Turk. J. Fish.& Aquat. Sci. 19(4), 305-312
http://doi.org/10.4194/1303-2712-v19_4_05

Turkish Journal of
FISHERIES and
AQUATIC SCIENCES

RESEARCH PAPER

The Course of Growth, Feed Intake and Feed Efficiency of Different Turbot (*Scophthalmus maximus*) Strains in Recirculating Aquaculture Systems

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Article History
Received 10 August 2017
Accepted 16 April 2018
First Online 19 April 2018

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Keywords
Turbot
Breeding strains
Nutrition modelling
Biological traits
Recirculating aquaculture systems

Abstract

We fitted the flexible nonlinear model $y = a * \exp(-b * x - c/x)$ to long-term data of daily gain (DG), feed intake (FI) and feed efficiency (FE) of different strains of communally-reared turbot from a recirculating aquaculture system (RAS). We modelled each trait (y = DG, FI, FE) as a function of actual body size (x). We used the coefficient of determination (R^2) to display the suitability of the model. The curves of each trait were analyzed via shape, location of the point of inflection (POI), minimum (Min.) and maximum (Max.). The relationships between FI and FE to actual size were the same for both strains although the magnitude of the curves diverged. Diversion of the growth curves, related to sexual dimorphism, occurred similar in both strains at 460-500 g body weight. We observed a major change in turbot growth characteristics with a POI between 60-110 g weight, 15.7-18.6 cm length respectively. Our results verify several distinct life-stages, which cause changes in trait characteristics, as well as strong sexual dimorphism. Accordingly, findings from experiments with juvenile fish cannot be extrapolated to mature fish. We could prove that the biological processes related to growth are still the same in different breeding strains.

Introduction

The number of farm raising aquatic organisms has increased rapidly during the last decades and numerous new candidate species have been evaluated for production. Accordingly, primary aquaculture research focuses on finding the optimal rearing conditions for new emerging species. Compared to other livestock, only few trait-specific breeds have been developed in aquaculture so far. Recognizing this, regional, national or company based breeding programs have tried to establish strains with increased growth rates, feed utilization or pathogen resistance vis-á-vis the wild genotypes they were based on.

Wild turbot populations show little genetic distance and generally low genetic diversity, although local environmental adaption exists in some populations (Blanquer, Alayse, Berrada–Rkhami, & Berrebi, 1992; Bouza *et al*., 2014). In reverse, local environmental adaption might affect the future productivity of breeding lines, originating from such wild populations.

Today, strong diversity in individual growth characteristics occurs in each commercial turbot strain. This leads to unequal production cycles with massively varying individuals. Fish have to be graded several times (Bouza *et al*., 2014). As feed supply is the major factor of costs in aquaculture production, traits such as feed intake (FI), feed efficiency (FE) and daily gain (DG) are becoming key issues of trait specific breeding programs.

For most livestock, the rate of growth is strongly correlated to feed intake (Parks, 1982). Feed efficiency, feed intake and daily gain are strongly related to each other (Kanis & Koops, 1990). Therefore, it is possible to shift the growth curve to a more economic one by manipulation feed intake (Parks, 1982; Krieter & Kalm, 1988; Kanis & Koops, 1990). Thus, precise knowledge of the course of these traits can be used in selection and breeding purposes (Krieter & Kalm, 1988; Kanis & Koops, 1990). To do so, the limits and mathematical relations of these traits must be known, in order to manipulate the feed intake, either by feeding management or selective breeding (Kanis & Koops, 1990).

Only limited aquaculture studies refer to growth-response as a direct function of feed intake. Pleuronectiformes undergo numerous changes in life-history, during larval stage, metamorphosis, juvenile stages and maturation. Each change influences the growth characteristics, feeding behavior and feed efficiency. Most studies regarding turbot exclusively focus on juvenile fish. In order to improve trait-specific breeding programs and production efficiency, long-term studies are required to understand the underlying biological principles related to growth and the according changes that occur during different life-stages. In turbot, to date little is known about the interaction of feed intake, feed efficiency and daily gain in relation to actual body size, across different life-stages and the biological patterns, that control these.

The aim of the study was therefore, to describe the course of these different traits, and to characterize the patterns of growth, feed intake and feed-growth response in two established turbot strains using a flexible nonlinear model. The obtained information can be used to develop more efficient feeding schedules, and management plans. Further, the obtained information can be used in selection of parental animals for trait specific breeding programs.

Materials and Methods

Experimental Design

Turbot (n=1966) of two different established European breeding strains (strain A and B) were reared in a prototype marine recirculation aquaculture system (RAS) at the ”Gesellschaft für Marine Aquakulture mbH (GMA)” in Büsum, Germany. The RAS contained 10 identical round tanks of 2.2 m in diameter and a water depth of 1.0 m. The entire water volume of the RAS was 40 m³. Fish were kept at ≈ 16.5°C (SD ± 1.0) water temperature over the entire grow-out period. Water parameters were kept at: O_2 ≈ 9.3 mgL^{-1} (SD ± 0.5); NH_4 ≈ 0.4 mgL^{-1} (SD ± 0.7); NO_2 ≈ 0.9 mgL^{-1} (SD ± 0.9); salinity ≈ 24.8 ‰ (SD ± 2.6). All fish were individually marked intraabdominally with passive integrated transponder (PIT) tags (Hallprint, PTY Ltd., Hindmarsh Vally, Australia). Growth data were recorded every 28 days to the nearest 0.1 g. Both strains were communally stocked (Moav & Wolfarth 1974) at an initial stocking density of 8.6 kgm^{-2}. All fish were fed twice a day by hand to obvious saturation (ad libitum) using commercial fish feed for turbot (Emsland-Aller Aqua GmbH, Golßen, Germany). Fish where graded in 4 different size groups according to actual body size during grow-out and re-graded when necessary (Bouza *et al*. 2014). Stocking density met common production standards and did not exceed 60 kgm^{-2} in large individuals.

Calculations and Statistics

All calculations as well as fitting of the model were performed using the open-source software R version 3.0.2 (R Development Core Team, 2013).

Fish weight increase (ΔW) was calculated as $\Delta W = W_{(t+1)} - W_{(t)}$. According growth rate was calculated as daily weight gain (DWG): ΔW/Δt (Prein, Hulata, & Pauly, 1993).

Data for total body length were obtained by transformation via Length-Weight relationship: $W = aL^b$ (Le Cren, 1951). Daily length gain (DLG) was, in accordance to daily weight gain (DWG), calculated as ΔL/Δt (Prein *et al*., 1993). Feed intake (FI) was calculated on a daily basis as the total amount of feed per tank divided by the number of fish in the tank. Feed efficiency (FE) was calculated as $FE = \frac{daily\ weight\ gain}{feed\ intake}$ (Ponzoni *et al*., 2013). Further we calculated feed intake (FI) as percentage of actual body weight (FI%).

Modelling the Course of Traits

We used the nonlinear model: $y = a * \exp(-b * x - c/x)$ (Kanis & Koops, 1990) to present the course of daily weight gain, daily feed intake and feed efficiency. In this model y is the dependent variable (DWG, DLG, FI, FE, FI%), x is the independent variable (total body length or total body weight) and *a*,*b*,*c* are parameters. The model was fitted by non-linear least squares (nl-LS) using the Levenberg-Marquardt algorithm implemented in the “minpack.lm” package (Elzhov, Mullen, Spiess, & Bolker, 2013) in the open-source software R (R Development Core Team 2013). We fitted the model to the data of each specific trait as a function of life body weight. All trait specific data were used based on individual fish (n = 1966) without any corrections or removal of outliers. We did not statistically weight any data. We used the coefficient of determination (R^2) to describe model performance and the fit to the data. Split of growth characteristics between the strains was calculated via a deviation bound set at a 2.5% level. The split between the sexes within each strain were also determined via a deviation bound set at a 2.5% level. The shape of curves were analysed via the location of the point of inflection (POI), minimum (Min.) and maximum (Max.).

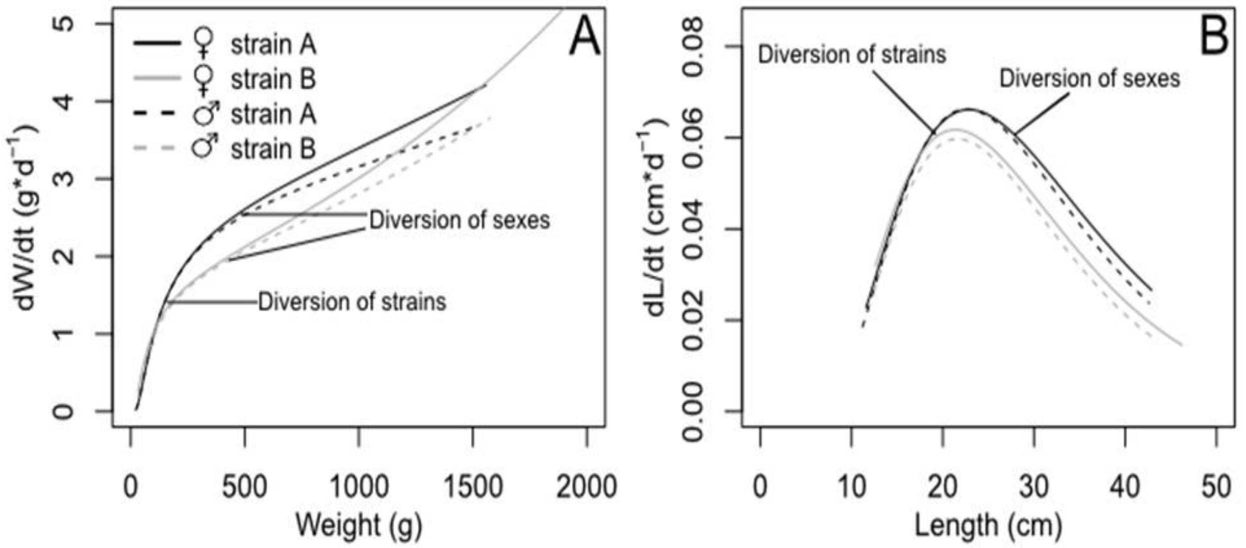

Figure 1. Average course of daily weight gain (dw/dt) as a function of life body weight (A) and average course of daily length gain (dL/dt) as a function of actual body length (B) in ad libitum fed RAS farmed turbot of different strains and sexes.

Results

The Course of Weight Gain

The results of our analysis show that the growth curves of turbot ≥35 g can be subdivided into three phases. Phase one (subsequently: juvenile phase) describes a strong and almost linear increase in body weight with a daily weight increase of approximately 0.014% per gram of body weight. This increase is similar in both strains involved in the trial. A linear regression can be fitted to this part of the growth curve with an R² of 0.99 (data not shown). Maximum growth in relation to body size (Figure 1A) occurs at 110 g body weight in females and at 111 g body weight in males of strain A. This maximum in growth also marks the point of inflection in the growth curve (Figure 1A, Table 1A). In strain B the POI was determined to be at 65 g body weight in females and at 75 g body weight in males. The diversion of strains occurs at 121 g of body weight (Figure 1A). After the POI the second phase (subsequently: transitional phase) of the growth curve is of diminishing return behavior. This curve is similar for both sexes in each strain. Both sexes diverse in growth at a weight of 462 g in strain A and 499 g in strain B. This diversion of sexes also determines the end of the transitional phase. Afterwards growth rate is higher in females than in males and diversion between sexes increases with increasing body weight. The third phase (subsequently: maturing phase) describes a linear but downgraded growth rate as a function of weight. This linear behavior can be observed in both sexes of strain A, but only for males of strain B. Females of strain B follow a slight exponential course of growth rate. The model fitted good to the data giving R² of 0.69 in females and 0.66 in males of strain A. In Strain B the model performed a bit lower giving R² values of 0.48 in both sexes (Table 1A). Estimated parameters of the model were almost similar for both sexes of each strain (Table 1A), expressing the similarity of the curves.

The Course of Length Gain

The growth in length can also be subdivided into three phases (e.g. the course of weight gain). The juvenile phase shows a strong increase in daily length gain as a function of total body length. After reaching a POI, growth rate again shows a decreasing curve. The POI was determined at 18.3 cm total body length in females of strain A and 18.5 cm in males. In strain B females reach the POI at 17.9 cm total body length and males at 17.3 cm respectively. In comparison to weight gain, length gain reaches a maximum in the middle of the curve, at a total length of 22.6 cm in females of strain A and 22.5 cm in males (Table 1 B). Strain B reaches a maximum length increase at 21.6 cm total length in females and 21.4 cm in males respectively. The transitional phase is extended in length gain compared to weight gain. It covers sizes between the POI up to approximately 28cm. Afterwards growth rate shows tendency to reverse-exponentially until it levels out (maturing phase) (Figure 1B). The two strains disconnect in growth rate at approximately 19 cm total body length. Males and female of strain A clearly diverse at a total body length of 28.5 cm while sexes of stain B distinguish in length growth rate during the entire trial. They are never within the defined 2.5% bounder. Lowest diversion occurs at a total body length of 23.2 cm with a value of 3.1% (Figure 1B). Parameters of the model varied widely between strains and sexes within strains. The fit was generally lower in all length

Table 1A. Daily weight gain as a function of actual body weight

Strain	N observations	Fit	Parameters			Weight (g)			dW/dt (g*d⁻¹)		
		R²	a	b	c	Min.	Max.	POI	Min.	Max.	POI
A♀	6583	0.69	2.75	-0.00031	106.8	25	1557	110	0.04	4.2	1.0
A♂	5584	0.66	2.81	-0.00022	108.1	22	1529	111	0.02	3.7	1.1
B♀	7128	0.48	1.89	-0.00046	72.5	32	1972	65	0.3	5.4	0.7
B♂	6134	0.48	1.80	-0.00057	62.5	32	1574	75	0.2	3.8	0.7

dW/dt (cm*d^{-1}) = daily weight gain, N = no of observations, R² = coefficient of determination, a,b,c = estimated parameters of the model, Min. = minimum, Max. = maximum, POI = point of inflection

Table 1B. Daily length gain as a function of actual body length

Strain	N observations	Fit	Parameters			Length (cm)			dL/dt (cm*d⁻¹)		
		R²	a	b	c	Min.	Max.	POI	Min.	Max.	POI
A♀	6583	0.38	5.71	0.0974	6.75	11.6	42.9	18.3	0.022	0.066	0.059
A♂	5584	0.41	9.29	0.0035	55.9	11.2	42.6	18.5	0.019	0.066	0.059
B♀	7128	0.32	11.8	0.1223	57.1	12.6	46.2	17.9	0.015	0.062	0.056
B♂	6134	0.35	6.33	0.1083	49.5	12.5	43.0	17.3	0.016	0.059	0.054

dL/dt (cm*d^{-1}) = daily length gain, N = no of observations, R² = coefficient of determination, a,b,c = estimated parameters of the model, Min. = minimum, Max = maximum, POI = point of inflection

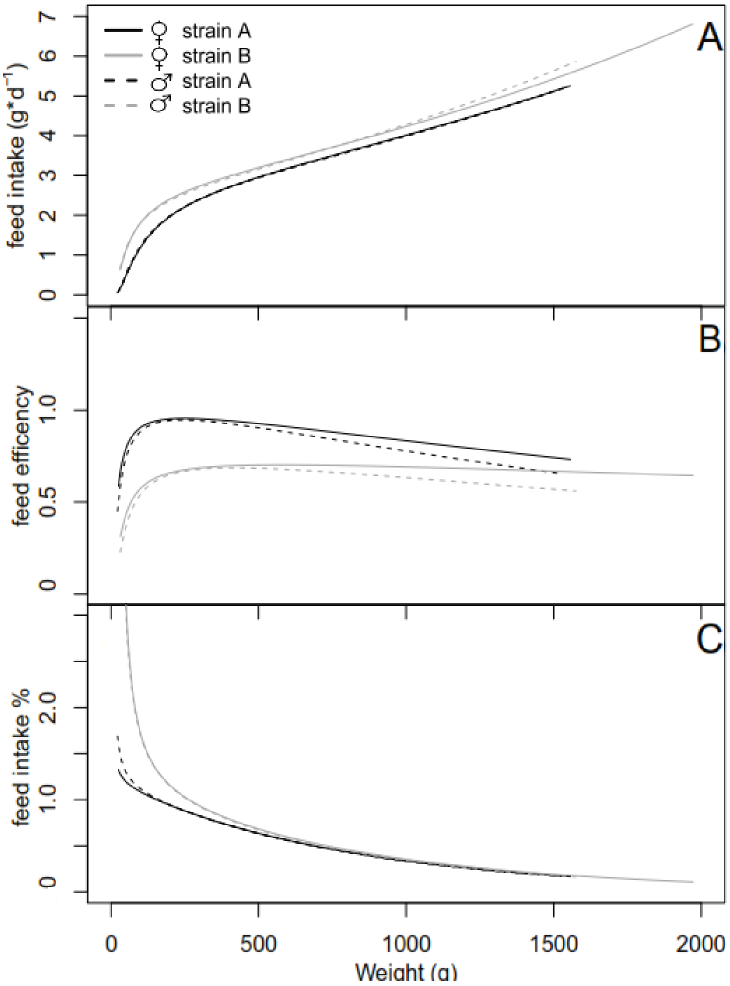

Figure 2. The course of daily feed intake (A), feed efficiency (B) and feed intake as % of live body weight (C), of both sexes of both strains of turbot reared in the trial.

data than it was in weight data. Differences in fit were minor between strains and sexes, with slightly higher values in males than in females. R^2 was 0.38 in females of strain A and 0.41 in males, respectively. In strain B R^2 was 0.32 in females and 0.35 in males (Table 1B).

The Course of Feed Intake

Feed intake data are presented as feed intake in g*d^{-1} (FI) (Figure 2A), feed efficiency (FE) (Figure 2B) and as % feed intake of actual body weight (FE%) (Figure 2C). A strong similarity between the feed intake curve (Figure 2A) and the daily weight gain curve (Figure 1A) can be recognized, indicating a strong correlation between feed intake and body weight**.** The curves can be subdivided into the same three segments as previously seen in the weight and length gain curves. The juvenile phase describes a steam linear increase in FI. This increase is almost similar in both strains involved in the trial. No difference in terms of sexes was detected in this segment of the curve. However, the diminishing return behaviour of the transitional phase is not as distinct in FI as it is in DWG. The FI curves of strain A also specifies a POI. At 47 g body weight in females and 44 g body weight in males. The FI curve of strain B does not comprise a POI. Both strains describe the same shape of FI curve although the magnitude differs, with strain B having constantly higher FI. In strain A no diversion of FI between the sexes could be defined during the experiment. In Strain B diversion in FI between sexes occur at approximately 1260 g body weight. Accordingly maximum FI is higher in females than it is in males (Table 2A). The model fitted well to the course of FI giving an R^2 of 0.93 for both sexes of strain A. Fit was somewhat lower in both sexes of strain B (R^2=0.80) (Table 2A).

The Course of Feed Efficiency

Within the course of feed efficiency (FE), we could again observe the three distinct phases. However, a significant difference in the magnitude of the curves was observed between the two strains, although the shape of was the same. In both strains FE increased rapidly in small fish, reflecting the juvenile phase. FE curves of both strains do not comprise a POI but a maximum (Figure 2B, Table 2B). This maximum was 95% FE in both sexes of strain A, while it was 70% in females of stain B and 69% in males, respectively. Accordingly, FE was about 25% lower in strain B than in strain A at a body weight of approximately 250 g. After the maxima (0.69% / 0.95%) (Table 2B), the FE curves follow a decreasing linear pattern (Figure 2B). This negative slope is steeper in strain A than in strain B and steeper in males than in females. The females of strain B keep a constant linear level of FE at approximately 70% while males of strain A have the steepest negative slope. Sexual diversion occurs at 502 g body weight in strain A and 510 g body weight in strain B. Altogether strain A seems to be more efficient in smaller individuals, while specimens of strain B are more efficient in larger individuals > 2000g. Females even out at a higher level of FE than males. R^2 values are lowest in this trait (0.13-0.19) (Table 2B).

Table 2A. Feed intake

Strain	**N observations**		**Fit**		**Parameters**		**Feed intake (g*d^{-1})**	
		R^2	a	b	c	Min.	Max.	POI
A♀	6583	0.93	2.88	-0.00045	93.1	0.07	5.3	0.4
A♂	5584	0.93	2.81	-0.00044	86.8	0.05	5.2	0.4
B♀	7128	0.80	2.79	-0.00046	43.3	0.7	6.8	n.d
B♂	6134	0.80	2.67	-0.00052	44.5	0.6	5.9	n.d

N = no of observations, R^2 = coefficient of determination, a,b,c = estimated parameters of the model, Min . = minimum, Max. = maximum, POI = point of inflection, n.d. = not defined.

Table 2B. Feed efficiency

Strain	N observations		Fit		Parameters		Feed efficiency	
		R^2	a	b	c	Min.	Max.	POI
A♀	6583	0.13	1.08	0.00024	14.9	0.58	0.95	n.d.
A♂	5584	0.16	1.12	0.00034	19.8	0.45	0.95	n.d.
B♀	7128	0.19	0.78	0.00009	29.1	0.31	0.70	n.d.
B♂	6134	0.15	0.84	0.00024	40.1	0.23	0.69	n.d.

N = no of observations, R^2 = coefficient of determination, a,b,c = estimated parameters of the model, Min . = minimum, Max. = maximum, POI = point of inflection, n.d. = not defined.

Table 2C. Feed intake (%) as a function of live body weight

Strain	N observations		Fit		Parameters		Feed intake (%)	
		R²	a	b	c	Min.	Max.	POI
A♀	6583	0.78	1.19	0.0013	-3.49	0.17	1.3	n.d.
A♂	5584	0.77	1.16	0.0143	-8.90	0.17	1.7	n.d.
B♀	7128	0.80	1.13	0.0013	-5.30	0.11	6.0	n.d.
B♂	6134	0.81	1.11	0.0020	-5.54	0.16	5.8	n.d.

N = no of observations, R² = coefficient of determination, a,b,c = estimated parameters of the model, Min . = minimum, Max. = maximum, POI = point of inflection, n.d. = not defined.

The Course of Feed Intake as % of Actual Body Weight

No differences in feed intake as percentage of actual body weight (FI%), could be found in any of the two strains in regards of sex. The maximum of all curves were determined at the very beginning in the smallest fish. FI% continuously decreased while fish grew. Fish of strain A have a lower feed intake as fish of strain B from 35 g body weight to 500 g body weight. After 500 g body weight no differences could be found regarding sexes nor strains. All fish level out at approximately 0.10 – 0.17 FI% when they exceed 1500 g body weight. The model fitted good to the course of this trait, giving R² values ranging between 0.77 and 0.81. However, values were a bit lower in strain A than they were in strain B (Table 2C).

Discussion

In aquaculture operations, growth output and feed intake are of major importance regarding cost-benefit analysis. Accordingly, feeding studies are of great relevance for the aquaculture sector. In such experiments, fish must be of equal sizes at the beginning of the trial, if results shall be analyzed via descriptive statistics. In contrast, growth models are not limited by equal initial sizes. When fitting a model to a set of data, the comparison of the growth curves is done via regression parameters used in the function (e.g. L_∞, k, Φ). Accordingly, modelling the course of a trait allows for different initial sizes and ages (Hopkins, 1992). Currently, the most frequent used models in analyzing fish growth are the von Bertalanfy growth model (Von Bertanlanffy, 1938), the Gompertz growth equation (Gompertz, 1825), and the Logistic function (Ricker, 1975), or the Schnute–Richards model (Schnute & Richards, 1990) (Katsanevakis, 2006). These functions have proven good suitability when displaying growth as a function of age (Lugert *et al*. 2016). However, all of these equations reflect the animal as an output system only (Parks, 1982). The feed intake is not taken into account. Accordingly, they are not suitable to describe the course of feed specific traits.

During the last decade, trait specific breeding programs and animal nutrition modelling have gained increasing interest in aquaculture research (see. Dumas, France, & Bureau, 2010). These approaches have first taken specific life-stages in aquatic species into account. Following the results of such studies, the aquaculture feed industry has developed specific feeds for certain life-stages in the most commonly reared fish species, for example rainbow trout (*Oncorhynchus mykiss*).

In turbot specific live-stages and according shift in habitats and feeding behavior are well documented in wild fish. Déniel (1990) points out that: “growth cannot be studied without investigating the general biology of the species”, as growth is rooted in specific physiological processes (Katsanevakis, 2006). Turbot are an oceanodromous species (Riede, 2004). They spawn during spring and summer (April – August) when water temperatures are high (Déniel, 1990). Eggs are pelagic and juveniles approach the shallow warm waters of the intertidal coastal zone, where they find sufficient amount of small pray items. As they grow and mature, the need for increasing pray items drives them towards deeper waters. All of our results document very distinct life-stages in turbot, which do reflect the natural life cycle of this species. However, no aquaculture study has yet taken this into account.

Kanis and Koops (1990) argue that in animal husbandry, it is more functional to display growth as a function of size rather than a function of age, as all environmental determinants and feed supply are controlled by human interaction. Though Arneri, Colella, & Giannetti (2001) describe changes in growth of turbot related to seasonal pattern, this does not apply when using RAS, where seasonal cycles do not occur. Accordingly, changes in traits and life stages are not only driven by age, or season, but also by actual size. The present study is a first approach to refer daily gain (DG), and feeding specific traits (FI and FE) to actual body size in different breeding lines of turbot grown in a RAS.

The course of such traits is commonly described using polynomial functions (e.g. Krieter, 1986). Although, polynomials can achieve adequate fit to such data, their parameters do not have biological meaning. In order to model the course of these interactions, we chose the nonlinear model $y = a * \exp(-b * x - c/x)$, provided by Kanis and

Koops (1990). This flexible function allows multiple shapes of curves and can therefore adequately describe the course of the different traits. The model also takes into account the "mathematical interrelationship between the traits daily gain, feed intake and feed efficiency" (Kanis & Koops, 1990: 72). Accordingly, FE can easily be derived through dividing DG by FI (Kanis & Koops, 1990). Especially this interaction between FI and DG is of great interest when the growth curve shall be shifted towards a more economical one (Krieter & Kalm, 1988).

In terms of goodness of fit, the model varied widely between strains, sexes within strains and the specific traits. The wide range of distribution within the data can explain the low fit of the model in some of the traits. Turbot is a very recently domesticated species (Bouza *et al*., 2007), which is known for huge variance in individual growth potential and distinct sexual dimorphism. Such individual growth differences are one of the major challenges for producers and breeders. Accordingly, not only growth output, but also feed intake varied massively between individuals, resulting in low fit of the model in such traits. In addition, the large amount of collected data advantages a wider distribution of data. The cloud of plotted data was mostly so dense and widely spread, that no general pattern could be determined visually. According to Kanis and Koops (1990), we modelled our data additionally via a 2nd degree polynomial function, which resulted in approximately the same fit (data not shown). This proves a wide dispersion of data as cause of low fit, rather than unsuitability of the chosen model. Our results approve the same suitability of the model for turbot data as findings of Kanis and Koops (1990) for pigs. In reverse, the large distribution of data indicates the necessity of profound and target orientated breeding programs.

All of our results document very distinct life-stages in turbot, which do reflect their natural life cycle. As all curves in each trait describe the same course, we conclude, that even tough, specific breeding can change the magnitude of a trait, the underlying biological principles, which determine the course and shape of a trait are still inviolated. Weight gain curves and length gain curves indicate a strong shift between juvenile and maturing fish including a point of inflection between 65 - 110 g life body weights (15.7 – 18.6 cm body length). Common recommendations regarding the switch from on-growth to out-growth of turbot in commercial aquaculture are set at this bound (50 – 100 g body weight) (Person-Le Ruyet, 2002; Bouza *et al*., 2014). This implies that hatcheries and breeders have knowledge about the point of inflection. Thus, little information regarding this has yet been published. Also the strong similarity between the feed intake curve and the weight gain curve, indicates a strong linear relationship between the two traits. Indeed, correlation between feed intake and weight gain was 0.8. However, no life-stage specific feed has yet been developed for turbot.

Our results also prove a distinctive sexual dimorphism, as generally described in this species (Robledo *et al*., 2015). However, only few studies focus on the diversion of growth characteristics related to this. Most literature refers sexual dimorphism to age, e.g. age at first maturation (Froese & Pauly, 2015) as it is generally of interest in fisheries studies. Since growth is known to differ between males and females (Imsland, Folkvord, Grung, Stefansson, & Taranger, 1997), most recommendations regarding breeding programs suggest monosex female breeding lines (Aydın, Küçük, Şahin, & Kolotoğlu, 2011; Bouza *et al*., 2014). Novel approaches target gene based analysis to determine sex in early stages (Robledo *et al*., 2015). As our results demonstrate, differences in growth and feed efficiency first appear at approximately 500 g body weight, independent of strain, implying enduring fundamental biological processes related to maturation. The exponential shapes of the DWG curve in females of strain B also indicates an increased development of gonads, which was also described by Imsland *et al*., (1997). The differences in growth and feeding patterns of the different life-stages and sexes can be linked to the ontogenetic shift in wild fish (Déniel, 1990), which is still present in domesticated specimen. A quick and reliable test for sexing and corresponding grading of sexes at specific size (approx. 500 g) could significantly increase the effectivity of turbot aquaculture.

Conclusion

Growth and growth-related traits are not linear nor isometric in turbot. The species undergoes massive morphometric changes throughout its life, which are strongly reflected in DG, FI and FE. Accordingly, results from studies with juvenile fish are intransferable to other life-stages. Findings cannot be extrapolated to larger or mature fish. Attention should be paid performing growth experiments in this species, due to the extended transitional phase these fish undergo. Sexual grading, adjusted feeding schedules and specific feeds for different life-stages could increase the efficiency of turbot rearing.

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