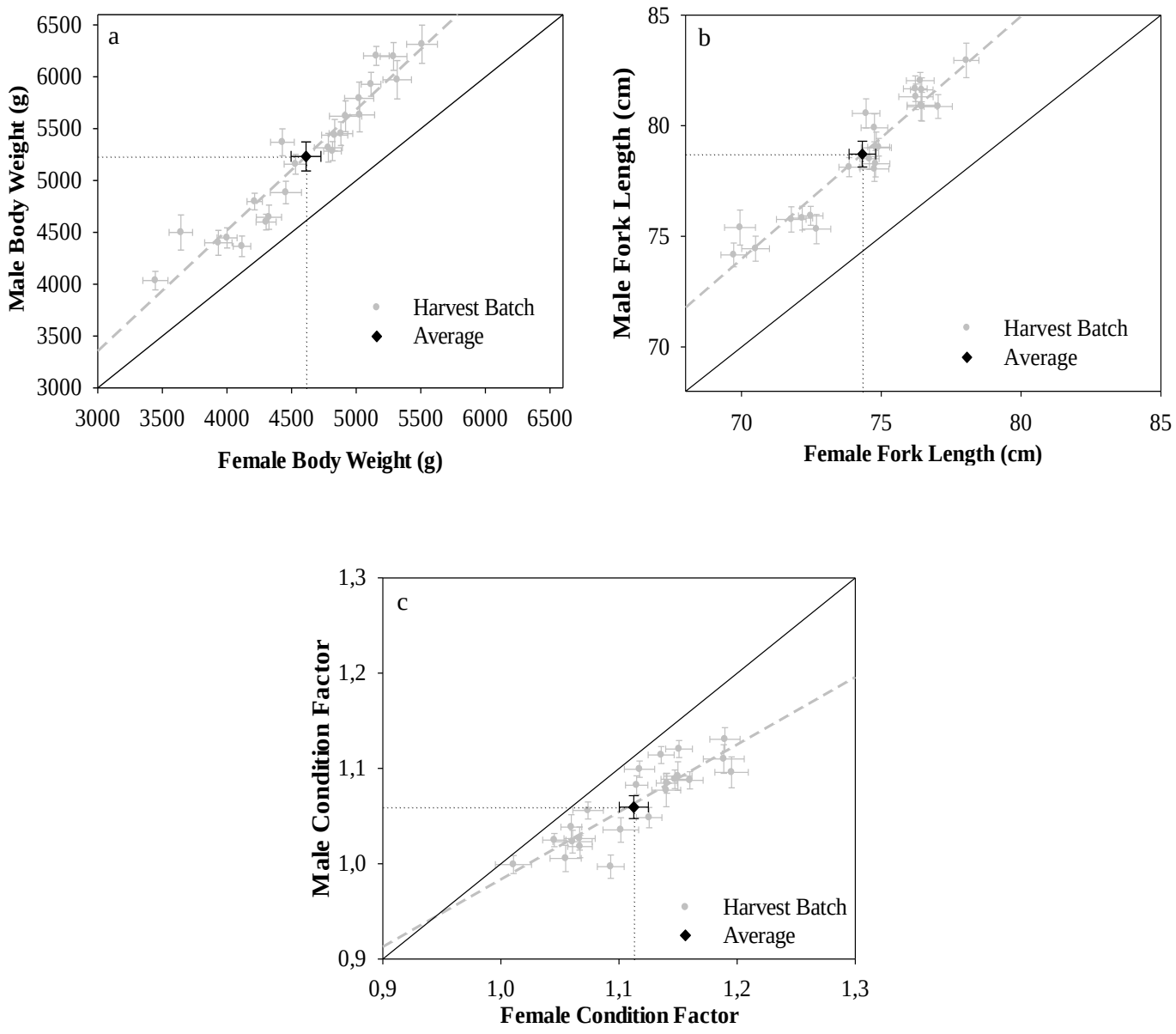

a
Male Body Weight (g)
Female Body Weight (g)
6500
6000
5500
5000
4500
4000
3500
3000
3000 3500 4000 4500 5000 5500 6000 6500
Harvest Batch
Average
b
Male Fork Length (cm)
Female Fork Length (cm)
85
80
75
70
70 75 80 85
Harvest Batch
Average
c
Male Condition Factor
Female Condition Factor
1,3
1,2
1,1
1,0
0,9
0,9 1,0 1,1 1,2 1,3
Harvest Batch
Average

Figure 3.

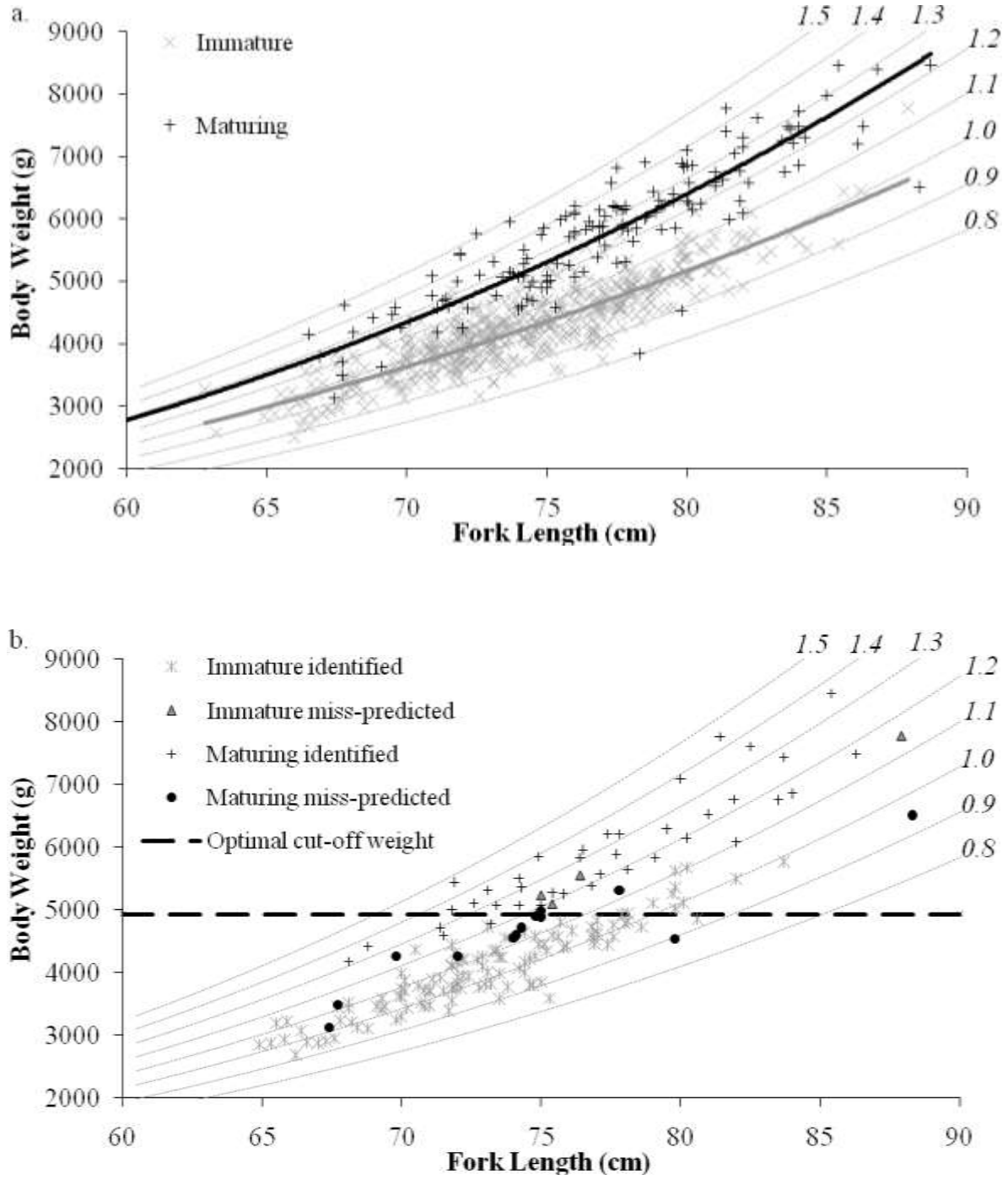
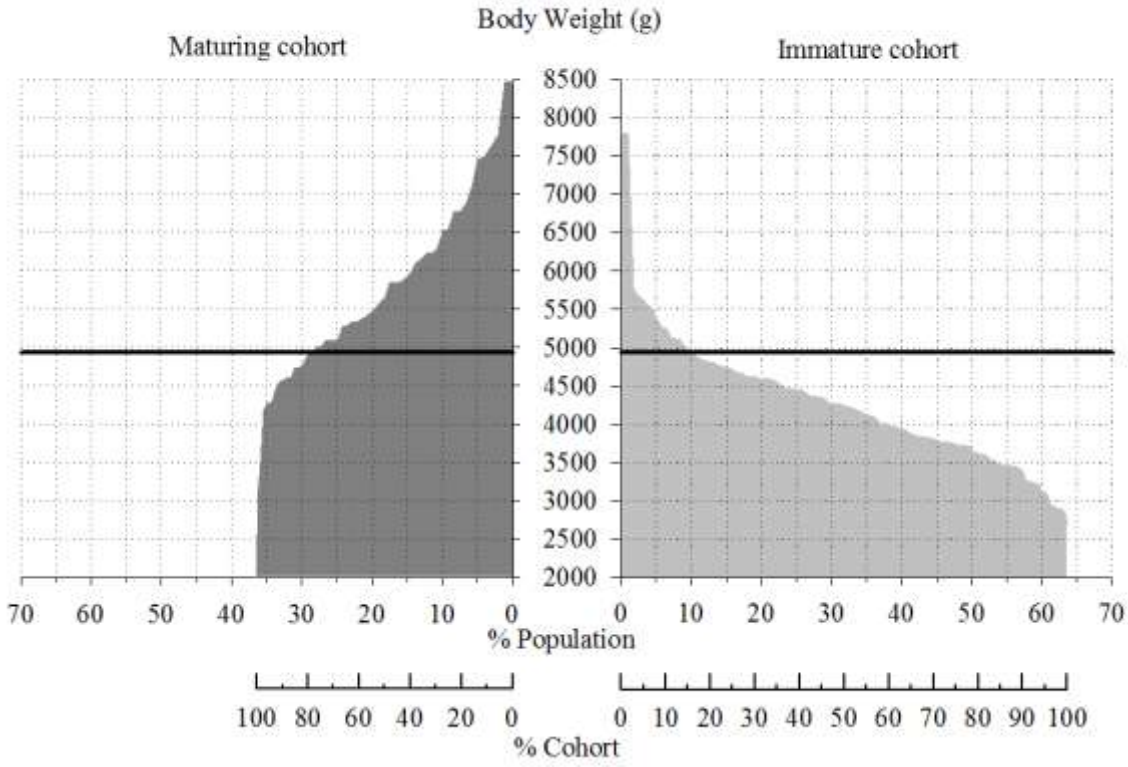

a.
Immature
Maturing
1.5
1.4
1.3
1.2
1.1
1.0
0.9
0.8
Body Weight (g)
9000
8000
7000
6000
5000
4000
3000
2000
60
65
70
75
80
85
90
Fork Length (cm)
b.
Immature identified
Immature miss-predicted
Maturing identified
Maturing miss-predicted
Optimal cut-off weight
1.5
1.4
1.3
1.2
1.1
1.0
0.9
0.8
Body Weight (g)
9000
8000
7000
6000
5000
4000
3000
2000
60
65
70
75
80
85
90
Fork Length (cm)

Figure 4.


Body Weight (g)
Maturing cohort
Immature cohort
8500
8000
7500
7000
6500
6000
5500
5000
4500
4000
3500
3000
2500
2000
70 60 50 40 30 20 10 0
0 10 20 30 40 50 60 70
% Population
100 80 60 40 20 0
0 10 20 30 40 50 60 70 80 90 100
% Cohort