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Sorren Lund Hansen

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**SCOPE FOR ACTIVITY, SPECIFIC DYNAMIC ACTION
AND GROWTH IN EARLY JUVENILE STAGES
OF ATLANTIC COD, *GADUS MORHUA***

By

Søren Lund Hansen

B.S. Roskilde University (Denmark), 1999

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(in Marine Biology)

The Graduate School

The University of Maine

May, 2003

Advisory Committee:

Ione Hunt von Herbing, Associate Professor of Marine Sciences

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Pete Jumars, Professor of Marine Sciences and Oceanography

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An Abstract of the Thesis Presented
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Growth rates of early life stages of Atlantic cod (*Gadus morhua*) are very high, but decline, as the fish grow larger. Little is known about the physiological processes that facilitate and regulate this growth pattern. In this study, feeding and swimming metabolism were measured in individual juvenile Atlantic cod (*Gadus morhua*) in order to investigate how energy is allocated to swimming and growth in fast growing stages of fishes. Metabolic rates were measured by the means of oxygen consumption using two "Brett-type" respirometers. The metabolic measurements were repeated several times in individual juvenile Atlantic cod with a wet body mass of 0.5-5.0 g over a period of 100 d. Wet body mass and total length of individual cod were measured biweekly during the

experimental period and used together with metabolic measurements to determine the relationship between energy utilization and growth.

The study consisted of two parts, 1) determination of aerobic scope for activity (the difference between standard and active metabolism), and 2) measurement of specific dynamic action (SDA, which represents the energy expenditure for ingesting, digesting, absorption of foodstuff, biochemical transformation of nutrients and assimilation of proteins).

Power-performance relationships between oxygen consumption and swimming speed were established for juvenile Atlantic cod for the first time. Standard metabolic rate (R_s) and active metabolic rate (R_a) were calculated from the power-performance relationships by extrapolating to zero swimming speed and maximum sustained swimming speed, respectively. Scope for activity was calculated as the difference between active and standard metabolism ($R_a - R_s$). SDA duration, amplitude and magnitude were calculated by measuring oxygen consumption of fed and unfed fish swimming at a low cruising speed.

Specific growth rates (G) ranged from 1.4 - 4.4% wet body mass d^{-1} and decreased with increasing body mass. Scope for activity ranged from 10.2 to 40.7 $\mu\text{mol O}_2 h^{-1}$ for juvenile cod with a mass of 0.53-2.89 g. Scope for activity increased with increasing body mass, while mass-specific scope for activity ($\mu\text{mol O}_2/M$) decreased with increasing body mass. SDA peaked within 1 h after feeding for juvenile cod with a wet body mass of 0.45-4.20g, and peak values were 1.12-2.22 times the unfed values. SDA duration for juvenile Atlantic cod ranged from 2 to 8 hours. SDA magnitude ranged from 2.8 to 60.0 $\mu\text{mol O}_2$ and increased with increasing wet body mass. Relative magnitude of

SDA (percentage of the energy value of the ingested food) was found to be 0.18-3.84%.

SDA amplitude accounted for 14.8-44.0% of the scope for activity.

Results from this study suggest that the swimming and feeding metabolism in early stages of juvenile Atlantic cod differs from that of larger juvenile and adult cod. Major physiological differences include higher specific growth rates, shorter time to peak SDA, shorter SDA duration, lower relative SDA magnitude and a smaller portion of scope for activity taken up by SDA. Physiological differences among early juvenile and adult cod may be the result of the metabolic demand for high growth rates in small juvenile cod. Further research is needed to determine the physiological differences and the underlying mechanisms for different life stages of Atlantic cod and other temperate fishes.

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CHAPTER 1

INTRODUCTION

Atlantic cod

Atlantic cod (*Gadus morhua*) has been a commercially important finfish for centuries (Kurlansky, 1998). Extensive fishing on Georges Bank during the 60s caused a decline of the stock, which has not yet recovered (Campana *et al.*, 1989). Much research effort has been expended in order to understand the factors that influence yearly fluctuations in recruitment (Lough *et al.*, 1985; Campana *et al.*, 1989; Auditore *et al.*, 1994; Werner *et al.*, 1999). According to Lough *et al.*, (1985), fluctuations in year-class strength are strongly influenced by processes operating during the first year of their life. Factors affecting growth and survival during the early juvenile stages may particularly influence year-class success (Campana *et al.*, 1989; Tupper & Boutilier, 1995a,b).

Growth and survival are closely linked in Atlantic cod and other fishes (Pepin, 1991). Small fish are more vulnerable to predation than large fish, and high growth rates therefore increase the likelihood of survival by reducing the exposure time of being small. Growth rates during early life stages of Atlantic cod (*Gadus morhua*), as in all fishes, are very high but decline as the fish grow larger. Little is known about the physiological processes that facilitate and regulate this growth pattern.

Though many physiological studies have been performed on cod eggs and larvae (Laurence, 1978; Hunt von Herbing & Boutilier, 1996; Hunt von Herbing *et al.*, 2001; Finn *et al.*, 2002), as well as large juvenile and adult cod (Sundnes, 1957; Saunders, 1963; Edwards *et al.*, 1972; Soofiani & Hawkins, 1982; Soofiani & Preide, 1985; Tang *et al.*, 1994; Claireaux *et al.*, 1995; Houlihan *et al.*, 1995; Reidy *et al.*, 1995; Nelson *et al.*,

1996; Schurmann & Steffensen 1997, Reidy *et al.*, 2000), only few studies have been performed on early juvenile cod (Hunt von Herbing & White, 2002; Peck, 2003). This is likely due to difficulties in captive rearing, as well as difficulties in catching and transporting wild juvenile cod (Peck, 2003). The last decade's effort in rearing Atlantic cod in an aquaculture setting has provided access to larval and early juveniles stages of Atlantic cod, and thereby made metabolic measurements of these stages possible. Metabolic measurements of early juvenile Atlantic cod could enable the development of bioenergetic models for juveniles. Such models are already in use for adult cod in fisheries as well as aquaculture to predict growth rates and food utilization (Krohn *et al.*, 1997).

The aim of this study is to bridge the gap between metabolic measurements made on larvae and adult Atlantic cod by measuring the feeding and swimming metabolism of early juvenile cod. This bridge will help expand understanding of how Atlantic juvenile cod utilize and allocate energy for growth and metabolism and how this energy allocation changes with body mass.

Energy for growth

Bioenergetics involves the investigation of energy expenditure, losses, gains and efficiency of transformation within the body (Brett & Groves, 1979; Jobling, 1994). Energy enters the fish in the form of food, which changes form chemically (usually to ATP) by oxidation, and is used in a variety of metabolic processes. It is of critical importance to understand how energy is allocated to growth and metabolic processes in order to estimate energy conversion efficiency and predict growth rates. Many authors

have proposed balanced energy equations that quantify various metabolic components of metabolism in fishes (Winberg, 1956; Kleiber, 1961; Paloheimo & Dickie, 1966; Warren & Davis, 1967; Brett & Groves, 1979). However, the interactions between the various components in the energy equation in relation to growth and swimming activity are not yet fully understood.

Bioenergetic transfer of energy conforms to the first law of thermodynamics called “conservation of mass”, which states that energy cannot be created nor destroyed, but can be changed from one form to the other (Kleiber, 1961). Therefore, the ingested energy (I) has to turn up through metabolism (R), growth (G) or excretion (E) (Brett & Groves, 1979). In a simplified form the energy equation is:

$$I = (R_s + R_{SDA} + R_a) + (G_s + G_g) + (E_f + E_u + E_s)$$

Where R_s , R_{SDA} and R_a are standard metabolism, feeding metabolism (specific dynamic action) and active metabolism respectively. G_s is somatic growth and G_g is gamete production. G_g is not a consideration in juvenile cod, due to their immature stage. E_f , E_u and E_s are energy lost due to excretion of feces, urea and ammonia, and loss of surface materials (mucus and sloughed epidermal cells) respectively. The prediction of somatic growth is of great importance in fisheries biology as well as aquaculture. It is useful to rearrange the bioenergetic equation to measure somatic growth as follows:

$$G_s = I - (R_s + R_{SDA} + R_a) - (G_g) - (E_f + E_u + E_s)$$

This study will focus on aerobic metabolism (R_s , R_{SDA} , and R_a) in the energy equation and will investigate how energy may be allocated for swimming activity and growth in juvenile Atlantic cod.

Metabolism

Metabolic energy can be divided into 3 categories 1) standard metabolism (R_s), which is the minimum required energy to maintain basic body functions, 2) active metabolism (R_a), which is energy loss associated with swimming activity and 3) specific dynamic action (R_{SDA}), which is energy expenditure associated with feeding (see section on specific dynamic action for a more detailed description).

Standard metabolism

Standard metabolic rate (R_s) is defined as the minimal observed post-absorptive metabolic rate of poikilothermic animals (Krogh, 1914; *as cited in* Brett and Groves, 1979). Standard metabolism represents the minimum rate of energy expenditure to keep the organism alive. This energy expenditure is used by respiratory and circulatory systems, as well as cellular maintenance functions like ion regulation and transport (Blaxter, 1989). The term is important in bioenergetics, because energy requirements for standard metabolism have to be fulfilled before any additional energy can be allocated for swimming and growth (Brett & Groves, 1979).

Due to early technical difficulties in measuring standard metabolism in fish different methodologies were developed, and consequently a number of terms exist that have all been used as synonyms to describe the “minimal metabolism of fish”. These

terms include, standard metabolism, basal metabolism, resting metabolism, least observed metabolic rate and low routine metabolism (Jobling, 1994). No definition of “minimal metabolism” has to date been universal accepted, but the term standard metabolism is most recognized (Jobling, 1994).

It remains a challenge to measure the metabolism of a fish at rest. However the introduction of tunnel respirometers by Brett (1964) in the 1960s allowed oxygen consumption to be determined as a function of swimming speed, and standard metabolic rate could be calculated by extrapolating back to zero swimming speed.

Active metabolism and aerobic scope for activity

Active metabolic rate (R_a) represents the maximum aerobic metabolism. Active metabolism is most often measured at the highest sustainable swimming speed (Brett & Groves, 1979), since locomotion is metabolic costly for fish in comparison with the metabolic cost of maintenance and feeding (Tang *et al.*, 1994).

The difference in energy expenditure between standard and active metabolism is normally referred to as “the aerobic scope for activity” (Fry, 1947; *as cited in* Brett & Groves, 1974). This term is thought to represent the energy available to the organism for energy demanding processes like swimming activity, feeding and digesting, reproductive effort, foraging, etc. (Brett & Groves, 1979; Jobling, 1994). Aerobic scope for activity may therefore give information about the condition of the fish as well as the potential for growth, swimming and other processes leading to increased fitness.

True aerobic scope for activity has not been estimated for early juvenile cod in the range of 1-10 g wet body mass (wbm). Hunt von Herbing & White (2002) estimated

relative scope for activity ($R_a - R_r$ (routine metabolism)) in early juvenile cod with a mass from 1.0-8.0 g. Hunt von Herbing & White (2002) used low routine values in the calculation of relative scope for activity, which may have underestimated true aerobic scope for activity. To calculate the true scope for activity a relationship between swimming speed and oxygen consumption has to be established for early juvenile cod. One of the objectives of this study is using tunnel respirometers to establish power-performance relationships between oxygen consumption and swimming speed for early juvenile cod. This will allow the estimation of standard metabolism for the first time in early juvenile cod.

Specific dynamic action

SDA will be quantified and examined for early stages of juvenile Atlantic cod in this study. An increase in metabolic rate after an ingestion of a meal was first discovered and quantified around 1780 by Lavoisier and Laplace (Brown & Cameron, 1990) and the phenomenon was in 1902 termed “specific dynamic effect” by Rubner (*see* Kleiber, 1961). The phenomenon was later renamed “specific dynamic action” (SDA), the heat increment, the calorogenic effect or the thermic effect of feeding (Garrow, 1974). SDA, now the most commonly used term, is believed to represent the energy expenditure in relation to nutritive processes including the energy expenditure for ingesting, digesting, absorption of foodstuff, biochemical transformation of nutrients and assimilation of proteins (growth) (Jobling, 1981; Beamish & Trippel, 1990; Brown & Cameron, 1991). Recent research has shown that the synthesis of proteins is a major component of SDA (Brown & Cameron, 1990; Carter and Brafield, 1992; Lyndon *et al.*, 1992; Houlihan *et*

al., 1995). Brown & Cameron (1990) found a correlation between increased oxygen consumption and increased protein synthesis in the channel catfish (*Ictalurus punctatus*), following infusion of an essential amino acid mixture. The increase in oxygen consumption associated with the infusion of the amino acid mixture stopped after pre-treatment with the protein synthesis inhibitor cycloheximide (Brown & Cameron, 1990). This indicated that a cause and effect relationship might exist between SDA and protein synthesis.

Three variables define SDA; 1) SDA duration, which is the time from a post-prandial (following a meal) increase in oxygen consumption is observed after the ingestion of a meal and until the post-prandial oxygen consumption reaches the pre-feeding level, 2) SDA amplitude, which is the difference between the fed and unfed oxygen consumption of the fish, 3) SDA magnitude, which is the total amount of oxygen used for processing the meal (Fig. 6)

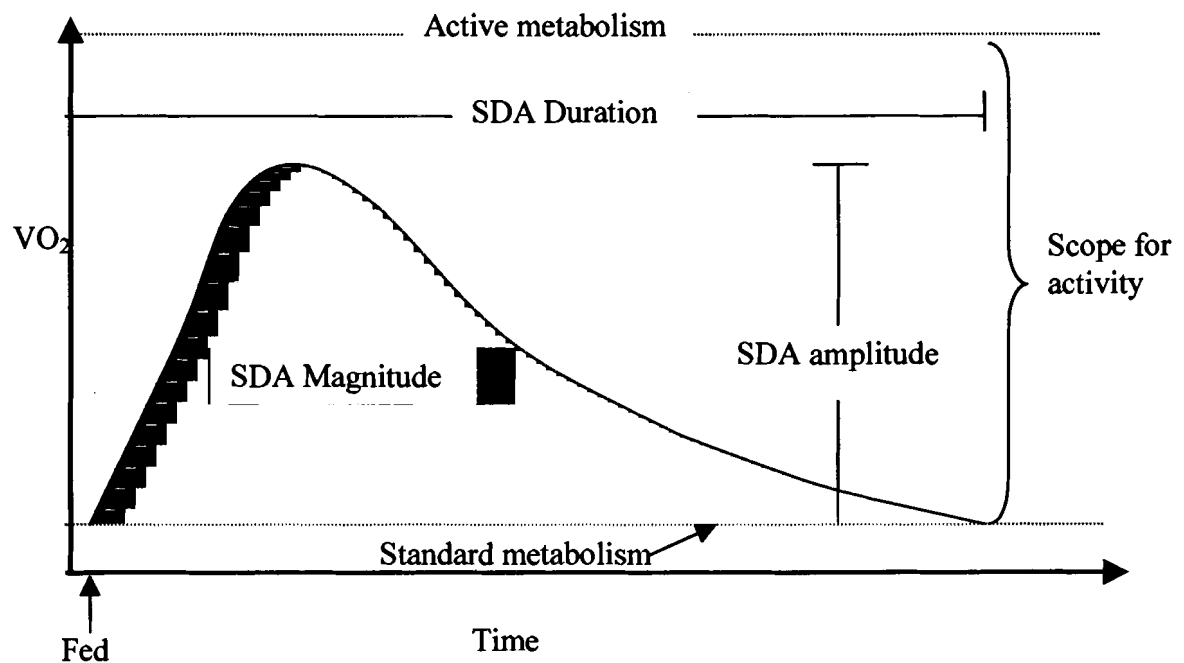


Figure 6. Schematic illustration of SDA

Various factors may influence the magnitude, amplitude and duration of SDA. These factors include meal size and meal composition (Muir & Niimi, 1972; Beamish, 1974; Tandler & Beamish, 1979; Vahl & Davenport, 1979; Jobling & Davies, 1980; Soofiani & Hawkins, 1982), temperature (Saunders, 1963; Jobling & Davies, 1980; Soofiani & Hawkins, 1982), and fish size (Jobling, 1981).

SDA can take up a significant portion of the aerobic scope for activity (Soofiani & Hawkins, 1982; Soofiani & Priede, 1985; Houlihan *et al.*, 1988; Alsop & Wood, 1997), which may limit further foraging, reduce swimming capacity and predator avoidance capability (Vahl & Davenport, 1979; Brown & Cameron, 1990). Oxygen consumption after a meal increased to 60-80% of the maximum rate of oxygen consumption (R_a) in juvenile rainbow trout (*Salmo gairdneri*) (LeGrow & Beamish, 1986). Soofiani and Hawkins (1982) showed that SDA could take up as much as 98% of the aerobic scope for activity in large juvenile Atlantic cod (29.3-82.9 g).

Ideally SDA should be measured as the increase of postprandial oxygen consumption over standard metabolic rate. This is technically difficult to achieve because it requires measurements of oxygen consumption of fed and unfed fish at zero swimming activity. Consequently, SDA is often measured in fish at low routine swimming speeds (see the “section specific dynamic action” in the discussion for more details). In the present study, tunnel respirometers were used for the first time to measure the feeding metabolism of early juvenile cod. SDA was calculated from measurements of oxygen consumption of fed and unfed juvenile cod swimming at controlled low routine swimming speed.

Objectives

This study investigates aspects of the aerobic metabolism of individual juvenile Atlantic cod (*Gadus morhua*). Different metabolic variables will be measured using respirometry to explore how energy is directed toward growth and activity in fast growing stages of Atlantic cod. The study will consist of two parts, 1) determination of aerobic scope for activity, and 2) measurements of SDA. All experiments will be carried out at a temperature of 10°C.

Power-performance relationships between oxygen consumption and swimming speed will be established for the first time in early juvenile Atlantic cod. Standard and active metabolism will be determined from these power-performance relationships by extrapolating back to zero swimming speed and up to maximum sustained swimming speed, respectively. Aerobic scope for activity will then be determined as the difference between standard and active metabolism.

SDA will be determined for individual juvenile cod by measuring the post-prandial increase in oxygen consumption. SDA amplitude, duration and magnitude will be determined for each experiment.

Wet mass and total length of individual cod will be measured every 2 wk over the 100 d experimental period and specific growth rates will be calculated.

Objectives of this study include:

- 1) Establish power-performance curves over swimming speed and oxygen uptake for individual juvenile Atlantic cod *Gadus morhua* in the size range 0.5 g- 4.0 g.

- 2) Determine standard metabolism (R_s), active metabolism (R_a), and the aerobic scope for activity in individual juvenile Atlantic cod.
- 3) Determine the specific dynamic action (SDA) for activity in individual juvenile Atlantic cod, *Gadus morhua* in the size range 0.5- 4.0 g, including amplitude, duration and magnitude of SDA.
- 4) Find the relative magnitude of SDA (SDA magnitude expressed as a percentage of the energy value of the ingested food)
- 5) Investigate the relationships between body mass, specific growth rates, aerobic scope for activity and SDA in early juvenile cod.
- 6) Explore the relationship between aerobic scope for activity and SDA (how much of the aerobic scope for activity is taken up by SDA?)

CHAPTER 2

MATERIALS AND METHODS

Hatching procedure and larval rearing

Fertilized cod eggs were obtained from the National Marine Fisheries Service (NMFS) in February 2001. The cod eggs were spawned from broodstock fish, which originated from Great South Channel in the Gulf of Maine. The eggs were transported 5 h from the Narragansett lab in Rhode Island to the Aquaculture Research Center (ARC) located on the University of Maine campus. The eggs were disinfected with a 200 ppm glutaraldehyde solution and placed in 75-L incubators containing artificial saltwater (Crystal Sea[®] Marine mix) at a temperature of $8.0 \pm 0.5^{\circ}\text{C}$ and salinity of 32.0 ± 1.0 ppt (parts per thousand). After hatching the cod larvae were transferred from the incubator to a recirculating larval rearing system for 109 d. During the larval rearing period the illumination was constant at 100 lux. Water temperature was adjusted gradually to $10.0 \pm 0.5^{\circ}\text{C}$. Larvae were fed live rotifers (*Brachionus plicatilis*) six times a day from 1 to 22 days post hatch (dph), then weaned to brine shrimp (*Artemia* sp.) and finally to microparticulate diet (MPD) by day 50. The MPD was a commercial diet (BioKyowa C[®]), and larvae were fed different pellet sizes ranging from 250 to 1000 μm according to the size of fish.

Juvenile rearing

At 109 days post hatch (dph), 250 juvenile cod were transferred to a 660-L juvenile holding system at the ARC where they were held during the 100 d experimental period (Fig. 1). The water in this system was kept at a temperature of $10.0 \pm 0.5^{\circ}\text{C}$ and a salinity of 30.0 ± 1.0 ppt.

A 2-wk acclimation period was provided before starting the experiments in order for the juvenile cod to adjust to the tank size, light conditions and feeding regime. Illumination was adjusted to 200 lux (measured by SPER Scientific light meter) and a photoperiod of 16 h light and 8 h darkness. During the 2-wk acclimation period the feeding schedule was adjusted to 5 daily feedings (7 AM, 11AM, 3 PM, 6 PM and 10 PM). Food pellet size was changed from 700 to 1000 μm . The cod were fed to satiation at every meal by adding a few pellets at a time by hand until all fish stopped feeding.

Juvenile holding system

The juvenile holding system consisted of twenty 20-L black tanks. The system had a total capacity of 660 L. Water was supplied from a 72-L head tank and distributed to each tank via PVC pipes and ball valves. Air-diffusers were provided to each tank to ensure sufficient oxygen concentration as well as water circulation. The water level in the tanks was regulated by standpipes, which allowed water to exit the tank and drain into a 240-L sump. Water was then pumped from the sump to the head tank by a $\frac{1}{2}$ hp centrifugal pump (TEEN model 4RJ85) and re-circulated back to the tanks.

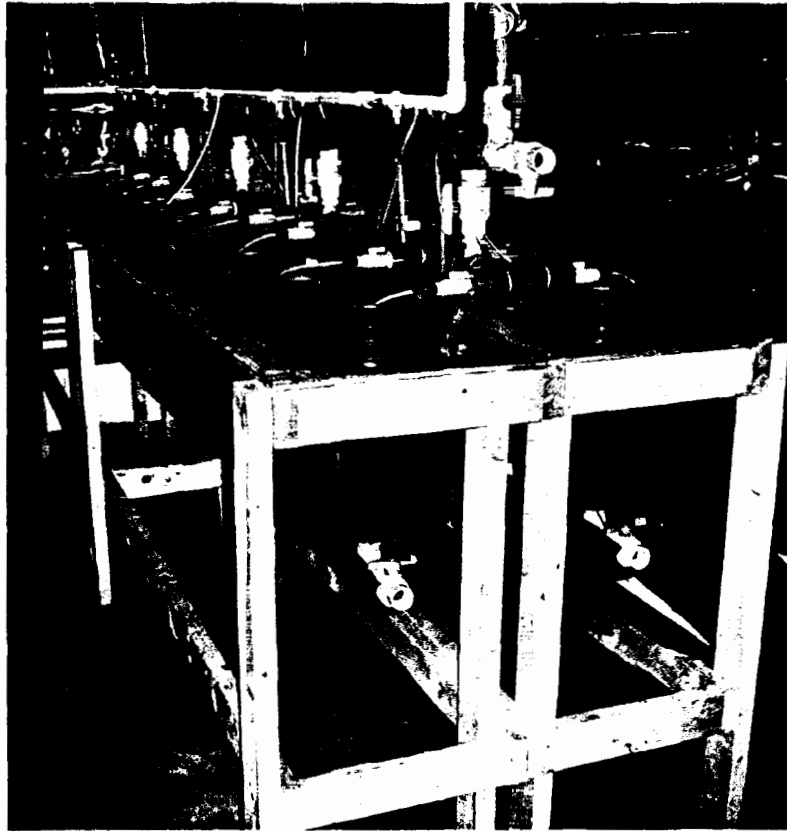


Figure 1. Juvenile holding system.

Water temperature was kept at $10.0 \pm 0.5^{\circ}\text{C}$ by two 1/3 horsepower chillers (AQUANETICS model AFC-4A).

Water quality

A number of different filters were incorporated into the recirculating system to maintain good water quality during the experimental period.

Biological filtration

Shredded PVC material was added to the sump and head tank to provide a large surface area for nitrifying bacteria. Nitrifying bacteria convert ammonia to nitrite, and nitrite to nitrate. This bacterial process called nitrification is crucial in any recirculating

system because it converts toxic by-products like ammonia and nitrite to the less harmful nitrate.

UV-sterilizer

Two UV-sterilizing units (AQUA ultraviolet) reduced bacteria and pathogens in the water. These units were mounted immediately downstream of the head tank so the water was sterilized before entering each tank.

Mechanical filtration

Two mechanical filtration units were installed between the sump and the head tank to filter out particulate matter. These units had filter cartridges with pore sizes of 50 and 25 μm . Filter cartridges were replaced every 2-wk.

Protein skimmer and ozone

A protein skimmer was designed and incorporated in the system. This device traps organic matter at an air-water interface. Many organic compounds are of a bipolar nature and therefore tend to “stick” to the air-water interface. A foam of organic matter is formed and extracted in a skimmer cup. The major advantage of the protein skimmer is that organic matter (OM) is removed from the water before it breaks down and adds to the load of dissolved organic matter (DOM). Maintaining DOM at a low level in the recirculating system is beneficial for several reasons: 1) reduction of bacteria growth due to a lower level of OM and DOM, 2) reduction of bacterial oxygen demand (BOD), which facilitates a higher and more stable oxygen concentration in the system, 3) more

stable pH of the water, because of reduced bacterial respiration (CO_2 expired from respiration causes a drop in pH) and, 4) reduces the risk of bacterial infections.

An ozone generator (APOKA) was connected to the protein skimmer to further help the skimming process as well as to sterilize the water. Water exiting the protein skimmer flowed through activated carbon, which absorbed any excess ozone as well as any leftover organic matter.

Water quality parameters

Water quality parameters were measured every day to ensure that good water quality was maintained throughout the experimental period. The following parameters were measured daily: 1) oxygen, 2) pH 3) temperature and, 4) salinity. Ammonia and nitrite were measured every other day. Oxygen, salinity and temperature were measured with a multi-meter (YSI 85) with a precision of $\pm 2.0\%$, ± 0.1 ppt and $\pm 0.1^\circ\text{C}$ respectively. Ammonia and nitrite were measured with a HACH test kit, which had a precision of $\pm 0.05 \text{ mg l}^{-1}$; pH was measured with a HACH pH meter (EC 30 benchtop) with a precision of ± 0.02 .

Environmental parameters were as follow: 1) oxygen concentration = $8.07 \pm 0.52 \text{ mg l}^{-1}$ ($\pm \text{SE}$), 2) pH = 8.0 ± 0.2 ($\pm \text{SE}$), 3) salinity = 30.55 ± 0.85 ppt ($\pm \text{SE}$), and 4) temperature = $10 \pm 0.4^\circ\text{C}$ ($\pm \text{SE}$). Ammonia and nitrite levels never exceeded values of 0.05 mg/l and 0.09 mg/l respectively.

Experimental setup

Respirometry system

Two identical closed Brett-type respirometers were used to measure metabolic variables (Fig. 2). The swim tunnel was built of Plexiglas and consisted of a swimming chamber and two end pieces (Fig. 2). The end pieces were conical and designed to suppress turbulence in the swimming chamber. The internal diameter of the swimming chamber was 50.8 mm and the length was 181.9 mm. Steel screens between the swimming chamber and the two end pieces reduced the magnitude of velocity perturbations and secondary circulations, produced a uniform velocity profile in the swimming chamber and confined the experimental fish in the swimming chamber. One respirometer was used for SDA experiments only and the other for scope for activity experiments only. Volumes of the SDA respirometer and the scope for activity respirometer were 1195 and 1140 ml, respectively.

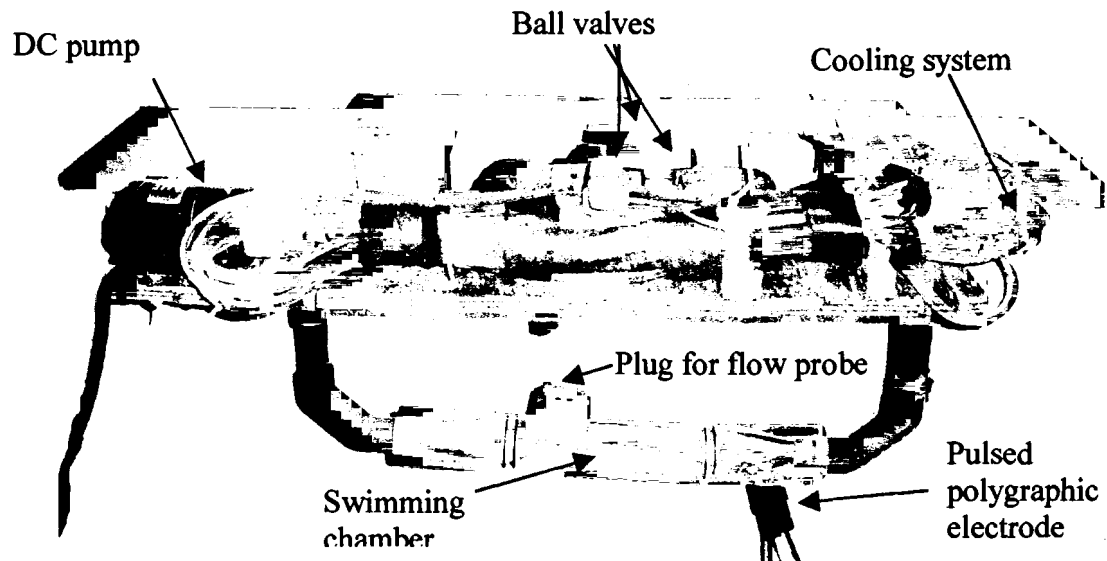


Figure 2. Brett-type respirometer used for metabolic measurements of juvenile cod

The velocity of water flowing through the swimming chamber could be adjusted from 4.26 ± 0.05 to $26.40 \pm 0.29 \text{ cm s}^{-1}$ (\pm SE) by a direct current magnetic drive pump (Cole Palmer, 316 SS) connected to a variable transformer (VARIAC).

Two pulsed polarographic oxygen electrodes (Endeco Inc.) were placed in the downstream plexiglas endpiece via custom-built inserts (Fig. 2). Temperature sensors with a precision of $\pm 0.01^\circ\text{C}$ were built into the oxygen probes.

The respirometers were operated by three ball valves (Hayward $\frac{3}{4}$ ") positioned at the top of the respirometer. These ball valves could be positioned in two modes: 1) "closed" position, where water circulated in a closed loop in the respirometer, and 2) "open" position, where water flowed from the respirometer tank to the respirometer, flowed through the respirometer and finally was discharged back into the respirometer tank. The open position was used to supply a constant flow of oxygenated water to the juvenile cod during the 12-h acclimatization period prior the initiation of the experiment. The closed position was used when the experiments were in progress. Oxygen consumption of the juvenile Atlantic cod was calculated by measuring the decrease of the oxygen concentration in the water over time.

Each respirometer was partly submerged into a tank (Fig. 3), which served two functions, 1) to control the water temperature in the respirometer, 2) to supply oxygenated water during the acclimation period. The two tanks were connected to a recirculating system to keep good water quality and stable temperatures during the experiments.

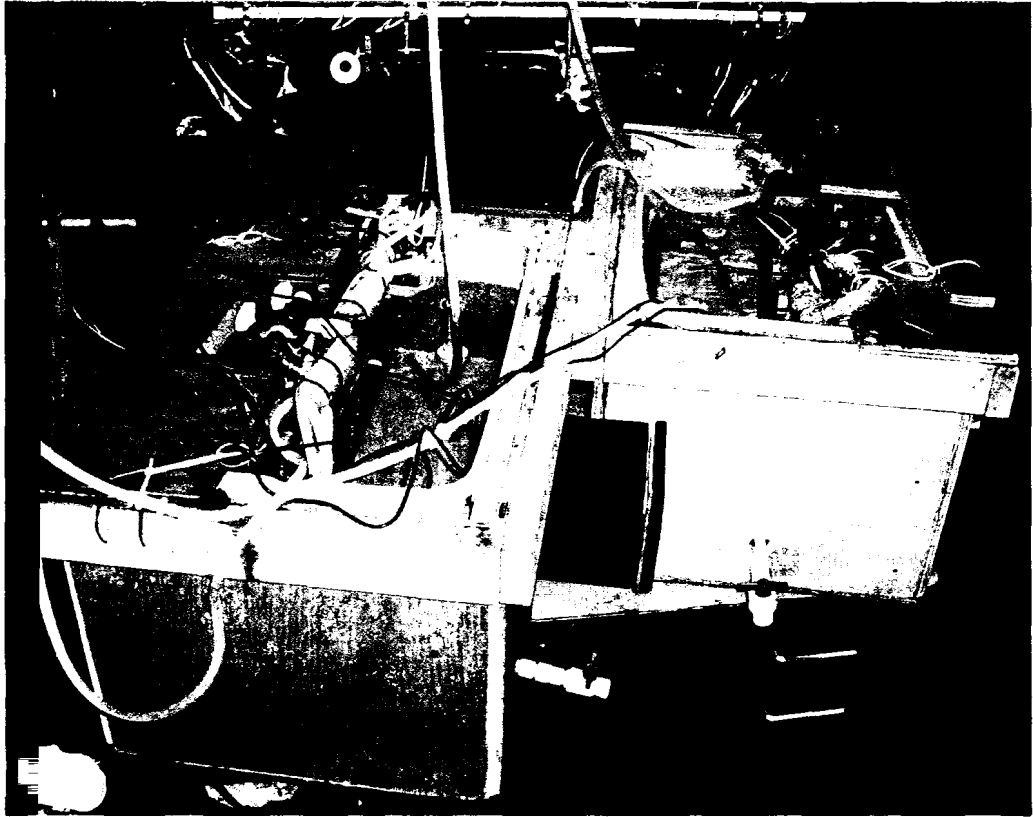


Figure 3. Respirometers partly submerged in the cooling tanks.

Each tank was equipped with a plexiglas window to allow video recording of the swimming cod during experiments. An insulated box held the video camera safely, prevented fogging of the lens and kept light from entering the tank through the window (Fig. 3). The video camera was connected to a monitor so swimming behavior, or any unusual behavior, of the juvenile cod could be observed without disturbing the experimental fish.

Flow rate determination

Flow rates in the two respirometers were measured with a low-speed flow probe (Streamflo probe, Nixon Instrumentation Limited). The flow probe was placed via a custom built insert (Fig. 2) in the top of the swimming chamber. Water velocity was measured in the center of the swimming chamber approximately 2.5 cm anterior to the stainless steel mesh at the inflow side of the swimming chamber. This was also the position where the cod would swim during the experiments. A total of 100 readings were recorded for each speed. Flow rates were measured at 18 different speeds ranging from 4.26 ± 0.05 to 26.40 ± 0.29 cm s⁻¹ (\pm SE).

Cooling system for respirometers

Frictional heat from the magnetic drive pump in the respirometer caused the water temperature in the respirometer to increase, which led to supersaturation of the dissolved air. This process forced dissolved oxygen out of solution, which resulted in a drop in the dissolved oxygen concentration. The pump produced more heat at higher speeds, resulting in a higher degree of supersaturation. Having the respirometers partly submerged in the 10.0°C water was not enough to eliminate supersaturation of the water in the respirometers.

An additional cooling system was added to compensate for the heat output from the DC pump and thereby reduce background oxygen consumption. This was done by coiling 30 feet of silicone tubing (3/8" ID X 1/16 wall) around the exposed part of the respirometer (see Fig. 2). The hose was attached to a temperature bath (EXACAL NESLAB) connected to a chiller (ENDOCAL 350). Cooling fluid (ethylene glycol) was

pumped from the temperature bath through the cooling tubing and back. The temperature of the ethylene glycol in the temperature bath could be adjusted from -50°C to +150°C. The temperature was adjusted for each speed, because a higher cooling effect was necessary at higher velocities. This method proved successful in compensating for the heat input into the water in the respirometer to $\pm 0.4^{\circ}\text{C}$ (\pm SE), which was sufficient to maintain stable background oxygen consumption.

Recirculating system for respirometry setup

The respirometer tanks were connected to a recirculating system, which was independent from the juvenile holding system. This recirculating system consisted of a 72-L head tank, a 200-L sump, a ½ hp chiller (AQUANETICS model AFC-5b) and a ½ hp centrifugal pump (TEEL model 4RJ85). The total volume of the system was 552 L. A number of filters were added to the recirculating system to ensure good water quality and thereby keep bacterial oxygen demand (BOD) at a low level. Three mechanical filters (AQUANETICS model 105) in serial connection filtered the water down to 16 μm and a UV-sterilizer (AQUANETICS model 30IL) reduced bacterial activity. A filter bag with activated carbon was added to the sump to removed organic matter from the water. Water quality was measured at the same intervals and with the same equipment as described under the juvenile holding system. Environmental parameters were kept at the same levels as the juvenile holding system to reduce stress caused by moving the fish to a different system when conducting the experiments.

Oxygen electrodes

Two pulsed polarographic oxygen electrodes were connected to each respirometer, which ensured that the electrodes were in good working order and gave stable and consistent readings. The electrodes were attached downstream from the swimming chamber with the end of the probes flush with the internal wall of the respirometer (Fig. 2). This prevented any air bubbles from interfering with the electrodes and maintained a laminar flow over the Teflon membranes.

The oxygen electrodes were connected to a laptop PC via a control unit (type 1125 pulsed D.O. sensor controller). Oxygen readings were taken every two minutes during experiments and automatically downloaded onto a spreadsheet. There was a 2-s lag between successive readings of the four oxygen electrodes, so the electric pulse emitted at the time a reading took place would not interfere with other oxygen electrodes.

To ensure good performance and precision of the oxygen electrodes, all Teflon membranes and the electrolyte solution were replaced before experiments started. The oxygen electrodes were tested for leakage and error with a digital multimeter (Radio Shack model 22-666B). The electrodes were then calibrated with a four-point calibration using a temperature bath (EXACAL NESLAB) in connection with a chiller (ENDOCAL 350). The four points in the calibration were; 1) 5°C – 100% air saturation, 2) 5°C – 0% air saturation, 3) 15°C – 100% air saturation, and 4) 15°C – 0% air saturation. Nitrogen gas was used to flush all oxygen for the 0% air saturation. The electrodes proved to be stable after the 4-point calibration and drifted only a couple of times during the experimental period. When drifting of the electrodes was observed, a two-point calibration was done to correct the error.

Procedures for SDA experiments

Fish used for SDA experiments

SDA experiments were carried out on individual cod over a 100-d experimental period. A total of 6 individual cod were used for the measurements of SDA. Each fish went through 2-3 SDA experiments as well as 1-2 unfed controls over the 100-d experimental period. Individual cod had a 14-d recovery period between each experiment. A total of 15 SDA experiments and 11 unfed control experiments were conducted over 100 d.

Feeding and transfer to the respirometer

Prior to each SDA experiment the fish were starved for 48 h. Starvation time was determined based on gastric evacuation time (see section on gastric evacuation time). On the day of the experiment, the cod were fed to satiation in the juvenile holding system with food pellets (BioKyowa C[®], 1000 µm pellets) 10 min before being introduced to the respirometer. Ideally, juvenile cod would have been transferred to the respirometer 12 h prior to the experimental start to allow longer acclimation. However this was not possible because the juvenile cod would not eat in the respirometer. After the 10-min feeding period the juvenile cod was carefully caught by gently guiding the fish into a 1000-ml beaker, which was submerged into the tank. The fish was moved from the juvenile holding system in the 1000-ml beaker, and transferred to the swimming chamber by: 1) detaching the swimming chamber from the two end-pieces, 2) detaching the stainless steel mesh of one end of the swimming chamber, 3) holding the swimming chamber at a 45° angle partly submerged in the respirometer tank, 4) gently pouring the

water and cod from the 1000-ml beaker to the swimming chamber, 5) re-attaching the stainless steel mesh, 6) carefully attaching the swimming chamber to the two end pieces and making sure that no air bubbles were trapped in the swimming chamber, and 7) starting the magnetic drive pump. This 7-step procedure took about 2 min. Swimming speed for the SDA experiments was $4.26 \pm 0.05 \text{ cm s}^{-1}$, which was the slowest speed where the juvenile cod would swim continuously and allowing sufficient speed to ensure mixing and uniform distribution of oxygen in the water.

Respirometer operation for SDA experiments

The respirometer was adjusted to the “closed position” immediately after the transfer of the juvenile cod, and the experiment was started. The first 10 min of data were discarded to reduce errors related to stabilization of the oxygen electrode as well as any stress of the juvenile cod induced by the transfer from the juvenile holding system to the respirometer.

Oxygen measurements were taken every 2 min over a time period of 12 h, which was sufficient time for the SDA to peak and return to pre-feeding metabolism for all the juvenile cod tested. Flushing periods were introduced to replenish oxygen in the respirometer if oxygen levels decreased to 80% of air satiation before the end of the 12-h experimental period. Flushing periods lasted 4 min, which was sufficient time for the water in the respirometer to return to 100% saturation. The first 10 min of data were discarded after a flushing period to allow stabilization of the oxygen electrode.

Measurement of wet body mass and total length

SDA experiments were terminated after 12 h. The juvenile cod was removed from the respirometer by detaching the swimming-chamber, removing one of the two steel mesh screens and gently pouring the cod into a fine-mesh. After excess water was allowed to drip from the net, the cod was transferred to a transparent, preweighed Plexiglas container with water. The Plexiglas container, water and fish were weighed using a Mettler Scale (Toledo AG) with a precision of ± 0.02 g. The mass of the juvenile cod was calculated by difference.

A ruler was placed underneath the transparent Plexiglas container and a 1-min recording was taken of the juvenile cod with a Hi8 video camera (Sony model CCD-TRV101). A digital picture was then later prepared from the recording, and Optimas software was used to measure the length of the juvenile cod. The precisions of the weighing and length measurements were ± 0.1 g and ± 0.50 mm, respectively. Measurements of wet mass and length took approximately 2 min, and the gentle procedure rendered anesthesia unnecessary. The juvenile cod was transferred from the Plexiglas container to its respective 20-L tank immediately following the mass and length measurements.

Oxygen consumption of unfed juvenile cod

Oxygen consumption of unfed juvenile cod (unfed reference) was established for individual juvenile cod. Following a SDA experiment and a 2-wk recovery period, the juvenile cod would go through an unfed control experiment. Oxygen consumption of unfed juvenile cod followed the same procedure as the SDA experiments, except the cod

was not fed prior to the experiment. Due to high growth rates of the juvenile cod it was not possible to use fed and unfed oxygen consumption from an individual cod measured with a 2-wk interval for the calculation of SDA magnitude. A relationship between wet body mass (wbm) and oxygen consumption of unfed juvenile cod was therefore established. The equation from this relationship was used to calculate the unfed oxygen consumption of juvenile cod with a specific body mass.

Background oxygen consumption

Background oxygen consumption in the respirometer was measured twice a week. This was done by measuring background oxygen consumption over a 12-h period at the same water velocity as with the SDA experiments, but without fish in the swimming chamber.

Procedures for scope for activity experiments

Scope for activity fish

Scope for activity experiments were carried out on individual cod over a 100-d experimental period. A total of 6 individual cod was used for the scope for activity experiments. Each cod went through 4-6 scope for activity experiments over the 100-d experimental period. Individual cod had a 2-wk recovery period between experiments. A total of 20 scope for activity experiments were conducted.

Respirometer operation for scope for activity experiments

Experimental cod were starved for 48 h prior to each scope for activity experiment. Starvation time was determined based on gastric evacuation time (see section on gastric evacuation time). The fish was transferred from the juvenile holding system to the scope for activity respirometer 12 h before the start of the experiment. The transfer followed the 7-step procedure explained previously.

The scope for activity experiments consisted of a series of swimming trials, starting at a slow cruising speed and continuing with progressively higher swimming speeds. The juvenile cod would swim for 46 min at each swimming speed. A 10-min flushing and recovery period at low velocity (4.26 cm s^{-1}) separated speed trials. Oxygen concentration was measured every 2 min by the pulsed oxygen electrodes. Each scope for activity experiment consisted of measurements of oxygen consumption of one individual juvenile cod swimming at 7 different speeds ($4.6 \pm 0.05 \text{ cm s}^{-1}$, $6.0 \pm 0.05 \text{ cm s}^{-1}$, $6.3 \pm 0.07 \text{ cm s}^{-1}$, $7.1 \pm 0.11 \text{ cm s}^{-1}$, $7.9 \pm 0.07 \text{ cm s}^{-1}$, $8.8 \pm 0.10 \text{ cm s}^{-1}$, and $9.6 \pm 0.11 \text{ cm s}^{-1}$ (mean \pm SE). Oxygen consumption of juvenile cod could not be measured with precision at velocities higher than $9.6 \pm 0.11 \text{ cm s}^{-1}$. This was due to unstable background oxygen consumption caused by supersaturation at high velocities ($> 9.6 \text{ cm s}^{-1}$).

The first 10 min of each swim-trial was discarded for each swimming speed to reduce errors related to stabilization of the oxygen electrode. Oxygen consumption for each swimming speed was calculated from the remaining 36 min.

Measurement of maximum sustainable swimming speed

Maximum sustainable swimming speed was measured after all 7 swim-trials were carried out. A ½ hour flushing and recovery period at low velocity (4.6 cm s^{-1}) was executed before measurement of maximum sustainable swimming speed would begin. The velocity of the water was gradually increased until the fish started to burst swim. Maximum sustainable swimming speed was determined as the swimming speed just prior burst swimming. Oxygen consumption at maximum sustained swimming speed could not be measured accurately, due to unstable background oxygen consumption at velocities higher than 10 cm s^{-1} . Active metabolism was therefore estimated by extrapolation from the power-performance relationships between oxygen consumption and swimming speed.

Wet body mass and total length of the juvenile cod was measured after each experiment, following the procedure described previously. Juvenile cod would have a two-week recovery period between scope for activity experiment.

Standard and active metabolism

Power-performance relationships between swimming speed and oxygen consumption were established for individual juvenile cod. These power-performance curves allowed the calculation of standard metabolism (R_s) and active metabolism (R_a). This was achieved by extrapolating the power-performance curves back to zero swimming speed for standard metabolism and up to maximum sustained swimming speed for active metabolism.

Background oxygen consumption

Background oxygen consumption for the scope for activity experiments was measured twice a week. The procedure for measuring the background oxygen consumption was the same as for the scope for activity experiments, but without a fish in the swimming chamber.

Juvenile Atlantic cod

Juvenile Atlantic cod were divided into three different groups: 1) the experimental group (EG), i.e., the fish that went through swim-trials in the respirometers; 2) the experimental control group (ECG), i.e., the fish that went through the same feeding regimen as the EG, but did not go through any swim-trials in the respirometers; and, 3) the weight control group (WCG), i.e., the fish that experienced the same feeding regime as the EG and ECG, but did not go through any swim trial in the respirometers and were not starved for 48 h every 2 wk.

Experimental group

The experimental group (EG) of juvenile cod was divided into SDA fish and scope for activity fish. SDA fish were used for the SDA experiments only and scope for activity fish were used for the scope for activity experiments only. The experimental fish were randomly selected at the beginning of the 100-d experimental period. Each of the 12 selected fish was assigned a 20-liter tank in the juvenile holding system. This was necessary for easy identification and to control feeding and starvation regiment for each individual cod.

Wet body mass and total length was recorded for experimental fish after each experiment (every 2-wk). Specific growth rates (G) were calculated for individual cod for every two-week period over the 100-d experimental period. Specific growth rates were also calculated for grouped data to make comparisons between the ECG and the WCG

Experimental control group

The experimental control group of juvenile cod served as a growth control for the EG. The ECG went through the same feeding and starvation regimen as the EG, but did not go through any swim-trials in the respirometer. Any difference in growth between the EG and the ECG would provide information about stress-related effects of the respirometer trials on growth.

The ECG consisted of 25 juvenile cod that were randomly selected at the beginning of the 100-d experimental period. Wet body mass and total length of the ECG were recorded every 14 d during the 100-d experimental period. Specific growth rates (G) were calculated from mean values of wet body mass (wbm) of the 25 juvenile cod.

Growth control group

The growth control group (GCG) of fish did not go through any swim-trials in the respirometer and were not starved for 48 h every 2 wk like the EG and the ECG. Growth comparisons between the GCG and the two other groups of cod (i.e. EG and ECG) would provide information about the effect of the 48-h biweekly starvation period.

Every week during the 100-d experimental period 10 juvenile cod were sampled for measurements of wbm, total length, dry weight and crude ash. A mean value of wbm from each weighing period was used to calculate G.

Dry weight and crude ash determination

Each week 10 fish from the ECG would be sampled for dry weight and crude ash determination. After measuring the total length and wbm, the juvenile cod were euthanized with MS222 and rinsed with deionized water to remove any saltwater from the skin. Each juvenile cod was then placed in a pre-weighed weighing boat (aluminum foil) weighed and transferred to the drying oven (Fisher isotemp model 225G). The juvenile cod were dried for 48 h at a temperature of 102°C. The dried cod were then taken out of the oven, placed in a desiccator and allowed to cool for ½ h before recording the weight on a Mettler scale (Toledo AT20) with a precision of $\pm 2 \mu\text{g}$.

For the crude ash determination each dried cod was placed in a pre-weighed ceramic crucible. The mass of the crucible and cod was then weighed. The crucibles were placed in a muffle oven (Sybron Thermolyne model FA 1730) for 6 h at a temperature of 600°C. After cooling down to 200°C the samples were transferred from the muffle oven to a drying oven (Fisher isotemp model 225G), which had a temperature of 101°C. The samples were taken out of the drying oven the following day and placed in a dessicator for ½ h to allow the samples to cool before they were weighed. Crude ash was measured on the same Mettler scale.

Gastric evacuation time of juvenile cod

A starvation study was carried out to find the gastric evacuation time of juvenile cod in the size range 0.5-4.0 g. Starvation time of the juvenile cod prior to the scope for activity and SDA experiments was determined based on gastric evacuation time.

Ten juvenile cod were selected randomly and starved for 24 h. All fish were fed to satiation before the starvation experiments were started. Wet body mass and total length were measured for the 10 juvenile cod, following the procedures previously described. At the end of the starvation time the juvenile cod were given an overdose of MS222 and prepared for dissection. It was noted if any digesta was present in the stomach or intestine.

If any digesta was present in the stomachs or intestines of any of the 10 juvenile cod another batch of 10 juvenile cod would be sampled and starved for 12 h longer than the previous group. The starvation experiment was terminated when no digesta was present in the stomachs and intestines of any of 10 cod in a batch.

Data analyses

Prior to data analyses all numeric data were tested for normality using graphical probability plots (Systat, 2002) and for homogeneity of variance using appropriate residual plots.

Scope for activity experiments

A one-way analysis of variance (ANOVA) was used to detect any difference in background oxygen consumption in the respirometer for the seven different velocities used in the scope for activity experiments. A Bonferroni post hoc test was used for pairwise comparison of background oxygen consumption between the seven different velocities.

Oxygen consumption of juvenile cod used in the scope for activity experiments were calculated from linear regression of oxygen concentration ($\mu\text{mol O}_2$) in the respirometer over time (hours). A regression was done for each of the 7 different speeds, which lasted 46 min. Relationships between swimming speed and oxygen consumption were established for juvenile Atlantic cod. Standard (R_s) and active (R_a) metabolism were found for each juvenile cod from this relationship by extrapolation of the regression from the logged data to zero swimming speed for R_s and to maximum sustained swimming speed for R_a .

To determine the effect of body mass on active and standard metabolic rate, \log_{10} transformed oxygen consumption of standard and active metabolism were regressed against \log_{10} transformed body mass. Analysis of covariance (ANCOVA) was applied to the data by first testing the homogeneity of slopes to determine if the slopes for R_s and R_a were significantly different ($P > 0.05$). Data were then fitted to the ANCOVA model to test if the R_s and R_a were significantly different after adjustment of the covariate (\log wbm).

One-way ANOVA were used to test if there was any significant difference between three weight classes of juvenile cod (0-1, 1-2, and 2-3 g) for 1) wet body mass,

2) mass-specific standard metabolism (R_s/M), 3) mass-specific active metabolism (R_a/M), and 4) mass-specific scope for activity. A Bonferroni post hoc test was used for pairwise comparison of weight classes.

SDA experiments

One-way ANOVA's were used to determine if there was significant difference among the 12 measurements of background oxygen consumption. Oxygen consumption of juvenile cod used in the SDA experiment was calculated from linear regression of oxygen concentration ($\mu\text{mol O}_2$) over time (hours) in the respirometer. Regressions were done for each 60 min of data over the 12-h experiment to calculate oxygen consumption per hour for the duration of the experiment.

SDA duration was defined as the time from an increase in oxygen consumption, following a meal, was observed and until the oxygen consumption reached the pre-feeding level (student *t*-test; $P < 0.05$).

SDA magnitude was calculated for each SDA experiment, by subtracting the oxygen consumption of the unfed reference from the oxygen consumption of the fed fish ($R_f - R_{ref}$) for every hour of the SDA duration. In this fashion the area between the curves for fed and unfed oxygen consumption over the SDA duration was calculated.

One-way ANOVA's was used to test if there was any significant difference between four weight classes of juvenile cod (0-1, 1-2, 2-3, and 3-4 g) for 1) wet body mass, 2) mass-specific SDA magnitude (SDA_{mag}/M), and 3) mass-specific SDA maximum amplitude (SDA_{amp}/M). A Bonferroni post hoc test was used for pairwise comparison of the four weight classes.

SDA and scope for activity

Log₁₀ values of 1) standard metabolism, 2) unfed reference, 3) peak SDA, and 4) active metabolism were graphed against log₁₀ wbm and linear regression was applied. The 4 regression lines were compared by means of ANCOVA (as previously explained)

Growth

One-way ANCOVA's were used to compare slope values of growth (change in wet body mass over time) among the 3 groups of juvenile cod, 1) EG, 2) ECG, and 3) WCG. Log₁₀ values of wet mass for the 3 groups of cod were graphed against time in days post hatch (dph). One-way ANCOVA's were again used to compare slopes of the three regression lines.

CHAPTER 3

RESULTS

Growth

Growth (change in wet body mass over time) was compared among the three groups of cod to determine if stress caused by the experimental procedures affected growth. The three groups of cod were: 1) experimental group (EG), i.e. the fish that went through swim-trials in the respirometers, 2) experimental control group (ECG), i.e. the fish that went through the same feeding regimen as the EG, but did not go through any swim-trials in the respirometers, and 3) weight control group (WCG), i.e. the fish that experienced the same feeding regime as the EG and ECG, but did not go through any swim trial in the respirometers and were not starved for 48 h every two wk.

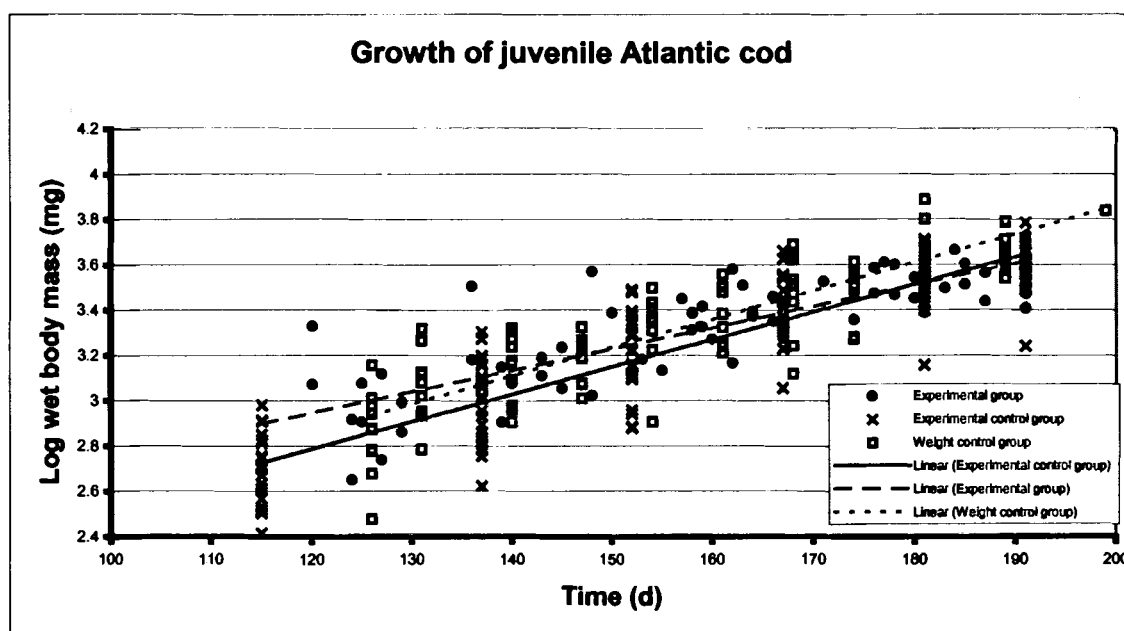


Figure 4. Growth of juvenile Atlantic cod. The 3 groups are: 1) Experimental group ($Y = 0.009x + 1.81$, $r^2 = 0.71$), 2) Experimental control group ($Y = 0.012x + 1.33$, $r^2 = 0.81$), and 3) Weight control group ($Y = 0.013x + 1.36$, $r^2 = 0.76$).

Wet body mass (wbm) increased exponentially with time (days post hatch) and increased about 8-fold from 0.50 g (wbm) at 115 days post hatch (dph) to 4.50 g wbm at 190 dph (Fig. 4).

Analysis of covariance (ANCOVA) was applied to the data to find any differences in growth among the three groups. The test for homogeneity of slopes showed that there were no significant differences among the three slope values ($P < 0.25$, $F_{1,3} = 1.41$). Data were fitted to the ANCOVA model to test if the three groups of cod showed significant differences in growth after the groups of cod (treatments) had been adjusted for time (covariate). Growth was not significantly different among the three groups after adjustment for time ($P < 0.49$; $F_{1,3} = 0.72$). The data for wbm and dph can be found in the Appendix. Consequently stress from experimental runs did not substantially affect growth.

Specific growth rates

Specific growth rates (G) were calculated for the 3 groups of fish; EG, ECG and WCG (Table 1) from the following equation:

$$G = (e^g - 1) * 100$$

Where $g = (\ln W_2 - \ln W_1) / (t_2 - t_1)$ and W is wet body mass (g) at days t_2 and t_1 respectively. Units are percent wet body mass per day (% wbm d⁻¹). G was calculated from mean values of each group at time 1 and 2 (t_1 and t_2).

Experimental fish		
Days post hatch	Specific growth rate % wbm d ⁻¹ ± S.D.	wbm g ± S.D.
115-140	3.0 ± 1.1	1.19 ± 0.7
140-165	1.9 ± 1.0	2.05 ± 0.8
165-180	1.6 ± 0.6	3.25 ± 0.7
Experimental control group		
Days post hatch	Specific growth rate % wbm d ⁻¹	Wbm g ± S.D.
115-140	3.4	1.07 ± 0.5
140-165	3.1	2.05 ± 0.7
165-180	1.4	3.84 ± 0.3
Weight control group		
Days post hatch	Specific growth rate % wbm d ⁻¹	Wbm g ± S.D.
115-140	4.4	0.80 ± 0.4
140-165	3.5	2.25 ± 0.9
165-180	1.8	3.43 ± 0.8

Table 1. Specific growth rates in percent wet body mass d⁻¹ (% wbm d⁻¹), and mean mass ± S.D. of the three groups of juvenile Atlantic cod. S.D. is not given for G of the ECG and the WCG, because G is calculated from mean values of wet body mass.

G ranged from 1.4 - 4.4 % wbm d⁻¹ for the three groups of cod. G decreased in all three groups, with increasing mass of fish. G for individual experimental cod can be found in appendix.

Conversion of body mass and length

In order to convert among wet body mass, dry body mass, crude ash and total length of juvenile cod, relationships between these variables were established.

Wet body mass and total length

A relationship between wet body mass and total length of juvenile Atlantic cod was established (Fig. 5). The data were pooled for the three groups of fish (EG, ECG and

WCG), since no significantly difference was found among the three groups of fish. Best fit was obtained by a powerrelationship ($P < 0.001$, $F_{1,241}$, $r^2 = 0.98$). Conversion from wbm to total length follows the equation:

$$\text{wbm (g)} = 50.47 * \text{total length (mm)}^{0.35}$$

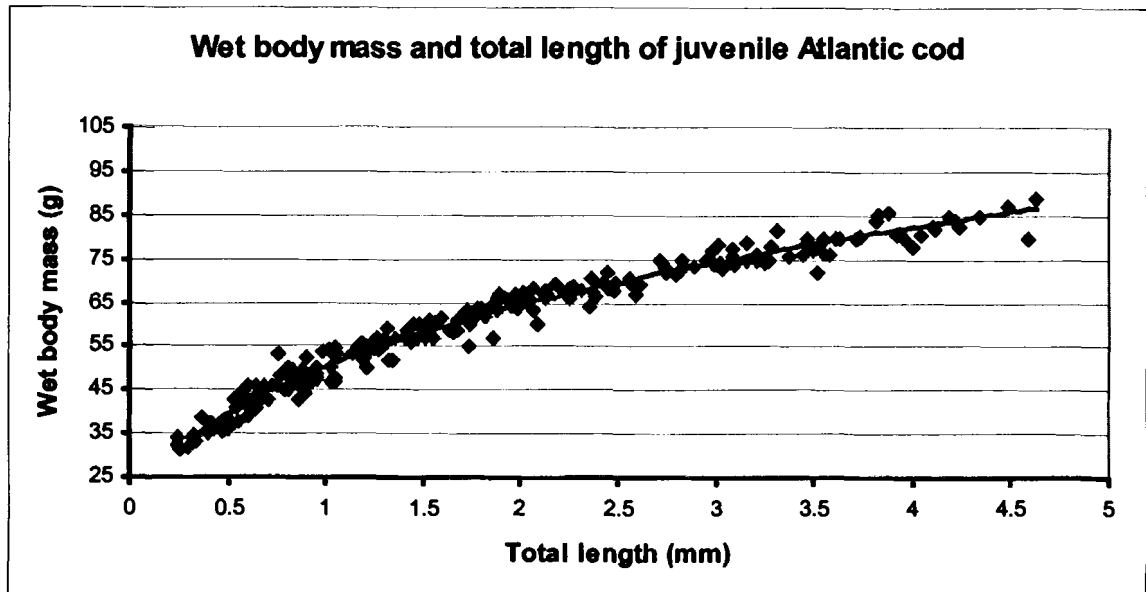


Figure 5. Mass-length relationship of juvenile Atlantic cod. Data are pooled for the three groups of cod (e.g. EG, ECG and WCG). Equation is $y = 50.47X^{0.35}$. $r^2 = 0.98$.

Wet body mass and dry body mass

A relationship was established between wbm and dry body mass (dbm) (see appendix for figure). The best fit was obtained by a power relationship ($P < 0.001$, $F_{1,96} = 19909$, $r^2 = 0.995$). The conversion from wbm to dbm follows the equation:

$$\text{Dry body mass (mg)} = 0.166 * \text{wbm (g)}^{1.18}$$

Wet body mass and crude ash

A relationship was established between wbm and crude ash (see appendix for figure). The best fit was obtained by linear regression. ($P < 0.001$, $F_{1,96} = 6845$, $r^2 = 0.986$). The conversion from wbm to crude ash follows the equation:

$$\text{Crude ash (mg)} = 28.68 * \text{wet body mass (g)} - 6.51$$

Gastric evacuation time

Juvenile Atlantic cod were starved for 24, 36 and 48 h in order to find the gastric evacuation time. Wet mass of the 30 juvenile cod ranged from 0.41 to 4.15 g, and the mean mass for the three groups of cod was 1.45 ± 0.92 , 1.44 ± 1.09 , and 1.78 ± 1.21 g for starvation time of 24, 36 and 48 h, respectively. No digesta was present in the stomach of any of the juvenile cod after 24, 36 or 48 h of starvation. Digesta was present in seven of the ten fish starved for 24 h and three of the nine fish starved for 36 h. No digesta was present in the stomachs or intestines in any of the 10 juvenile cod that were starved for 48 h. Gastric evacuation time was < 24 h for juvenile cod in the weight range 0.41 g to 4.15 g. Total throughput time of the gastric intestinal tract was < 48 h for the same fish.

Scope for activity experiments

Background oxygen consumption for scope for activity experiments

Background oxygen consumption was a function of bacterial oxygen demand (BOD) and degassing due to supersaturating of dissolved gas. The supersaturating was caused by the slight increase in water temperature ($0.1 - 0.3^\circ\text{C}$) in the respirometer due to

heat output from the DC pump. One-way analysis of variance (ANOVA) was applied to the data to find if the background oxygen consumption in the respirometer varied significantly at different water velocities. A total of 7 different (4.6, 6.0, 6.3, 7.7, 7.9, 8.8 and 9.6 cm s⁻¹) velocities were tested. There was no significant difference between any of the 7 different velocities ($P < 0.17$, $F_{1,56} = 1.60$). Data from the 7 different velocities were grouped and a mean value of 7.18 ± 0.51 (SE) was used for the background consumption of oxygen.

Swimming speed and oxygen consumption

Power-performance relationships between swimming speed and oxygen consumption were established for a total of 15 swim trials representing 6 individual fish in a weight range between 0.53 – 2.89 g (Fig. 6). Oxygen consumption increased exponentially with swimming speed in all swim trials. Swimming speeds from 4.6 to 9.6 cm s⁻¹ were used for these power-performance relationships. The lowest speed of 4.6 cm s⁻¹ was the slowest speed at which the DC pump would operate. The highest velocity of 9.6 cm s⁻¹ was not the maximum sustainable swimming speed for any of the cod, but was chosen because oxygen readings became unstable at velocities higher than 9.6 cm s⁻¹. This was probably due to increased degassing caused by extra heat input to the respirometer from the DC pump and interference from air bubbles and pressure changes at higher velocities.

The relationships between swimming speed and oxygen consumption were significant for all 15 swim-trials (see appendix for statistics and equations).

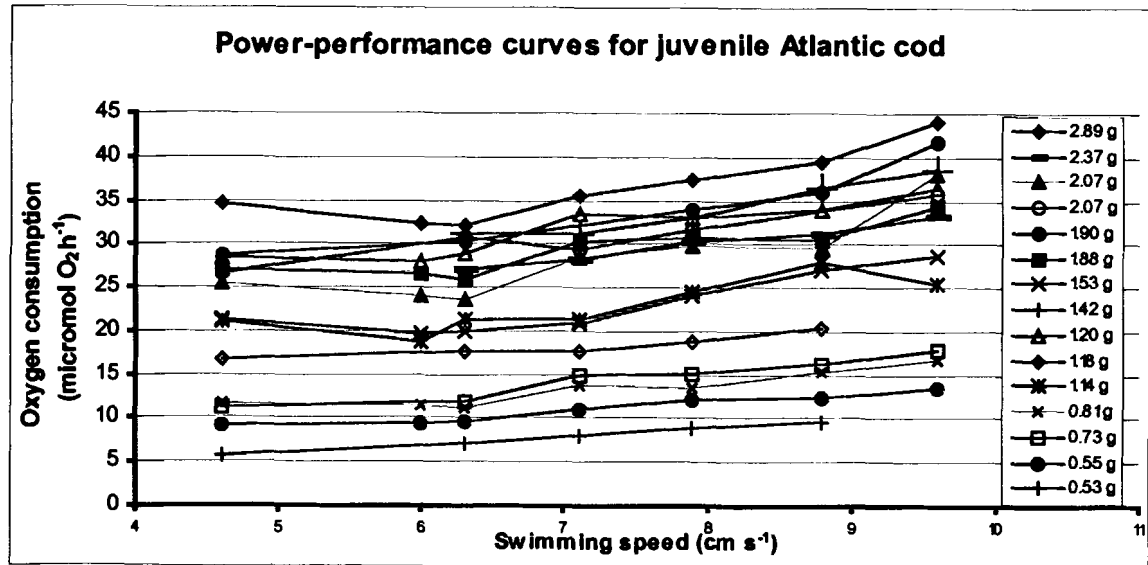


Figure 6. Power-performance curves of 15 individual juvenile Atlantic cod with a mass ranging from 0.53- 2.89 g wbm. Oxygen consumption increased exponentially with increasing swimming speed for all 15 cod.

Standard metabolism, active metabolism and scope for activity

Data for swimming speed and oxygen consumption were \log_{10} transformed and regression analysis fitted to the data (see appendix for regression statistics). Standard metabolism was found by extrapolating the regression to zero swimming speed, and active metabolism was found by extrapolating the regression to the maximum sustained swimming speed. Aerobic scope for activity was calculated as the difference between standard and active metabolism ($R_a - R_s$) (Table 2).

Exp. Fish No	Wet mass (g)	R_s ($\mu\text{mol O}_2 \text{ h}^{-1} \pm \text{SD}$)	R_A ($\mu\text{mol O}_2 \text{ h}^{-1} \pm \text{SD}$)	Aerobic scope for activity ($\mu\text{mol O}_2 \text{ h}^{-1} \pm \text{SD}$)	V_{\max} (cm s^{-1})
1	0.53	1.8 ± 0.3	12.0 ± 0.8	10.2 ± 1.2	12.0
6	0.55	3.5 ± 0.5	16.6 ± 2.7	13.1 ± 3.2	14.4
2	0.73	4.0 ± 0.6	24.1 ± 3.7	20.1 ± 4.3	15.8
5	0.81	4.7 ± 0.6	19.6 ± 3.5	14.9 ± 4.1	14.4
4	0.83	5.6 ± 1.1	34.6 ± 8.1	29.0 ± 0.2	13.3
6	1.14	10.0 ± 1.3	32.2 ± 11.5	22.2 ± 12.8	15.8
3	1.18	10.9 ± 0.7	21.7 ± 6.2	10.8 ± 6.9	13.3
5	1.20	15.4 ± 0.9	44.2 ± 9.8	28.8 ± 10.7	17.2
4	1.42	11.2 ± 1.0	51.9 ± 10.3	40.7 ± 11.3	17.2
5	1.53	9.0 ± 1.3	36.7 ± 12.5	27.7 ± 13.8	18.7
6	1.88	15.0 ± 1.1	42.8 ± 12.7	27.7 ± 13.8	21.2
5	1.90	13.5 ± 1.1	52.7 ± 12.2	39.2 ± 13.3	18.7
2	2.07	14.9 ± 0.9	44.6 ± 10.0	29.7 ± 10.9	18.7
4	2.07	10.2 ± 1.5	46.9 ± 15.8	36.7 ± 17.3	18.7
2	2.37	11.0 ± 0.4	45.6 ± 4.0	34.6 ± 4.4	18.7
4	2.89	18.2 ± 1.5	50.0 ± 17.3	31.8 ± 18.8	17.2

Table 2. Standard metabolism (R_s), active metabolism (R_A), aerobic scope for activity and maximum sustained swimming speed (V_{\max}) for individual Atlantic juvenile cod. The column for experimental fish No. indicates individual juvenile cod.

Both R_s and R_A increased exponentially with wbm and followed an allometric relationship with the equation $\text{VO}_2 = aW^b$, where VO_2 is the rate of oxygen consumption in $\mu\text{mol O}_2 \text{ h}^{-1}$, W is wet body mass (g), and a and b are constants. The allometric equations were $y = 6.69x^{0.96}$ for R_s and $y = 25.67x^{0.81}$ for R_A . The slopes of R_s and R_A scaled with a mass exponent $b = 0.96$ and 0.81 , respectively. A log-log plot of R_s and R_A over wbm allowed linear regression and consequently analysis of covariance (Fig. 7). Linear regression was significant for both R_s ($P < 0.001$, $F_{1,12} = 54.77$, $N = 13$) and active metabolism ($P < 0.001$, $F_{1,12} = 62.75$, $N = 14$). Homogeneity of slopes was tested to find any significant interactions between the covariate (log wet mass) and the treatments (R_s and R_A). The slopes for R_s and R_A were not significantly different ($P > 0.37$, $F_{1,23} < 0.83$, $N = 27$). Data were fitted to the ANCOVA model to test if the two treatments were significantly different after the treatments had been adjusted for the covariate (log wbm).

The test showed significant difference between the two treatments ($P < 0.001$, $F_{1, 24} = 30.79$, $N = 24$). R_s is therefore significantly different from R_a .

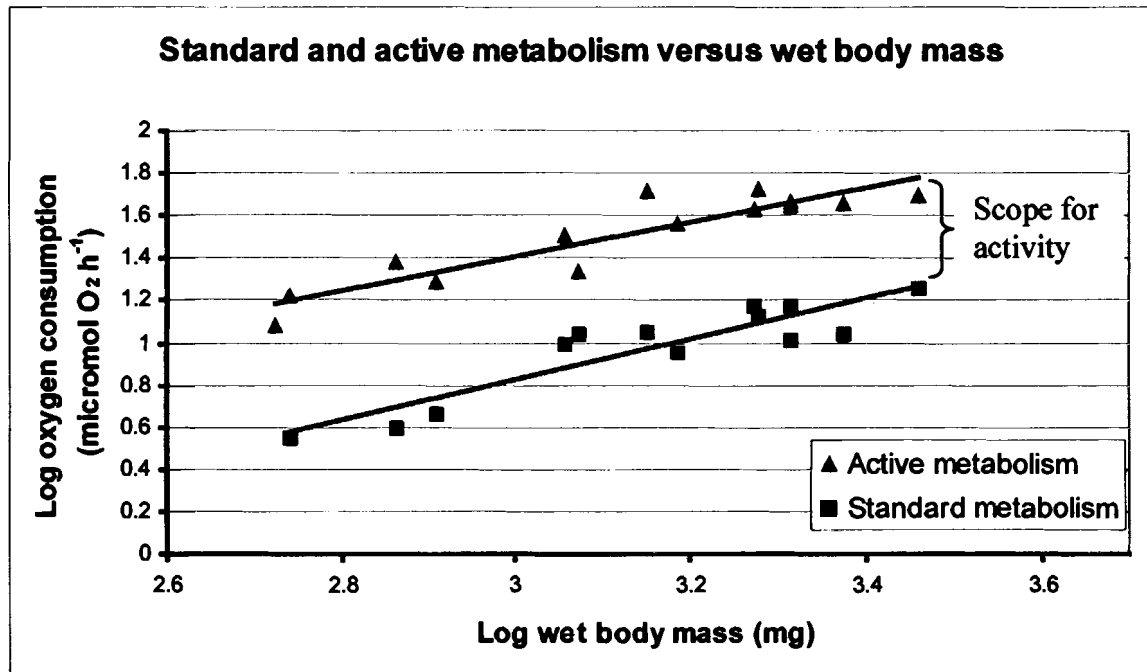


Figure 7. Standard and active metabolism versus wet body mass. The difference between the regression lines represents aerobic scope for activity. Each data point represents one individual Atlantic cod. Regression equation for R_a was $y = 0.81X - 1.02$ ($r^2 = 0.84$), and $y = 0.96X - 2.06$ ($r^2 = 0.83$) for R_s .

Mass-specific oxygen consumption

Mass-specific values of standard and active metabolic rates were calculated so comparisons could be made to other metabolic studies of Atlantic cod. Due to a large variation in the data for mass specific respiration and to ease comparison, the juvenile cod were divided into three weight classes: 1) 0-1, 2) 1-2, and, 3) 2-3 g. One-way ANOVA's followed by Bonferroni post hoc tests were conducted for: 1) wet mass, 2) standard metabolism (R_s), 3) active metabolism (R_a), and 4) scope for activity ($R_a - R_s$).

Mass-specific oxygen consumption ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ wet mass h}^{-1}$)					
Weight Class (g)	Mean wet mass (g \pm S.D.)	R_s (\pm S.D.)	R_a (\pm S.D.)	Scope for activity (\pm S.D.)	N
1 (0-1 g)	0.69 ± 1.42^a	6.10 ± 0.60^a	30.34 ± 7.65^a	26.18 ± 6.93^a	5
2 (1-2 g)	1.51 ± 0.33^b	7.82 ± 1.20^b	26.28 ± 6.18^a	18.46 ± 6.48^{ab}	6
3 (2-3 g)	2.35 ± 0.39^c	5.77 ± 1.19^a	20.18 ± 2.39^a	14.35 ± 3.35^b	4

Table 3. Mass-specific oxygen consumption. Mass-specific standard metabolism (R_s), active metabolism (R_a) and scope for activity of three weight classes of Atlantic juvenile cod. Letters in superscript indicates results from ANOVA ($P < 0.05$).

The three weight classes are significantly different from each other ($P < 0.001$; $F_{2, 12} < 34.38$). There was a significant difference in mass-specific standard metabolism between weight class 1 and 2 ($P < 0.01$), as well as weight class 2 and 3 ($P < 0.03$), but no significant difference between weight class 1 and 3 ($P < 1.00$). No significant differences were found between any of the three weight classes for mass-specific active metabolic rate ($P < 0.08$, $F_{2, 12} = 3.13$). There was a significance difference in mass specific scope for activity between weight class 1 and 3 ($P < 0.05$), but no significant difference was found between weight class 1 and 2 ($P = 0.07$) or 2 and 3 ($P = 1.00$).

Specific dynamic action experiments

Background oxygen consumption for SDA experiments

A mean value of $3.18 \mu\text{mol O}_2 \text{ h}^{-1} \pm 1.46$ (S.D.) ($N = 12$) of background oxygen consumption was used. Each measurement for background consumption was based on oxygen measurements taken over a 12-h period in an empty respirometer with a water velocity of 4.24 cm s^{-1} .

Oxygen consumption of fed juvenile cod

Oxygen consumption increased rapidly after consumption of a meal and fell slowly after feeding (Fig. 8). Post-prandial (following a meal) oxygen consumption then decreased until it reached the prefeeding level.

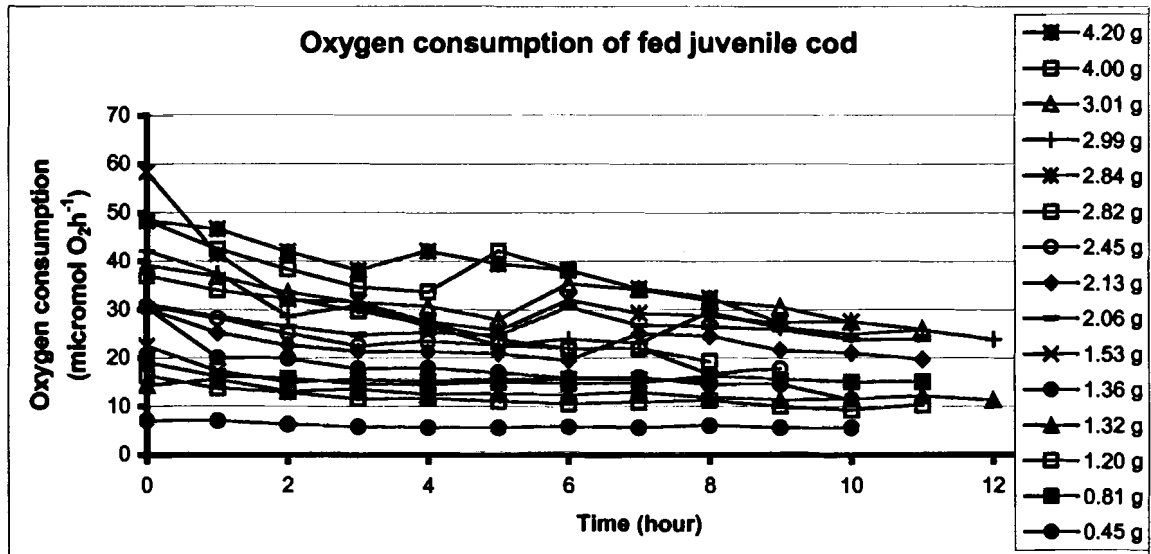


Figure 8. Oxygen consumption of fed juvenile Atlantic cod. Each line represents an individual cod. Prefeeding level for each cod is not shown on figure.

Oxygen consumption of post-absorptive juvenile cod

A relationship between oxygen consumption of post-absorptive (unfed) juvenile cod and wbm was established so that the prefeeding oxygen consumption of individual cod could be calculated (Fig. 9). The relationship between post-absorptive oxygen consumption and wbm was significant ($P < 0.001$, $F_{1,9} = 137$, $r^2 = 0.94$).

The conversion from wbm to post-absorptive oxygen consumption from this study follows the equation:

$$\text{Post absorptive oxygen consumption} = 10.46 * \text{wbm}^{0.88}$$

where post absorptive oxygen consumption is in $\mu\text{mol O}_2 \text{ h}^{-1}$ and wbm is in g. This equation was used to calculate the prefeeding level of metabolism of each individual juvenile cod according to the mass of the juvenile cod on the day of the SDA experiment.

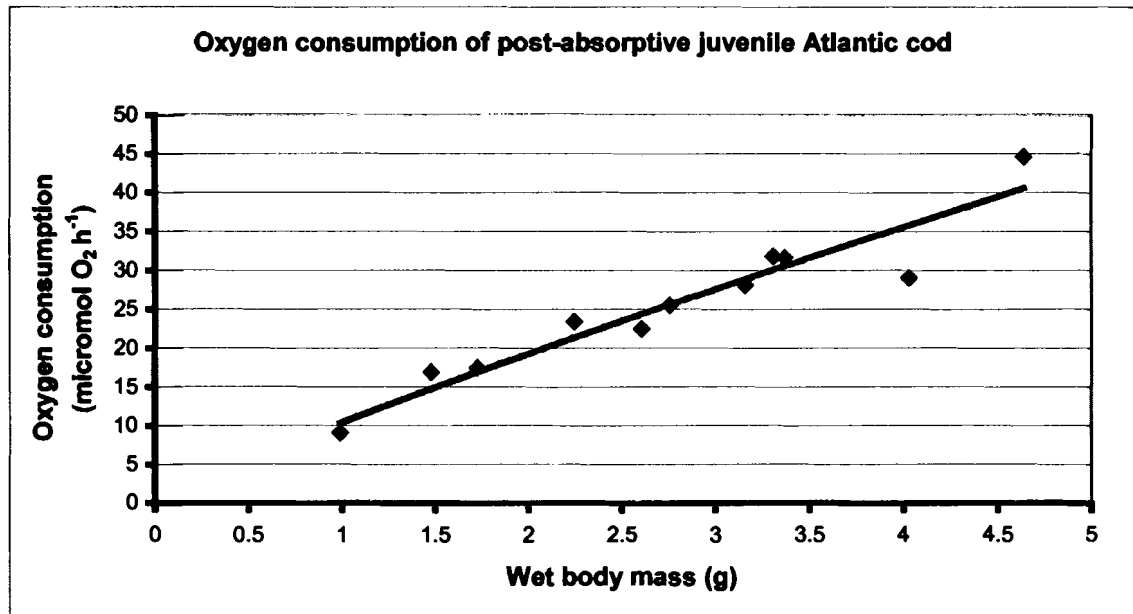


Figure 9. Oxygen consumption of post-absorptive juvenile Atlantic cod swimming at a velocity of 4.25 cm s^{-1} . The relationship followed a power curve with the equation $10.46x^{0.88}$, $r^2 = 0.94$.

Amplitude, magnitude and duration of SDA

All cod were fed to satiation ($1.20 \% \text{ wbm} \pm 0.62 \text{ (S.D.)}$) prior to each experiment. The effects of: 1) body mass, 2), meal size, and 3) specific growth rate (G), on SDA magnitude, amplitude and duration were investigated (Table 5).

wbm (g)	Unfed VO ₂ ($\mu\text{mol O}_2 \text{ hr}^{-1}$)	SDA mag. ($\mu\text{mol O}_2$)	Peak SDA ($\mu\text{mol O}_2$)	SDA amp. ($\mu\text{mol O}_2$)	SDA amp. (% of unfed VO ₂)	SDA dur. (hours)	SPG (% wbm d ⁻¹)	Meal size (Mg)	Meal size (% wbm)
0.45	5.2	2.8	7.0	1.9	36.4	3	3.9	8.7	1.9
0.81	8.7	5.0	12.5	3.8	44.1	3	3.0	23.5	2.9
1.20	12.3	6.3	16.3	4.1	33.0	3	3.6	11.4	1.0
1.32	13.4	2.5	14.9	1.6	11.6	2	2.1	16.8	1.3
1.36	13.7	45.5	30.5	16.7	121.9	8	1.2	20.1	1.5
1.53	15.2	9.3	22.5	7.2	47.5	2	1.4	22.8	1.5
2.06	19.8	9.9	31.2	11.4	57.5	3	1.7	20.1	1.0
2.13	20.4	19.6	30.2	9.8	48.2	7	0.8	18.8	0.9
2.45	23.1	14.9	30.7	7.6	32.8	3	2.5	34.9	1.4
2.82	26.2	29.8	37.0	10.8	41.4	5	2.0	30.2	1.1
2.84	26.3	60.0	58.4	32.1	122.4	5	2.8	18.8	0.7
2.99	27.5	29.3	42.1	14.6	53.0	4	0.8	11.4	0.4
3.01	27.7	33.9	39.1	11.4	41.1	6	1.4	26.2	0.9
4.00	35.6	20.6	47.5	12.0	33.8	3	0.1	47.6	1.2
4.10	36.4	40.7	48.4	12.0	32.8	7	1.8	22.8	0.6

Table 4. Summary of SDA data for Atlantic juvenile cod, *Gadus morhua*. Data are presented with increasing wbm from top to bottom. Columns from left to right; wet body mass (wbm), Unfed reference (unfed VO₂), SDA magnitude (SDA mag.), Peak SDA, SDA amplitude (SDA amp.), SDA amplitude % of unfed reference, SDA duration (SDA dur.), specific growth rate (G), meal size in mg, and meal size in % wbm. Each row represents one individual cod.

Variables	Best fit & equation	R ²	Levels of significance	F-value	df
Unfed ref. & wbm	Exponential	0.94	P<0.001	136.68	1, 9
MS & wbm	Linear regression	0.33	P< 0.026	6.28	1, 13
SDA dur. & wbm	Linear regression	0.12	P< 0.208	1.75	1, 13
Peak SDA & wbm	Exponential	0.90	P< 0.002	15.29	1, 13
SDA amp. & wbm	Exponential	0.54	P< 0.002	15.29	1, 13
SDA mag. & wbm	Exponential	0.59	P< 0.001	18.37	1, 13
SDA dur. & MS	Linear regression	0.00	P<0.917	0.01	1, 13
SDA amp. & MS	Exponential	0.16	P<0.149	2.35	1, 13
SDA amp. & MS	Exponential	0.15	P<0.160	2.22	1, 13
SDA mag. & G	Exponential	0.44			
SDA amp.& G	Linear regression	0.56	P< 0.002	15.47	12
SDA dur. & G	Linear regression	0.11	P< 0.238	1.53	13

Table 5. Statistical summary of SDA variables; Unfed reference (unfed ref.), wet body mass (wbm), SDA duration (SDA dur.), peak SDA, SDA amplitude (SDA amp.), SDA magnitude (SDA mag.), meal size (MS), and specific growth rate (G).

Mass specific SDA ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ wet mass h}^{-1}$)				
Weight class (g)	Wet body mass (mean (g) \pm S.D.)	SDA magnitude (mean \pm S.D.)	SDA amplitude (mean \pm S.D.)	N
1 (0-1 g)	0.6 \pm 0.3 ^a	6.2 \pm 0.1 ^a	4.5 \pm 0.4 ^a	2
2 (1-2 g)	1.4 \pm 0.1 ^b	11.7 \pm 14.6 ^a	5.4 \pm 4.8 ^a	4
3 (2-3 g)	2.6 \pm 0.4 ^c	10.3 \pm 5.8 ^a	5.6 \pm 2.9 ^a	6
4 (3-4 g)	4.0 \pm 0.1 ^d	8.2 \pm 4.3 ^a	3.4 \pm 0.6 ^a	2

Table 6. Mass-specific SDA for four weight classes of juvenile cod. One-way analysis of variance (ANOVA) was performed for wet body mass, SDA magnitude and SDA amplitude. Letters in superscript indicate significance (ANOVA, P< 0.05)

SDA duration

SDA duration was determined at the point where there was no significant difference between oxygen consumption of the fed cod and the unfed reference (student *t*-test, $P < 0.05$). SDA lasted from 2 to 8 h for juvenile cod with a size ranging from 0.45 to 4.20 g wbm. There was no significantly relationship between SDA duration and wbm ($P < 0.21$, $F_{1,13} = 1.75$) (Table 5). There was also no significantly relationship between SDA duration and meal size ($P < 0.92$, $F_{1,13} = 0.01$) (Table 5), or between SDA duration and specific growth rates (G) ($P < 0.24$, $F_{1,13} = 0.53$).

SDA amplitude

SDA amplitude is defined as the difference between the post-prandial oxygen consumption (R_f , following a meal) and the standard metabolism ($R_f - R_s$). In this study both post-prandial oxygen consumption and unfed reference was found for individual cod at low swimming speed (4.26 cm s^{-1}). Swimming speed is accounted for because both starved and fed cod swam at the same velocity.

SDA amplitude increased from ingestion of the meal and until peak SDA (Fig. 8), which occurred 0.5 – 1.0 hour after ingesting the meal. Following peak SDA, the SDA amplitude decreased until post-prandial oxygen consumption was no longer different from the unfed reference.

Maximum SDA amplitude was found as the difference between peak SDA and the unfed reference. Relationships between peak SDA, unfed reference and wbm were investigated in order to understand the nature of maximum SDA amplitude. Peak SDA was 12% to 122% higher than (1.12-2.22 times unfed reference) compared to the unfed

reference (Table 4). There was a significant relationship between peak SDA and wbm ($P < 0.002$, $F_{1,13} = 15.29$, $R^2 = 0.90$). Peak SDA increased with increasing wbm and followed a power relationship with the equation $y = 15.26x^{0.91}$ (Fig. 10).

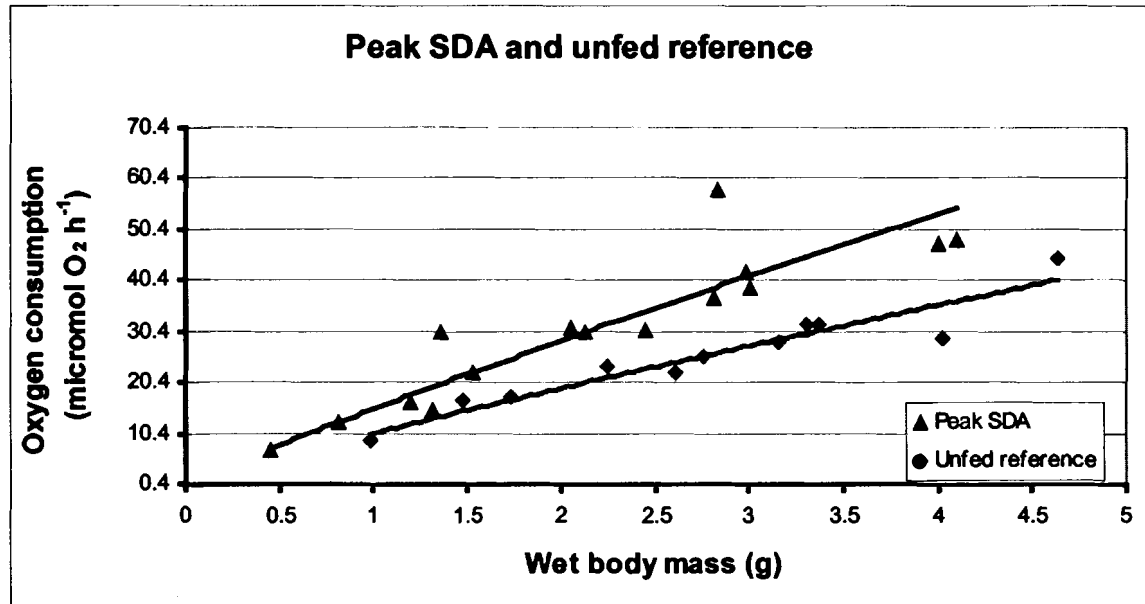


Figure 10. Peak SDA and unfed reference of juvenile Atlantic cod graphed against wbm. Peak SDA followed a power relationship with the equation $15.26x^{0.91}$, $r^2 = 0.90$. Maximum SDA amplitude is represented as the difference between the peak SDA and unfed reference. See also figure 6 for unfed reference.

Maximum SDA amplitude is represented as the difference between the two regression lines in figure 10, and it appears that maximum SDA amplitude increase with increasing wbm. Using data for peak SDA and unfed reference for individual cod (Table 4) it was established that there was a significant relationship between maximum SDA amplitude and wbm. Maximum SDA amplitude increased with increasing wbm and followed a power relationship with the equation $4.29x^{0.98}$ ($P < 0.002$, $F_{1,13} = 15.29$).

In order to find if maximum SDA amplitude varied on a mass-specific basis, the juvenile cod were divided into four weight classes: 1) 0-1, 2) 1-2, 3) 2-3, and 4) 3-4 g, and one-way ANOVA's were applied to the data. No significant difference in mass-

specific maximum SDA amplitude was found between any of the four weight classes ($P < 0.87$, $F_{3,10} = 0.24$). No significant relationship was found between SDA amplitude and meal size ($P < 0.15$, $F_{1,13} = 2.35$).

Maximum SDA amplitude and scope for activity

SDA amplitude accounted for 14.83-44.01% of the scope for activity for the three weight classes: 1) 0-1, 2) 1-2, and 3) 2-3 g (Table 7). Maximum SDA amplitude took up a larger percentage of scope for activity in larger juvenile cod compared to smaller juvenile cod. However, this is not conclusive since no significant difference was found for scope for activity or maximum SDA amplitude between the three weight classes.

Weight class	Scope for activity ($\mu\text{mol O}_2 \text{ hour}^{-1}$) (\pm S.D.)	Max SDA amplitude ($\mu\text{mol O}_2 \text{ hour}^{-1}$) (\pm S.D.)	% max SDA amplitude of scope for activity
0-1 g	19.3 ± 7.1^a	2.9 ± 1.4^a	14.8
1-2 g	28.1 ± 11.0^a	7.4 ± 6.7^a	26.3
2-3 g	32.7 ± 3.6^a	14.4 ± 9.0^a	44.0

Table 7. Mean values of scope for activity and maximum SDA amplitude for 3 weight classes of juvenile cod. Letters in superscript show results from ANOVA statistics ($P < 0.05$). Percentage maximum SDA amplitude of scope for activity is shown in column 4.

To further investigate the relationship between maximum SDA amplitude, scope for activity and wbm, data were logged for: 1) standard metabolism, 2) unfed reference, 3) peak SDA, and 4) active metabolism, and graphed against log wbm (Fig. 11). Linear regression was applied to the four slopes and the four regression lines were compared by means of ANCOVA statistics (test for homogeneity of slopes). No significant difference was found between any of the 4 regression lines (Table 8).

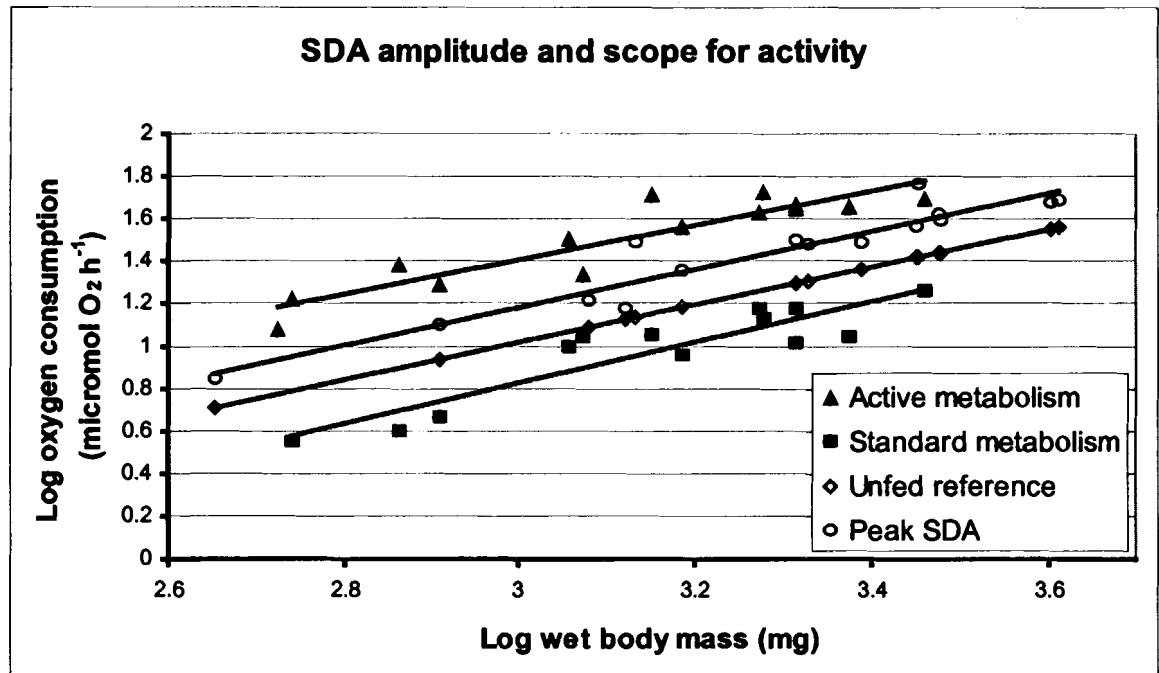


Figure 11. SDA amplitude and scope for activity. Logged data for 1) standard metabolism (R_s), 2) unfed reference, 3) peak SDA, and 4) active metabolism (R_a), and graphed against logged wbm.

The two regression lines for the unfed reference and peak SDA are located between the two regression lines for standard metabolism and active metabolism. The regression line for the unfed reference is located higher on figure 11 compared to the regression line for standard metabolism. This is due to the added energy expenditure of the juvenile SDA cod swimming at a slow speed (4.24 cm s^{-1}). Maximum SDA amplitude (peak SDA-unfed reference) takes up a part of the scope for activity and thereby temporarily reduces the scope for activity. The proportion of scope for activity taken up by maximum SDA amplitude increases with increasing wbm, since no significant difference was found between the four slope values (Fig. 11). Calculation based on the regression equation show that maximum SDA amplitude take up from 19 – 32% of the scope for activity for juvenile cod ranging from 0.5 – 3.0 g wbm (Table 9).

Variables	Levels of significance	F-value	Df
R_s & R_a	$P < 0.37$	0.83	1, 24
Unfed reference & peak SDA	$P < 0.79$	0.07	1, 26
R_s & unfed reference	$P < 0.87$	0.03	1, 24
Unfed reference & R_a	$P < 0.19$	1.78	1, 25
R_s & peak SDA	$P < 0.79$	0.07	1, 24
Peak SDA and R_a	$P < 0.40$	0.74	1, 25

Table 8. ANCOVA statistics (test for homogeneity of slopes) for comparison of slope values among the 4 variables; 1) standard metabolism (R_s), 2) unfed reference, 3) peak SDA, and 4) active metabolism (R_a).

Wet body mass (g)	Max. SDA amp. ($\mu\text{mol O}_2 \text{ h}^{-1}$)	Scope for activity ($\mu\text{mol O}_2 \text{ h}^{-1}$)	% reduction of scope for activity by max. SDA amp.
0.5	2.5	12.8	19.4
1.0	4.8	20.7	23.1
1.5	7.1	27.4	25.8
2.0	9.3	33.3	27.9
2.5	11.5	38.7	29.6
3.0	13.6	43.7	31.2

Table 9. Reduction of scope for activity by maximum SDA amplitude for cod with a mass from 0.5-3.0 g wbm. Values for maximum SDA amplitude and scope for activity is calculated from the regression equations shown in figure 11.

SDA magnitude

SDA magnitude was found for juvenile cod with a mass ranging from 0.45 to 4.10 g (Table 4). A significant relationship was found between SDA magnitude and wbm ($P < 0.001$, $F_{1,13} = 18.37$, $r^2 = 0.59$). SDA magnitude increased with increasing wbm, following a power relationship with the equation $6.64x^{1.26}$.

Mass-specific SDA magnitude was calculated for four weight classes of juvenile cod: 1) 0-1, 2) 1-2, 3) 2-3, and 4) 3-4 g. Mass-specific SDA magnitude ranged from 6.2 to $11.7 \mu\text{mol O}_2 \text{ g}^{-1} \text{ wbm h}^{-1}$ (Table 6). There was no significant difference in mass-

specific SDA magnitude between the 4 different weight classes (ANOVA, $P < 0.90$, $F_{3, 10} = 0.18$).

SDA magnitude and food energy

SDA magnitude was expressed in energy units (joules) using oxycalorific coefficients for the conversion between consumed oxygen and energy expenditure. By doing so it was possible to express SDA magnitude as a percentage of the energy value of the ingested food, which is referred to as the relative magnitude of SDA (Jobling, 1981). SDA magnitude was converted into energy units using oxycalorific equivalents of $1 \mu\text{mol O}_2 = 0.218 \text{ Joules}$ (converted from Brett & Grove 's (1979) conversion factor of $13.6 \text{ kJ g}^{-1} \text{O}_2$). In similar fashion ingested food for each individual cod was converted to energy units (joules) using the conversion $20.82 \text{ J mg dry mass}^{-1}$ (values from Peck, 2003). Peck (2003) determined food energy values for identical type of food used in this experiment (BioKyowa, 1000) using a bomb calorimeter (Gebttry) ($N = 15$). Relative SDA magnitude ranged from 0.2-3.8% (Table 12). There was no significant relationship between relative SDA and wbm.

Wbm (g)	SDA magnitude (joules)	Meal energy (joules)	Relative SDA magnitude % SDA mag. of meal energy
0.45	0.6	157.9	0.4
0.81	1.1	425.1	0.3
1.20	1.4	206.5	0.7
1.32	0.5	303.7	0.2
1.36	9.9	364.4	2.7
1.53	2.0	413.0	0.5
2.06	2.2	364.4	0.6
2.13	4.3	340.1	1.3
2.45	3.2	631.6	0.5
2.82	6.5	546.6	1.2
2.84	13.1	340.1	3.8
2.99	6.4	206.5	3.1
3.01	7.4	473.7	1.6
4.00	4.5	862.4	0.5
4.10	8.9	413.0	2.2

Table 10. SDA magnitude and ingested meal represented in energy units (joules).
Relative SDA magnitude was calculated as the percentage of food energy lost to SDA magnitude.

CHAPTER 4

DISCUSSION

This study is the first to establish power-performance relationships between oxygen consumption and swimming speed for juvenile Atlantic cod ranging from 0.5 to 4.0 g. Standard and active metabolism were estimated from these power-performance curves by extrapolation. Other important findings from this study include:

1. Specific growth rates (G) ranged from 1.4 - 4.4% wet body mass d^{-1} for juvenile cod with wet mass ranging from 0.45 to 3.99 g. G decreased with increasing wet body mass (wbm).
2. Standard and active metabolism scaled with a mass exponent of $b = 0.96$ and 0.81 , respectively.
3. Scope for activity increased with increasing body mass. Mass-specific scope for activity decreased with increasing body mass.
4. SDA duration was short (2-8 h) compared to larger juveniles or adult fish (> 48 h).
5. Maximum SDA amplitude temporarily reduced the aerobic scope for activity 19 - 44%, with larger cod having a higher percentage of their aerobic scope taken up by SDA.
6. Relative SDA magnitude (% SDA magnitude of food energy) was 0.4 % - 3.8 %.
7. Gastric evacuation time was < 24 hours and total throughput time was < 48 h for Atlantic juvenile cod with a mass ranging from 0.41 - 4.15 g.

These findings and their importance will be discussed in detail in the following sections.

Growth comparison

Growth rates of the experimental group of cod (EG) and the experimental control group (ECG) were not significantly different, which indicate that the experimental procedure resulted in little or no stress on the EG. However, both the EG and the ECG displayed compensatory growth. For example, the biweekly starvation regime of these two groups of cod did not result in significantly lower growth rates compared to the weight control group (WCG).

Specific growth rates (G) for all juvenile cod ranged from 1.4 - 4.4% wet body mass (wbm) d^{-1} during the 75-d experimental period. G of the juvenile cod from the present study was slightly higher than values reported from other studies (Hunt von Herbing & White, 2002). Hunt von Herbing & White (2002) found G of 1 - 4% wbm d^{-1} for juvenile cod with a weight ranging from 1.0 – 8.0 g wbm, and held at a temperature of $10.0 \pm 0.05^{\circ}\text{C}$.

In this study G decreased as the mass of the juvenile cod increased. This phenomenon is well documented in fishes, which grow throughout their life (Jobling, 1988). For example, larval stages of Atlantic cod can grow much faster, often exceeding G of 30% wbm d^{-1} (Finn *et al.*, 2002). In contrast, older juveniles and adult cod experience much lower growth rates. Jobling (1988) found growth rates of 0.4 - 0.9 % wbm d^{-1} for cod kept at a temperature of 8.0°C and with a size ranging from 250 to 2000 g wbm. Similarly, Houlihan (1988) found specific growth rates of 0.2 - 2.0% wbm d^{-1} for Atlantic cod with a mass of 73 - 492 g at a temperature of $10.0 \pm 0.5^{\circ}\text{C}$. Specific growth rates calculated from this study compare well with other studies and supported the growth pattern of decreasing growth rates with increasing size of fish.

Standard and active metabolism

Power-performance curves

In this study power-performance relationships between oxygen consumption ($\mu\text{mol O}_2 \text{ h}^{-1}$) and swimming speed (cm s^{-1}) were established for the first time for juvenile Atlantic cod with a size ranging from 0.53 to 2.89 g wbm. Standard and active metabolism was estimated from these power-performance relationships by extrapolation.

Metabolic scaling relationships

The allometric relationships of standard and active metabolism with body mass followed the equation $\text{VO}_2 = aW^b$, where a is the scaling constant (intercept), W is wet body mass and b is the scaling exponent (Burness, 2002). In this study, standard and active metabolism scaled with a mass exponent of $b = 0.96$ and 0.81 , respectively for juvenile cod with a wbm from $0.5 - 3.0$ g. This suggests that standard metabolic rate changes proportional to body mass in early juvenile fish, whereas active metabolism decreases on a mass unit basis with increasing body mass.

The discussion about the value of the metabolic scaling exponent in developing is currently being debated. One hypothesis is that the scaling relationship between metabolism and body mass changes as a function of fish developmental stage with a higher scaling exponent for fish larvae than for juvenile and adult fishes (Giguere, 1988; Post & Lee, 1996). For example, scaling exponents close to unity ($b = 1$) have been found for some fish larvae (Giguere *et al.*, 1988; Kaufmann, 1990; Wieser & Medgyesy, 1990; Rønnestad & Naas, 1993; Rombough, 1994; Finn *et al.*, 1995), whereas older

juvenile and adult fishes often have metabolic scaling exponents closer to the 0.75 power scaling coefficient first proposed by Kleiber (1932) (Post & Lee, 1996).

Recently, Finn *et al.* (2002) argued that isometric scaling cannot be generalized in larval fishes and several studies have reported metabolic scaling exponents of less than unity (Laurence, 1978; Grubner & Wieser, 1983; Wieser & Forstner, 1986; De Silva *et al.*, 1986; Bishop & Torres, 1999, Finn *et al.*, 2002). Finn *et al.* (2002) found the metabolic scaling exponent of larval Atlantic cod to be $b = 0.88 - 0.89$ for light adapted larvae and $b = 0.90 - 0.91$ for dark-adapted larvae. These values of scaling exponents in larval Atlantic cod are similar to values reported for older juvenile and adult cod (Saunders, 1963; Edwards *et al.*, 1972). For example, Saunders (1963) found that the routine metabolism (R_r) of Atlantic cod with a wet body mass of 190- 3230 g scaled with a mass exponent of $b = 0.89$. Edward *et al.* (1972) found a scaling exponent of routine metabolism in adult cod of $b = 0.82$. Finn *et al.* (2002) concluded that the scaling exponent for Atlantic cod is maintained throughout the life of Atlantic cod.

Scaling exponents reported for early juvenile Atlantic cod are lower than reported for both larval and adult Atlantic cod and therefore do not support either of the two schools of thought previously described. Hunt von Herbing & White (2002) found a mass exponent $b = 0.76$ for unfed routine metabolism and $b = 0.79$ for maximum metabolic rate (fish chased to exhaustion) of juvenile Atlantic cod with a mass of 1.0 - 8.0 g and at a temperature of $10 \pm 0.5^\circ\text{C}$. Peck (2003) found the scaling exponent for low routine metabolism of $b = 0.73$ for juvenile cod with a mass of 0.15 -23.01g. The scaling exponent from this study for active metabolic rate ($b = 0.81$) are close to Hunt von Herbing & White's (2002) value for maximum metabolic rate ($b = 0.79$). On the other

hand, the scaling exponent for standard metabolic rate ($b = 0.96$) from the present study is much higher than Hunt von Herbing & White's (2002) value for unfed routine ($b = 0.76$) and Peck's (2003) value for low routine ($b = 0.73$). This may, to some extent, result from different methodologies used in calculation the mass exponent. For example neither Hunt von Herbing & White (2002) nor Peck (2003), controlled for spontaneous activity of the juvenile cod in the respirometers. Further research needs to be done in this area to further knowledge of metabolic scaling at different life stages of fishes.

Mass-specific standard and active metabolic rates

Mass-specific values (VO_2/wbm) of standard and active metabolic rates for the EG were calculated to allow direct comparisons to other metabolic studies of Atlantic cod. Mean values for mass specific standard (R_s/M) and active metabolism (R_a/M) from this study were $6.4 \pm 1.6 \mu\text{mol O}_2 \text{ g}^{-1} (\text{wbw}) \text{ h}^{-1}$ and $24.3 \pm 4.5 \mu\text{mol O}_2 \text{ g}^{-1} (\text{wbw}) \text{ h}^{-1}$ respectively for juvenile cod in the size range 0.53 -2.89 g. The only other study in the literature reporting values of oxygen consumption of juvenile cod in the size range from 1.00 - 3.00 g is by Hunt von Herbing & White (2002). Their values for mass-specific routine metabolism (R_r) are lower than the R_s values found in this study and ranged from $3.6 - 2.4 \mu\text{mol O}_2 \text{ g}^{-1} (\text{wbw}) \text{ h}^{-1}$ for juvenile cod with a mass from 1.53 to 3.45 g.

Mass-specific standard metabolic rate is much higher for larval cod ($31.3 - 70.6 \mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$) than juveniles ($2.4 - 8.2 \mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$) or adults ($0.6 - 4.6 \mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$). This scaling relationship with a higher mass specific metabolism for smaller fish than larger fish also seems to apply to active metabolism (Table 11). Active metabolic

rates have not yet been measured in larvae of Atlantic cod since they are incapable of sustained high-speed swimming.

Mass specific values for standard and active metabolism from this study corresponded well with values reported from other similar studies and supports allometric scaling relationships between mass and metabolism in juvenile fish.

Author	Mass (g) Or size (mm)	Metabolic variable	VO ₂ μmol O ₂ g ⁻¹ h ⁻¹	Water Temperature	N
Hunt von Herbing & Boutilier (1996)	5-8 *	R _{routine}	70.6	10°C	
Davenport & Lonning (1980)		R _{resting}	31.3 – 62.0		
Hansen (2003)	1.39 ± 0.73	R _s	6.4 ± 1.6	10°C	13
	1.39 ± 0.73	R _a	24.3 ± 4.5	10°C	13
Hunt von Herbing & White (2002)	1.53 ± 0.06	R _{routine}	3.6 ± 1.8	10°C	12
	2.53 ± 0.14	R _{routine}	2.4 ± 1.2	10°C	10
	3.45 ± 3.45	R _{routine}	2.4 ± 0.4	10°C	7
Soofiani & Hawkins (1982)	29.3 – 82.9	R _{routine}	8.2 ± 1.0	10°C	
Soofiani & Priede (1984)	188.1	R _s	6.1	10°C	
	188.1	R _a	11.4	10°C	
Sundnes (1957)	280	R _{resting}	3.2	8.7-10.7°C	1
	1750	R _{resting}	4.6		1
Schurmann & Steffensen (1997)	371.1 ± 124.2	R _s	3.9 ± 0.7	10°C	11
	371.1 ± 124.2	R _a	12.4 ± 2.2		2
Tang <i>et al.</i> , (1994)	654-1472	R _a	3.3 – 5.1	5°C	10
Nelson, Tang & boutilier (1996)	1140 ± 0.06 (SSC)	R _s	0.6 – 0.8	2°C	5
	1030 ± 0.06 (BDC)	R _s	0.9 – 1.0	2°C	6
Saunders (1963)	500-6000	R _{routine}	4.6-3.5	10°C	4

Table 11. Literature values of respirometry data of Atlantic cod *Gadus morhua* L. * =

mm.

Scope for activity

Aerobic scope for activity represents the energy that is available to the fish for all activities like feeding, swimming, searching for prey, ingestion, digestion and growth.

Scope for activity is usually defined as the difference between active and standard metabolism ($R_a - R_s$).

The slope values for standard and active metabolism versus wbm are not significantly different over the weight range 0.53 - 2.89 g wbm (ANCOVA, $P > 0.35$, $F_{1,27} < 0.89$) (Fig. 7). This indicates that the scope for activity is higher per unit body mass in smaller juvenile cod than larger juvenile cod. ANOVA's performed on the three

significantly higher for juvenile cod with a wet body mass between 0.45-1.00 g (weight class 1) ($26.2 \pm 6.9 \mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$) compared to juvenile cod with a wet body mass between 2.00 –3.00 g (weight class 3) ($14.4 \pm 3.4 \mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$) (Table 3).

Values from other studies support the observation that larger Atlantic cod have a lower mass specific aerobic scope for activity (Soofiani and Priede, 1984). Soofiani and Priede (1984) found mass specific scope for activity for juvenile cod with a mean mass of 188.1 g wbm to be $5.29 \mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$ (at 10.0°C). This higher mass-specific scope for activity for smaller juvenile cod may translate into a higher growth potential, since more energy is available for nutritive processes on a per mass basis. It is well established that smaller cod have higher G's compared to larger cod (Edwards *et al.*, 1972; Houlihan, 1988; Finn *et al.*, 2002). However, whether there is a causal relationship between growth rates and aerobic scope for activity in fish requires further research.

Specific dynamic action (SDA)

Effects of body mass on SDA magnitude, amplitude and duration were investigated in juvenile cod in the size range 0.45 - 4.10 g. Post-prandial oxygen consumption in this study was measured while the experimental fish were swimming at a slow cruising speed of 4.26 cm s^{-1} . Consequently, oxygen consumption will be directed to energy demands for processing food and swimming activity simultaneously. To compensate for swimming activity, true SDA was calculated by subtracting the post-absorptive oxygen consumption of cod swimming at 4.26 cm s^{-1} . This methodology was used under the assumption that low cruising speed of the juvenile cod does not affect the magnitude, duration or amplitude of SDA. Alsop & Wood (1997) investigated the

impact of swimming activity on SDA in juvenile rainbow trout (*Oncorhynchus mykiss*) and found that SDA was not significantly dependent on swimming velocity.

Many studies that have reported values of SDA have measured SDA at low routine activity and allowed the fish to swim freely in the respirometer chamber (Jobling & Davies, 1980; Soofiani & Hawkins, 1982; Furnell, 1987; Wieser & Medgyesy, 1990; Carter & Brafield, 1991; Johnston & Battram, 1993; Finn *et al.*, 2002; Hunt von Herbing & White, 2002; Peck, 2003). However, the difference in oxygen consumption for fed and unfed fish under these conditions may reflect other factors besides SDA. For example, intensive feeding often stimulates spontaneous activity, whereas starvation reduces spontaneous activity (Beamish, 1964; Brett & Zala, 1975; Jobling, 1994). Brett & Zala (1975) found that oxygen consumption of juvenile sockeye salmon (*Oncorhynchus nerka*) peaked immediately prior the daily feeding. Also, in cases where SDA is measured on several fish in one respirometer, there might be added costs of social factors like aggression and overcoming flows generated by other fish (Christiansen & Jobling, 1990).

Only two studies have measured SDA in early juvenile cod in the mass range from 1.0 –10.0 g (Hunt von Herbing & White, 2002; Peck, 2003). Due to the respirometry system used, neither study accounted for spontaneous swimming activity. This could have led to an overestimation of SDA because energy expenditure of spontaneous and feeding related activity may have contributed to the true SDA value.

In the present study, tunnel respirometers were used for the first time to measure the feeding metabolism of early juvenile cod. Feeding-related spontaneous feeding activity was accounted for by measuring oxygen consumption of fed and unfed fish swimming at a controlled low routine swimming speed. Also, no social factor was

present because SDA was measured on individual fish. A more precise estimate of SDA may be obtained by controlling for swimming activity in this fashion, because feeding-related spontaneous swimming activity is removed from the measurements of SDA.

Meal size and wet body mass

Juvenile cod were fed to satiation (1.2 ± 0.6 % wbm (S.D.)) with BioKyowa food pellets (1000 μ m) prior to each SDA experiment. There was a significant relationship between wbm and meal size ($P < 0.03$, $F_{1,13} = 6.28$) with larger cod eating larger meals. However, smaller cod ate larger meals per unit mass basis than larger cod ($P < 0.001$, $F_{1,13} = 10.47$), which may be due to the demand of fueling a higher metabolic rate.

SDA duration

In this study SDA duration lasted from 2 to 8 h. Hunt von Herbing & White (2002) found SDA duration between 3 and 11 h for juvenile cod with a wbm of 1.00 – 8.00 g at a temperature of 10°C. Similarly Peck (2003) found SDA to last from 2.9 to 13.2 h in juvenile cod (0.2 -23.0 g wbm), with a temperature range from 4.5 to 15.5°C. SDA durations found in this study and other similar studies for small juvenile cod are much shorter than SDA durations found in larger juvenile cod. For example, Soofiani & Hawkins (1982) reported SDA duration of 1-2 d at 10°C for larger juvenile cod (29.3 – 82.9 g wbm). The shorter duration of SDA in small juvenile cod may be due to a higher rate of digestion needed to fuel a higher mass-specific metabolism and higher growth rates compared to larger cod. Gastric evacuation time for juvenile cod in the mass range 0.62 g – 4.15 g was < 24 hours in the present study. Jobling & Davies (1980)

demonstrated a correlation between gastric evacuation time (the time from ingesting the meal to no food is left in stomach or intestine) and duration of SDA in the plaice, *Pleuronectes platessa*. According to Jobling & Davies (1980), SDA may cause elevated oxygen consumption for some time after the food has been transported across the mucosa to the blood stream. Gastric evacuation time may therefore be an indicator of SDA duration.

A shorter duration of SDA may increase the survival of smaller juvenile cod, which are highly vulnerable to predators. The increased oxygen consumption caused by SDA temporarily reduces the energy available for activities like swimming, feeding and predator avoidance. Small fish digest a meal faster than larger fish. Therefore, small fish may have more energy available to them for other metabolic activities because of the reduced SDA duration.

SDA duration and wet body mass

There was no significant relationship between SDA duration and wbm ($P < 0.21$, $F_{1,13} = 1.75$), or SDA duration and meal size ($P < 0.91$, $F_{1,13} = 0.01$). SDA duration may be affected by a number of factors including temperature (Saunders, 1963; Jobling & Davies, 1980; Tupper, 1994), meal size (Soofiani & Hawkins, 1982; Vahl & Davenport, 1979; Peck, 2003), composition of meal (Vahl & Davenport, 1979), body mass of fish (Beamish, 1974; White, 2000) and gastric evacuation time (Beamish, 1974; Jobling & Davies, 1980). Results from this study do not support a strong relationship between SDA duration and meal size or a relationship between SDA duration and body mass.

SDA amplitude

Post-prandial oxygen consumption rose rapidly after ingestion of a meal and peaked (peak SDA) within 1 h after feeding for all juvenile cod. Post-prandial oxygen consumption gradually decreased after peak SDA until prefeeding levels were reached. The time to peak SDA in this study compares well with values from other studies. For example, Hunt von Herbing & White (2002) found that SDA peaked within 1 h after ingestion of a meal for juvenile cod in the mass range from 1.00 to 8.00 g at a temperature of 10°C. Peak SDA of 2-4 h has been observed in the largemouth bass, *Micropterus salmoides* (Beamish, 1974), and the bluegill, *Lepomis macrochirus* (Pierce & Wissing, 1974). In contrast, the time to peak SDA is much longer in larger juvenile and adult cod. Soofiani & Hawkins (1982) found SDA to peak almost 48 h after ingestion of a meal in larger juvenile cod (29.3 – 82.9 g wbm).

Peak SDA was 1.12-2.22 times the standard metabolic rate. Hunt von Herbing and White (2002) reported values of relative peak SDA (peak SDA/ R_r) to be 1.4-1.7 in juvenile cod with a wbm of 1 to 8 g. Similarly, Peck (2003) found values of relative peak SDA (peak SDA/ R_{resting}) to range between 1.48-1.68 for juvenile cod with a wbm between 0.2 and 23.0 g. Jobling (1981) listed values of relative peak SDA from the literature from many species of fishes and found that peak SDA range between 1.6 - 2.6 times the standard or low routine metabolism. Values of relative peak SDA from this study thus fall within the range of other published values.

SDA amplitude and scope for activity

Specific dynamic action will temporarily reduce the aerobic scope for activity, and may thereby limit any other metabolic activities (Soofiani & Hawkins, 1982; Alsop & Wood, 1997). In this study maximum SDA amplitude (peak SDA – unfed reference) accounted for 19-44% of the aerobic scope for activity, with larger cod having higher SDA amplitude. Reported values for the reduction of scope for activity by the post-prandial increase in oxygen consumption following ingestion of a meal is from 30 to more than 100% depending on fish species, size of fish, meal size, and methods of determining scope for activity and SDA (Muir & Niimi, 1972; Beamish, 1974; Vahl & Davenport, 1979; Hunt von Herbing & White, 2002). Hunt von Herbing & White (2002) found that apparent SDA reduced the relative scope for activity ($R_{\max} - R_r$) up to 98% in small (1.0 – 2.0 g) juvenile cod and exceeding 100% in larger (3.0 - 8.0 g) juvenile cod. Apparent SDA reduced the relative scope for activity ($R_{\max} - R_r$) up to 98% in larger juvenile cod (29.3 - 82.9 g) (Soofiani & Hawkins, 1982).

The proportion of scope for activity taken up by SDA was lower in this study compared to values from Hunt von Herbing & White's (2002) study on early juvenile cod and Soofini & Hawkins' (1982) study on larger juveniles and adult cod. This may partly be due to different methodologies used. For example, relative scope for activity ($R_a - R_r$ or $R_{\max} - R_r$) is smaller than true scope for activity ($R_a - R_s$), since routine respiration (R_r) is higher than standard metabolism (R_s). Similarly, apparent SDA is higher than true SDA since routine swimming activities are not accounted for and may therefore contribute a significant portion of the SDA. This may explain why some studies report SDA taking up more than 100% of the scope for activity, and why values from this study are in the

lower range of reported values. Despite the large variation in reported values for maximum SDA amplitude in relation to scope for activity it is clear that SDA does account for a substantial increase of the metabolism and can take up a great portion of the scope for activity. Fish experiencing a reduction in scope for activity caused by postprandial metabolism consequently may be limited in further swimming activities or food capture and be more vulnerable to predators.

The results from this study indicate that juvenile cod may not be limited by a reduction of scope due to SDA to the extent previously thought. The reduction of scope for activity by SDA measured in this study (19-44%) leaves a significant amount of energy for swimming. It might be an advantage for a fast growing fish to leave a surplus of energy for further searching for prey and predator avoidance. With more energy available for swimming activity while digesting and a short SDA duration (faster processing of a meal), juvenile cod may be adapted to small, frequent meals. In contrast, SDA takes up a larger percentage of the scope for activity in larger cod and SDA duration is longer (Soofiani & Hawkins, 1982). Adult cod therefore have less energy available for swimming activity while digesting a meal, but have less need to evade diverse predators.

SDA magnitude

In this study the relative SDA magnitude (% SDA of ingested food energy) ranged from 0.2-3.8 % for juvenile cod with a mass ranging from 0.45 to 4.10 g. Studies reporting values for relative SDA magnitude for larval and early juvenile fishes are rare. Peck (2003) reports mean values of relative SDA of 3.9 ± 0.1 % (N = 166) for juvenile Atlantic cod with a wet body mass ranging from 0.15 – 23.01 g and fed above

maintenance rations (temperature range of 4.5 – 15.5°C). There is strong agreement between Peck's (2003) study and this study for values of relative SDA magnitude in early juvenile Atlantic cod.

In contrast, Soofiani & Hawkins (1982) found values of relative SDA magnitude as high as 11.85% in larger juvenile cod (29.3 - 82.9 g.) fed to satiation and kept at a temperature of 10°C. Feeding metabolism in smaller juvenile cod therefore seems to differ from larger juveniles and adults. Observed major differences are shorter SDA durations and lower relative SDA magnitudes in smaller juvenile cod.

Summary

Results from this study indicate that the swimming and feeding metabolism in early stages of juvenile Atlantic cod differs from that of larger juvenile and adult cod (Table 12). Physiological differences between early juvenile and adult cod may be the results of the metabolic demand of high growth rates in small juvenile cod. Further research is needed to determine physiological differences and the underlying mechanisms in different life stages of the Atlantic cod and other fishes. Thus future research will increase knowledge about how energy is regulated in fast growing fishes in order to fuel the high growth rates.

Observed Bioenergetic differences from present study	
Early juvenile Atlantic cod	Large juvenile or adult Atlantic cod
High specific growth rates Appr. 4 %	Low specific growth rates < 2% (Jobling, 1988; Houlihan, 1988)
Short SDA duration < 8 h	Long SDA duration > 48 h (Soofiani & Hawkins, 1982)
Short time to peak SDA < 2 h	Long time to peak SDA Appr. 48 h (Soofiani & Hawkins, 1982)
Lower relative SDA 0.2 - 3.8% SDA magnitude of meal energy	Higher relative SDA ~12% (Soofiani & Hawkins, 1982)
SDA takes up smaller percentage of scope for activity. 19 - 44%	SDA takes up higher percentage of scope for activity, up to 98% (Soofiani & Hawkins, 1982)
High mass-specific scope for activity 14.4 -26.2 $\mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$	Low mass-specific scope for activity 5.3 $\mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$ (Soofiani & Priede, 1984)
Higher mass-specific standard metabolism 6.4 \pm 1.6 $\mu\text{mol O}_2 \text{ g}^{-1}$ (wbw) h^{-1}	Lower mass-specific standard metabolism 0.6 – 4.6 $\mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$ (Soofiani & Priede, 1984; Nelson, Tang & boutilier, 1996; Schurmann & Steffensen, 1997)
Higher mass-specific active metabolism 24.3 \pm 4.5 $\mu\text{mol O}_2 \text{ g}^{-1}$ (wbw) h^{-1}	Lower mass-specific active metabolism 3.3 – 12.4 $\mu\text{mol O}_2 \text{ g}^{-1}$ (wbw) h^{-1} (Soofiani & Priede, 1984; Tang <i>et al.</i> , 1994; Schurmann & Steffensen, 1997)

Table 12. Observed bioenergetic differences between early juvenile Atlantic cod from the present study and larger juvenile and adult cod.

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APPENDIX

DATA FOR GROWTH, GASTRIC EVACUATION TIME AND POWER-PERFORMANCE REGRESSIONS

Weight data and specific growth rate for juvenile Atlantic cod

Experimental group (EG)			Weight control group (WCG)		
Days post hatch	Wbw (g) (Mean \pm S.D.)	N	Days post hatch	wbw (g) (Mean \pm S.D.)	N
115	0.51 \pm 0.2	25	126	0.78 \pm 0.3	10
137	1.09 \pm 0.4	25	131	1.23 \pm 0.5	10
152	1.76 \pm 0.7	24	140	1.19 \pm 0.5	10
167	2.79 \pm 0.8	22	147	1.60 \pm 0.4	10
181	3.43 \pm 0.8	22	154	2.20 \pm 0.7	10
191	3.91 \pm 0.9	22	161	2.35 \pm 0.7	10
			168	3.32 \pm 1.1	10
			174	3.24 \pm 0.7	10
			181	5.00 \pm 1.2	10
			189	4.88 \pm 1.2	10
Experimental fish (EF)					
Days post hatch	wbm (g)	G (% wbm d ⁻¹)	Days post hatch	wbm (g)	G (% wbm d ⁻¹)
115 (1)	0.40	4.3	143 (6)	1.56	3.0
129 (1)	0.73	4.1	158 (6)	2.45	2.5
143 (1)	1.30	3.1	171 (6)	3.37	2.5
158 (1)	2.07	2.3	178 (6)	4.00	0.1
164 (1)	2.37	1.6	185 (6)	4.03	1.5
178 (1)	2.95	1.5	120 (7)	1.18	1.6
120 (2)	2.14	2.6	136 (7)	1.53	1.4
136 (2)	3.22	1.2	145 (7)	1.73	1.5
148 (2)	3.73	0.2	159 (7)	2.13	0.8
162 (2)	3.83	0.1	166 (7)	2.25	1.0
176 (2)	3.88	0.9	187 (7)	2.76	1.8
124 (3)	0.83	3.6	124 (8)	0.45	3.9
139 (3)	1.42	2.9	139 (8)	0.81	3.0
152 (3)	2.07	2.4	148 (8)	1.06	3.6
166 (3)	2.89	1.4	155 (8)	1.36	1.2
180 (3)	3.52	1.4	162 (8)	1.48	1.9
125 (4)	0.81	2.6	125 (9)	1.20	3.6
140 (4)	1.20	1.9	140 (9)	2.06	1.9
153 (4)	1.53	1.6	149 (9)	2.45	2.0
167 (4)	1.90	1.9	156 (9)	2.82	2.0
181 (4)	2.46	2.4	163 (9)	3.25	1.7
127 (5)	0.55	4.1	177 (9)	4.10	1.8
145 (5)	1.14	3.6	184 (9)	4.64	1.9
159 (5)	1.88	1.4	174 (10)	3.01	1.4
115 (6)	0.53	4.5	181 (10)	3.31	2.4
129 (6)	0.99	3.3	176 (11)	2.99	0.8
			183 (12)	3.16	2.1

Table A1. Weight data and specific growth rate for juvenile Atlantic cod. Data for ECG and WCG are given as a mean \pm S.D. Weight data for EG is given for individual juvenile cod. Numbers in parentages in the days post hatch column for the EG indicates individual juvenile cod. Specific growth rate (SGR) are shown for the EG.

Wet body mass and dry body mass for juvenile Atlantic cod

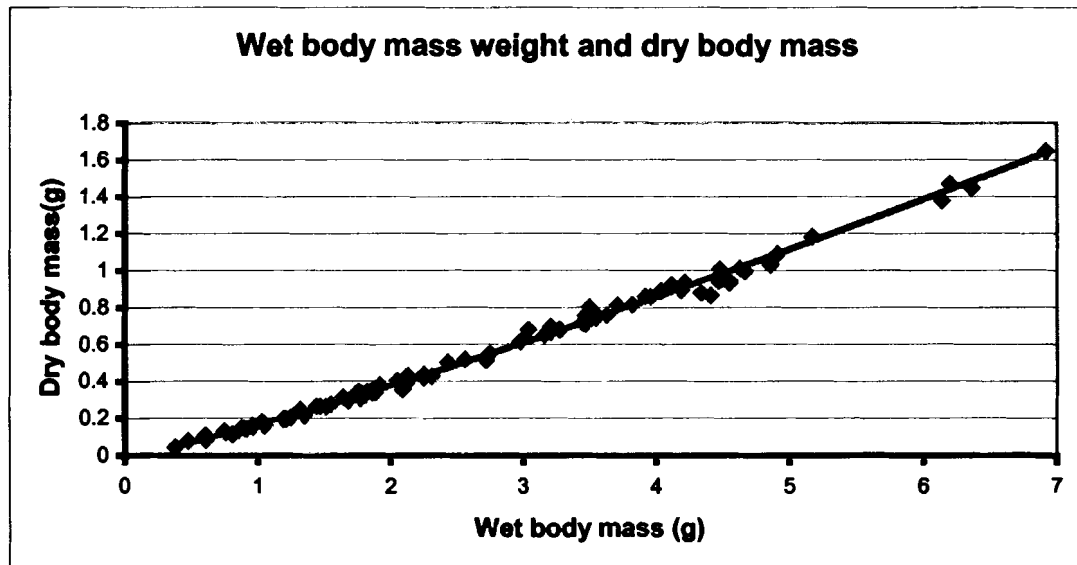


Figure A1. Wet and dry body mass for juvenile Atlantic cod. The relationship followed a power curve with the equation $y = 0.166X^{1.18}$, $r^2 = 0.995$.

Wet body mass and crude ash for juvenile Atlantic cod

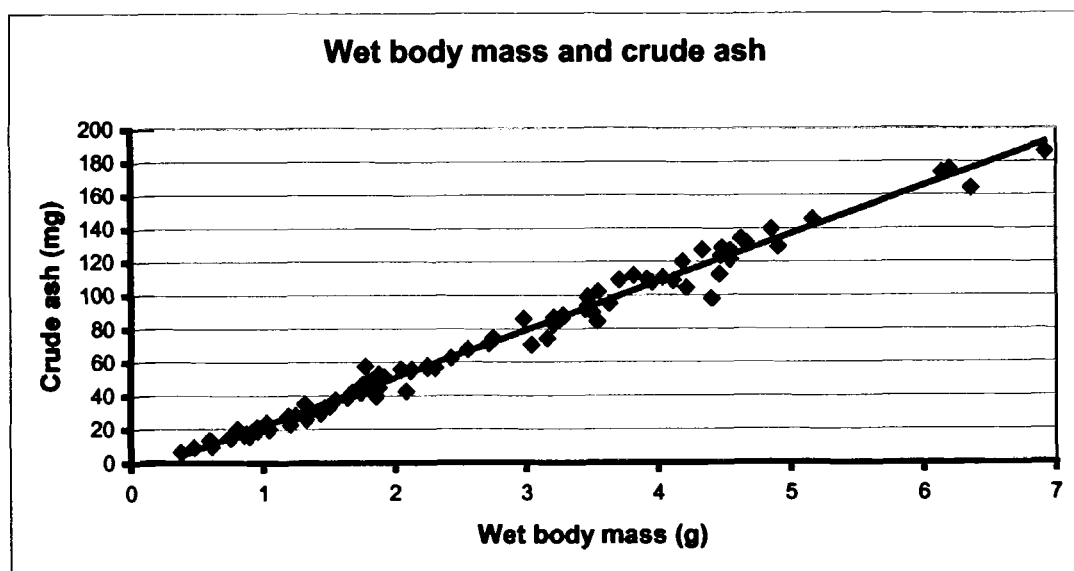


Figure A2. Wet body mass and crude ash for juvenile Atlantic cod. Linear regression equation was $y = 28.68X - 6.51$. $r^2 = 0.99$.

Gastric evacuation and total throughput time in juvenile cod

Starvation time (hours)	Wet body mass (g)	Total length (mm)	Digesta in stomach	Digesta in intestine
24	0.62	47	No	No
24	0.66	45	No	No
24	0.78	48	No	Yes
24	0.89	50	No	No
24	0.92	52	No	Yes
24	1.65	65	No	Yes
24	1.67	63	No	Yes
24	1.79	63	No	Yes
24	1.82	66	No	Yes
24	3.66	82	No	Yes
36	0.41	41	No	No
36	0.43	42	No	Yes
36	0.49	46	No	Yes
36	0.75	51	No	No
36	1.31	57	No	No
36	1.26	58	No	No
36	2.46	71	No	No
36	2.41	74	No	No
36	3.44	80	No	Yes
48	0.71	48	No	No
48	0.75	49	No	No
48	0.78	49	No	No
48	0.93	54	No	No
48	0.99	52	No	No
48	1.51	64	No	No
48	2.23	73	No	No
48	2.44	70	No	No
48	3.28	80	No	No
48	4.15	84	No	No

Table A2. Gastric evacuation and total throughput time in Juvenile Atlantic cod, *Gadus morhua*. Cod were starved for 24, 36 and 48 h. Observation of presence digesta in stomach and intestine is recorded in the two right columns.

Power-performance relationships

wbm	Intercept mean \pm SE	Slope mean \pm SE	r^2	P	F-value
0.53	0.77 \pm 0.05	0.25 \pm 0.05	0.99	P<0.000	F _{1,4} = 206.1
0.55	0.58 \pm 0.09	0.55 \pm 0.08	0.89	P<0.002	F _{1,5} = 39.1
0.73	0.60 \pm 0.09	0.65 \pm 0.10	0.89	P<0.003	F _{1,4} = 42.1
0.81	0.67 \pm 0.11	0.54 \pm 0.12	0.79	P<0.007	F _{1,5} = 18.8
1.14	1.00 \pm 0.13	0.42 \pm 0.15	0.61	P<0.038	F _{1,5} = 7.9
1.18	1.04 \pm 0.06	0.27 \pm 0.08	0.80	P<0.040	F _{1,3} = 12.2
1.20	1.19 \pm 0.07	0.37 \pm 0.08	0.80	P<0.006	F _{1,5} = 20.3
1.42	1.05 \pm 0.10	0.54 \pm 0.11	0.89	P<0.015	F _{1,3} = 25.3
1.53	0.96 \pm 0.14	0.48 \pm 0.16	0.63	P<0.032	F _{1,5} = 8.7
1.88	1.18 \pm 0.09	0.34 \pm 0.10	0.70	P<0.020	F _{1,5} = 11.4
1.90	1.13 \pm 0.09	0.46 \pm 0.11	0.86	P<0.023	F _{1,3} = 18.8
2.07	1.01 \pm 0.15	0.52 \pm 0.18	0.64	P<0.031	F _{1,5} = 8.8
2.07	1.17 \pm 0.07	0.37 \pm 0.08	0.87	P<0.021	F _{1,3} = 19.9
2.37	1.04 \pm 0.04	0.49 \pm 0.04	0.98	P<0.001	F _{1,3} = 128.2
2.89	1.26 \pm 0.11	0.36 \pm 0.12	0.62	P<0.034	F _{1,5} = 8.3

Table A3. Regression statistics for power-performance relationships. Regression statistics for log transformed oxygen consumption and swimming speed. Each row represents one individual cod.

Biography of the Author

Søren Lund Hansen was born in Næstved, Denmark on August 13, 1973. After graduating from Næstved Gymnasium (High School) in 1993 he went backpacking for over a year, traveling to Australia, New Zealand, Fiji and Indonesia. He then attended Roskilde University, Denmark and graduated in 1999 with a combination Bachelor of Science degree in Environmental Biology and Chemistry. Since he was young, Søren was always fascinated by the ocean and engaged in activities like fishing, sailing and scuba diving. In 1996 Søren became a PADI SCUBA instructor and since then a specialty instructor in drift diving and night diving. Every summer while he was an undergraduate student he taught SCUBA diving in Greece. He has certified more than 60 persons from 8 different nations in SCUBA courses from entry level to divemaster.

After completion of his Master's degree Søren plans to continue advanced studies at the University of Maine. He will pursue a Ph.D. degree in Marine Biology working with difficult-to-rear tropical reef fishes. While pursuing his Ph.D., Søren will be a co-owner of "Sea & Reef Aquaculture". This incubator business on campus will develop aquaculture techniques for the captive rearing of marine ornamental aquarium fish. Søren is a candidate for the Master of Science degree in Marine Biology from The University of Maine in May, 2003.