

INTERPOPULATION DIFFERENCES IN GROWTH,
FOOD CONVERSION EFFICIENCY AND SWIMMING
PERFORMANCE OF (0+) JUVENILE ATLANTIC COD
(*Gadus morhua*)

CENTRE FOR NEWFOUNDLAND STUDIES

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MANJUSRI PANDULA ATAPATTU WIJEKON

Interpopulation differences in growth, food conversion efficiency and swimming performance of (0+) juvenile Atlantic cod (*Gadus morhua*).

by

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A thesis submitted in partial fulfillment of the requirements for the degree of Master of
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Abstract

Studies have shown that geographically separated fish populations can exhibit life history variations in growth, and that environmental variability and /or genetic differences are responsible for such variations. It has been suggested that common garden experiments could be used to disassemble the environmental and genetic effects on growth in such latitudinally separated populations. The Counter-gradient variation (CnGV) hypothesis originated from such experiments, and predicts that northern populations will grow faster than their southern counterparts. The Atlantic cod (*Gadus morhua*) has a wide distribution over the North Atlantic Ocean and growth varies significantly among stocks. Understanding such differences in growth could be beneficial for both fisheries management practices and aquaculture of Atlantic cod.

In my thesis, I first examined the growth of cod from different populations, using common garden experiments. I compared the specific growth rate, food conversion efficiency, hepatosomatic index and survival of juveniles from two cod stocks (NAFO Division 3Ps- Placentia Bay, NF. 48°N; 54° W and 4T- Northumberland Strait, P.E.I. 46° N; 64° W) at two temperatures (7 °C & 11 °C) and rations (2% and 0.67% per day). I found no significant difference in growth, food conversion efficiency or hepatosomatic index; however, 3Ps juveniles had significantly higher survival rate (97%) than 4T juveniles (90%) with 2% ration at 11 °C. In addition, reaction norm analysis suggested that genetic differences did exist in certain traits (specific growth rate, hepatosomatic index etc.) between these two cod stocks.

The CnGV hypothesis also suggests that variations in growth among life-history stages of latitudinally separated populations may lead to trade-offs with other biologically important characteristics such as swimming performance. Thus, in my second experiment, I compared the swimming performance (*Ucrit*), metabolism (resting, active and scope) and cost of transport (COT) between these two populations. Juveniles from both populations spent more energy on swimming at higher temperature (11°C). There was no significant difference in metabolic scope for activity between 4T and 3Ps juveniles; however, 4T juveniles had a 20% higher metabolic scope for activity over 3Ps at high temperature suggesting a greater availability of energy for activity. I found no other significant differences in metabolic rate, *Ucrit*, metabolic scope or COT between 3Ps and 4T juveniles.

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Chapter 1.0

General Introduction

World aquaculture production currently accounts for 29% of the total yield of seafood, and aquaculture is currently the only worldwide seafood growth sector. (Anonymous, 2000). Starting from an insignificant total production before the 1950's, inland and marine aquaculture production has grown by about 10% per year since 1990. In contrast, the harvest from capture fisheries reached a plateau in the 1990's. This indicates that the aggregated stocks of the world are being harvested at or near their maximum sustainable yield (Aiken & Sinclair, 1995). With the rapidly increasing world demand for seafood protein in recent decades, it has been concluded that aquaculture will be the primary source of seafood protein by the 21st century (Drucker, 1999).

Given the need for, and significance of, the development in aquaculture, it is important to consider the status of capture fisheries. The global exploitation of many marine species follows the general trend described above, while the number of underexploited and moderately exploited fisheries resources continues to decline slightly. Further, the state of some of the highest producing stocks has worsened. A good example of this is the collapse of Atlantic cod *Gadus morhua* in Northwest Atlantic Ocean, a key ground fish stock that has been severely over exploited.

1.1 Atlantic Cod (*Gadus morhua*) - Background and the present situation

The Atlantic cod is one of 59 species of the family Gadidae, and has been the dominant commercial species of the Northwest Atlantic (Lear, 1989). This species is

widely distributed over the Northwest Atlantic, and occurs from inshore shallow waters (about 5 m) to the edge of the continental shelf (in water as deep as 600m). Adult cod generally average 2 to 3 kg in weight, and about 60 to 70 cm in length (Scott & Scott, 1988).

The Northern Atlantic cod fishery has experienced a collapse due to overexploitation (Myers *et al.*, 1997; Smedbol & Wroblewski, 2002), environmental changes (Rose *et al.*, 1994) and unbalanced predator-prey linkage (i.e. seals) to a certain extent (Larsen, 1993; Mohn & Bowen, 1996; Stenson *et al.*, 1997; Bundy *et al.*, 2000; Larsen, 2002). For example, it is estimated that the spawning biomass of Atlantic cod declined almost two orders of magnitude from 1962 to 1992 (Hutchings, 1996). This resulted in a fishing moratorium off Newfoundland in 1992 (Smedbol & Wroblewski, 2002).

Depletion of Atlantic cod stocks has created enormous interest in culturing this species (Anon, 2000; Avault, 2001; Adoff *et al.*, 2002; Anonymous, 2002; Broomfield, 2002). Cod is considered to have the same potential for large volume fish farming as salmon, and rainbow trout (Adoff *et al.*, 2002). However, identifying broodstock populations that possess characteristics (e.g. rapid growth rate, high food conversion efficiency, low mortality and delayed maturity) best suited for cod aquaculture is necessary to achieve this potential. Koljonen *et al.* (2002) have discussed the importance of assessing genetic diversity in wild and hatchery stocks for successful Atlantic salmon (*Salmo salar* L.) broodstock-breeding programs. Atlantic cod has a wide spread latitudinal distribution, and several populations of Atlantic cod have been shown to exist

(Bentzen *et al.*, 1996). Therefore, an approach similar to that suggested for salmon aquaculture by Koljonen *et al.* (2002) could benefit the cod aquaculture industry.

1.2 Stock structure of North Atlantic cod

The Department of Fisheries and Oceans (DFO) has divided cod in the Northwest Atlantic into stocks for the purpose of managing cod resources. These stocks are defined as recognizable units displaying characteristics unique to each stock, with very little intermingling between adjacent stocks (Lear, 1989). A variety of techniques have been used to investigate fish stock structure with early work focusing on age structure, growth, sexual maturity (reviewed by Halliday & Pinhorn, 1990) tagging, parasite (Boje *et al.*, 2002) and spine and vertebral counts (Templeman, 1981).

Delineation of population structure is fundamental to the assessment, conservation and management of Atlantic cod. Meristic characteristics such as number of vertebrae or fin rays have been used in delineating several other fish stocks (Hurlbut & Clay, 1998; Riget *et al.*, 1992), and attempts have been made in the past to differentiate Atlantic cod stocks using similar methods (Lear & Wells, 1984; Pepin & Carr, 1993) in the Northwest Atlantic. Studies have shown a strong environmental influence of temperature in particular on early development (Ali & Lindsey, 1974; reviewed by Lindsey, 1988), and thus, that there could be an environmental basis for the meristic differences between stocks of fish. This idea is reinforced by recent studies, where genetically homogenous groups of European anchovy *Engraulis encrasicolus*, displayed morphological differences (Kinsey *et al.*, 1994; Tudela, 1999). These consistent morphological

differences in certain areas have suggested the existence of “phenotypic stocks” even though such differences are not genetically based (Haddon & Wills, 1995; Jerry & Cairns, 1998).

Swain and Frank (2000) found spatial variation in the vertebral number of Atlantic cod in the southern Gulf of St. Lawrence and on the northeastern Scotian Shelf. They suggested a possible genetic, rather than environmental, basis for this variation. They concluded that vertebral number and habitat selection were closely linked among cod populations in this region. Similar studies have demonstrated a link between vertebral number and predation, and other fitness related traits such as burst swimming performance (Swain, 1992; Lindsey, 1988). Since most fitness related traits are adaptive, the factors mediating adaptive phenotypic plasticity (e.g. vertebral number) have become a topic of common debate (Via *et al.*, 1995). Swain *et al.* (2001), in a study examining five Atlantic cod populations, suggested that vertebral number provides valuable information, together with other characteristics, in delineating cod stocks because vertebral number is considered to have a strong genetic component both within (Tave, 1984; Leary *et al.*, 1985) and among fish populations (Billerbeck *et al.*, 1997). Swain *et al.*, (2001) discussed the tendency for the vertebral number to be higher in cold and high latitude Atlantic cod populations compared to their warm and low latitude counterparts.

In the past decade molecular techniques such as nuclear DNA, microsatellite DNA, mitochondrial DNA, and allozymes have been used to study genetic differences among fish populations (Ruzzante *et al.*, 1999). However, the sensitivity of these techniques for detecting differences can vary among fish populations. The genetic studies done to

investigate the population structure of Atlantic cod have given contradicting results. Pepin and Carr (1993), in a study of juvenile cod from NAFO divisions 3K, 3L and 3O, examined various factors including meristic parameters, vertebral counts and DNA sequence variations in order to support the hypothesis of stock separation between these areas. They did find meristic differences between stocks, which are consistent with the findings of Templemen (1981). However, they did not find evidence of any genetic basis for stock separation. Carr *et al.* (1995) reported similar results between near shore and off shore cod stocks from northeastern Newfoundland. However, Ruzzante *et al.*, (1996; 1997) provided evidence for a genetic basis in distinguishing cod stocks. They provided microsatellite DNA evidence to genetically distinguish inshore over-wintering Atlantic cod from Trinity Bay, Newfoundland, and offshore over wintering cod from the Grand Bank region. Bentzen *et al.* (1996) in a much broader study, provided evidence that cod in the Northwest Atlantic belonged to multiple genetically distinguishable populations and more significantly they were able to distinguish between north (Hamilton, Funk, and Bell Island) and south (northern Grand Bank area) cod stocks. In a recent study involving over 5000 cod from 19 inshore and off shore locations around Newfoundland, Beacham, (2002) found that cod from more distant locations tend to be more genetically distinct. However, some argue that recent genetic studies have only shown a weak population structuring of cod (Pogson *et al.*, 2001; Knutsen *et al.*, 2003), and it may be due to a post-collapse mixing among these cod populations (Ruzzante *et al.*, 2001).

1.3 Local adaptation

Studies have shown that variations in life history exist in cod. Brander (1994) found that cod grew faster and mature earlier in warm water. However, the evidence for the existence of genetically distinguishable populations of this species does not provide information on phenotypic and life history variation among stocks. Conover (1998) suggested that local adaptation may be more common in marine species than has been indicated by genetic studies. He provided extensive evidence of local adaptation in fitness related traits in *Menidia menidia* from “common garden” experiments. Adaptation may be defined as the process of becoming better suited to one’s environment in terms of morphology, physiology or biochemistry (Minkoff, 1983). Genetic variability and adaptiveness for present, and possible future conditions, is a very important phenomenon for the survival of an individual in a population. Phenotypic plasticity is one solution to the problem of adaptation to heterogeneous environments (Via *et al.*, 1995). The extent of genetic variation and/or environmental influence on phenotypic variation across environments is unknown for most marine species including Atlantic cod.

Adaptive variation in somatic growth rate across latitudinal clines is common in many species (Levinton, 1983; Conover & Present, 1990) and latitudinal differences in temperature, length of growing season, and severities of winter are the likely agents of selection (Conover, 1992, Conover & Schultz, 1997). Several species e.g. Summer flounder (*Paralichthys dentatus*; Malloy & Targett, 1994), Dover sole (*Solea solea*; Exadactylos *et al.*, 1999), and plaice (*Pleuronectes platessa*; Deniel, 1990) have shown

specific adaptation to different environments at the same latitude. This is termed local adaptation (Puvanandran & Brown, 1998).

1.4 Counter gradient variation hypothesis (CnGV)

Counter gradient variation (CnGV) is a theory put forward by Conover (1990) and Conover and Present (1990), which hypothesizes that growth and other life history traits in fishes of the same species can vary between latitudes. Counter gradient variation results due to a geographical pattern of genotypes (with respect to environments) in which genetic influences on a trait oppose environmental influences, and thereby minimize phenotypic change along the gradient (Conover & Schultz, 1995). This phenomenon is useful in understanding the cause of phenotypic variability or uniformity in nature. Phenotypic variance in a quantitative character (V_p) is shown in the formula (Conover & Schultz, 1995):

$$V_p = V_g + V_e + V_{g*e} + 2Cov(g,e)$$

where V_g and V_e represents the variance in phenotype resulting from genetic and environmental effects; V_{g*e} is the interaction between genotype and environmental effects; and $Cov(g,e)$ is the covariance between genotypic and environmental sources of variance. This covariance term expresses the degree to which genotypes, having a measurable effect on phenotypic expression, are non-randomly distributed among environments that influence the same phenotypic trait. Such effects on V_p in nature can either inflate or reduce V_p depending on whether the covariance is positive or negative. CnGV occurs when genotype diminishes the effect of environmental influences across a

gradient, minimizing phenotypic variation (Conover & Schultz, 1995). Therefore, testing individuals or genotypes from different geographic locations in common environment experiments is the only way to detect CnGV. Existence of CnGV across latitudes is supported by several studies (Bervan, 1982; Conover, 1990; Conover *et al.*, 1997; Svasand *et al.*, 1996; Jonassen *et al.*, 2000; Purchase & Brown, 2000a, b; Yamahira & Conover, 2002). CnGV was first recognized in *Drosophila* species (Levins, 1968), and later, Bervan *et al.* (1979; Bervan, 1982) provided documented evidence in frogs. In a common environment experiment *Rana sylvatica* larvae from mountain regions showed higher genetic capacity for growth and complete metamorphosis sooner than the larvae from low lands (Bervan *et al.*, 1979; Bervan, 1982). A CnGV in the capacity for growth has been shown for a number of marine invertebrates (Levinton, 1983; Lonsdale & Levinton, 1985) and vertebrates such as Atlantic cod (*Gadus morhua*: Svasand *et al.*, 1996; Purchase & Brown, 2000a & b), Atlantic halibut (*Hippoglossus hippoglossus*: Jonassen *et al.*, 2000), turbot (*Scophthalmus maximus*: Imsland *et al.*, 2000), striped bass (*Morone saxatilis*: Conover *et al.*, 1997) and Atlantic silverside (*Menidia menidia*: Yamahira, 2002).

Conover and Present (1990) showed in Atlantic silverside *Menidia menidia* that genetic capacity for growth varies inversely with length of the growing season across a latitudinal gradient. The length of the growing season declines by a factor of 2.5 with increasing latitude, but body size was not reduced at the end of the first growing season. Further, the fast growing northern fish displayed a higher growth rate, food conversion efficiency and a more efficient use of energy in somatic tissue production (Present &

Conover, 1992). There are benefits associated with the fast growth in high latitude fish. The rapid somatic growth during early life history tends to decrease the age at first maturity, shorten generation time and increase reproductive life span (Lewontin, 1965). Rapid somatic growth also reduces the risk of juvenile mortality by minimizing the time spent in vulnerable stages, and the larger body size increases fecundity in adult life (Wootton, 1990; Roff, 1982).

Growth rate has always been used as a measure of fitness when other fitness traits, such as reproductive success are not measurable (Stearns, 1992). Variation in growth rate may be due to various factors, such as limitations in food availability, temperature and/or genetic influences. Sibly *et al.* (1985) and Abrams *et al.* (1996) suggested that growth rates are likely to be optimized, but not maximized, by natural selection. For example, the costs involved with faster growth, such as increased mortality, can constrain the physiological capacity for growth. The evolution of sub-maximal growth rates in favorable environments for growth, would suggest the existence of tradeoffs with other fitness related traits (Billerbeck *et al.*, 2001). Thompson (1991) suggested that genotypic and environmental interactions result in ecotypic differences, and improved fitness in one environment can occur only at the expense of reduced performance in another environment. Several studies provide evidence for the existence of tradeoffs in biological and physiological traits. Fleming and Gross (1990) reported a tradeoff between egg number and size in Pacific salmon (*Oncorhynchus kisutch*), where the egg number increased significantly with latitude (38% increase from 47°N to 50°N), but egg size and total bio-mass were reduced. Schluter (1995) reported tradeoffs in two

species of stickleback (*Gasterosteus* sp.) and their hybrids, where the larger of the two species (the benthic) had a growth advantage over the second species (lentic) in the littoral zone of the lake. However, this was reversed in open waters. Specifically he found tradeoffs with growth rate (fitness), feeding efficiency and morphological specializations. Starck (1994) reported a tradeoff between growth rate and skeletal development in two bird species. When he compared the ossification of the leg and wing of a slow growing buttonquail *Turnix suscitator* and a fast growing budgerigar *Melopsitacus undulates*, the buttonquail contained a greater proportion of ossified tissue relative to cartilage i.e. ossification occurred at a faster rate in the slower growing species. Populations of pumpkinseed sunfish *Lepomis gibbosus* in lakes with bluegill sunfish *Lepomis macrochirus* have evolved faster growth rates than in lakes without bluegill (Arendt & Wilson, 1997) in order to compete for food. Further, Jeffrey and Wilson (1999) reported a tradeoff between cranial ossification and growth rate within two populations of pumpkinseed sunfish *Lepomis gibbosus*.

1.5 Phenotypic variation and reaction norms

Phenotypic and genetic variations have been used to understand the population structure of marine species. However, none of the above approaches provide direct insight into the geographic pattern or diversity of adaptive genetic variation between widely spread populations (Conover, 1998). Phenotypic variation in nature is the result of environmental influences during development, “genotype x environment” interactions and the covariance between genotypes and environments (Counter gradient variation)

(Conover, 1995; 2000). As discussed above, the covariance between genotype and the environment may be positive or negative (Conover, 2000). Understanding the geography of adaptive genetic variation is important as phenotypes, as they appear in nature, may give a very misleading impression of genetic tendencies (Conover, 2000).

Common environment experiments and reaction norms are widely used to explain genetic and environmental influences on phenotypic trait variation (Via *et al.*, 1995; Conover & Schultz, 1995; Conover, 2000; Pigliucci & Schlichting, 2002; Ricklefs & Wikelski, 2002). A reaction norm is a set of phenotypes that would be produced if a genotype were exposed to a defined set of environments (Via *et al.*, 1995). Reaction norms are measured for the main environmental parameter(s) that vary among habitats and would be expected to have major effect on the phenotypic trait of interest (Conover & Schultz, 1995). Reaction norms can take on any shape when visualized, and may be a simple set of lines connecting the mean phenotype in each environment (discrete environments) or a function in a continuous environment, (Via *et al.*, 1995). Depending on “genotype x environment” interactions (Billerbeck *et al.*, 2000) reaction norms may display parallel (no environmental effect on phenotype), non-parallel (one genotype is superior in all environments) or crossing reaction norms (rank order of performance for a given trait depends on the environment) (Conover & Schultz, 1995).

1.6 Swimming performance

Fishes are found in a wide range of habitats, which vary in temperature (Lowe-McConnell, 1987), light intensity (Price, 1981), salinity (Heisler, 1984), pH (Low-Mc

Connell, 1987), altitude, and water current velocity (Cao *et al.*, 1981). Irrespective of their habitats and life style, fishes are confronted with changes in their environment, and unlike endothermic vertebrates, many fishes show flexibility in their response to environmental change in traits such as growth, age at first reproduction and maximum life span (Wootton, 1990). However, fish needs to respond optimally to changing environment in order to maximize survivorship and fecundity.

Many studies have been conducted to understand the importance of swimming capacity, performance or ability to fishes. Most fish use swimming as a way to avoid and survive attacks from predators (Videler, 1993; Reidy *et al.*, 1995; Watkins, 1996), and maximal swimming performance strongly influences the ability of a fish to acquire food, find a mate, and avoid unfavorable conditions (Drucker, 1996). A fish's body form and the physical properties of water are influential determinants for effective propulsion. The study of fish locomotor capacity has a relatively long history (reviewed by: Beamish, 1978; Randal & Brauner, 1991; Hammer, 1995; Kolok, 1999; Plaut, 2001), with certain studies using the level of performance as a measure of fish health, stress level or the capacity to cope up with environmental change (Nelson *et al.*, 2002).

A fish's swimming performance is classified into three ecologically relevant categories (sustained, prolonged and burst) to evaluate their fitness or survival under different environmental conditions (Beamish, 1978). Sustained swimming performance applies to speeds that can be maintained for long periods, 200 - 240 min. without muscle fatigue (Brett, 1967; Beamish, 1966). This includes routine activity representing daily movements, steady and unsteady swimming, foraging and holding station. This type of

swimming is fuelled aerobically and is further divided into two subcategories (Beamish, 1978). Speeds achieved by migrating fish as well as the velocities attained by certain negatively buoyant species such as *Scombroid* and *Xiphoid* to maintain hydrostatic equilibrium, are considered cruising. Sustained schooling is the second category, which includes speeds displayed by groups of fish distributed in a regular array (Beamish, 1978).

Prolonged swimming is of shorter duration (20 sec to 200 min) than sustained swimming and is fuelled predominately by aerobic metabolism but ends in fatigue of the muscle (Beamish, 1978). This category is more commonly used for determining swimming speeds and the swimming velocity at which the fish fatigue can be determined using swim tunnels in laboratories (Beamish, 1978). However, sustained and prolonged swimming are hard to separate in the field due to the difficulty of tracking fish, and the inability to account for variability in swimming speed and type. Burst swimming performance applies to the highest speeds, and these speeds are maintained only for short periods (less than 20 sec) (Beamish, 1978). The ability for fish to attain higher swimming speeds in short time durations is essential for pray capture, avoiding predators, reacting to sudden disturbances and for maneuvering through strong current fields (Beamish, 1978; Reidy *et al.*, 2000; Plaut, 2001).

Critical swimming speed is most commonly used to assess the aerobic swimming capability of fishes (reviewed by: Beamish, 1978; Hammer, 1995; Koloc, 1999; Plaut, 2001). This technique was first developed and employed by Brett (1964) to evaluate the ability of salmonid fishes to ascend waters in streams. This is a graded water velocity

increment test where a fish is placed in a swim tunnel and forced to swim against water currents of different velocities (Beamish, 1978). In this technique, a fish is placed in a swim tunnel with a water velocity of 0.5 - 1 bls⁻¹ and left for a predetermined time to overcome handling stress. This period may range between 8 to 12 hrs (Plaut, 2001), but recent studies have not shown any significant difference in recovery time between fish left to recover overnight and fish left to recover 1-2 hrs (Kolok, 1991; Peake *et al.*, 1997). After the recovery period, water velocity is increased by a prescribed increment (cm or Body lengths s⁻¹) every 10-60 minutes, and this process of step-increases in velocity is repeated until the fish fatigues (Farlinger & Beamish, 1977). The critical swimming speed (*U_{crit}*) can be calculated (Brett, 1964, 1967) using the following formula:

$$U_{crit} = U_i + (U_{ii}(T_i/T_{ii}))$$

where U_i is the highest velocity (cm s⁻¹) maintained for the entire time interval, U_{ii} is the velocity increment (cm s⁻¹), T_i is the time elapsed at fatigue velocity (min), and T_{ii} is the prescribed interval time (min).

In addition to critical swimming speed, there are other ways of determining the aerobic swimming capability of fish. Beamish (1978) showed how to determine the endurance of fishes by measuring the time a fish can swim against a prescribed constant water velocity. Gait transition speed (Drucker, 1996) is another way of determining aerobic swimming activity. In this technique a fish is forced to swim against an incremental water velocity using a swim tunnel, and observed to determine the speed at which the fish changes from median and paired fin to body and caudal fin swimming.

However this method can only be used for species that change their mode of swimming with increases in swimming speed (Plaut, 2001).

According to Lindsey (1978) water as a medium for locomotion have both advantages and disadvantages. Water is denser and more viscous than air, which makes it a buoyant medium, and the effective propulsion by fishes is greatly influenced by the physical properties of water (Wootton, 1990). On the other hand, fishes are found in wide range of habitats with a variety of body shapes and life history patterns (Nelson, 1984). Such diversity and changing environments confront fish with adverse ecological effects in their habitats. However, fish have evolved the capacity to buffer any adverse effect, to a greater or lesser extent, with biochemical, physiological, behavioral, and morphological mechanisms (Wootton, 1990). Swimming ability is widely used to understand the effects of environmental factors on fishes; temperature (Randall, 1991; Kaufmann & Wieser, 1992; Claireaux *et al.*, 1995; Taylor *et al.*, 1996; Schurmann & Steffensen, 1997; Adams & Parsons, 1998; Kieffer *et al.*, 1998; Winger *et al.*, 2000), salinity (Claireaux, 1995; Nelson *et al.*, 1996; Swanson *et al.*, 1998; Plaut, 2000), feeding and growth (Soofiani & Hawkins, 1982; Bjornsson, 1993; Kolok & Oris, 1995; Gregory & Wood, 1998; Petrell & Jones, 2000; Hunt von Herbing & White, 2002), population or latitudinal effects (Nelson *et al.*, 1994; Hunt von Herbing & Boutilier, 1996; Schurmann & Steffensen, 1997; Billerbeck *et al.*, 2000; 2001), body form (Plaut, 2000; Webb, 2002), effects of externally attached tags or devices (Davidson *et al.*, 1999; Webber, *et al.*, 2001), internally attached devices (Webber *et al.*, 1998), transmitters (Counihan & Frost, 1999; Cote, 1999), and effects of pollutants (Kennedy *et al.*,1995).

Most fish swimming activities are associated with food capture, reproduction, migration or predator avoidance, and swimming speed limits and endurance are subject to strong selection pressures that enhance evolutionary response (Videler, 1993). For example Videler (1993) reported that territorial males in five species of herbivorous parrotfish (*Scaridae*), spent 90% of the time feeding, and 50% or more of the time during the day swimming. Further, he reported that all swimming activities were associated with feeding, reproduction, and occasionally predator avoidance. The energy budget for a fish is represented by the following formula (Wootton, 1990; Videler, 1993):

$$C = P + R + E$$

where C is the energy content of the food consumed, P is the energy put into growth and reproduction, R is the energy used for respiration or metabolism, and E is the energy lost in faeces and other excretory products. A significant portion of the energy budget is spent on P (growth, reproduction and tissue repair etc.) and R (active metabolism, standard metabolism and specific dynamic action-SDA), where SDA represents the costs involved with the digestion of food, and the storage, transport and assimilation of energy. However Videler (1993) reported that fractions of R are highly variable and depend on factors such as temperature and swimming speed etc.

Three types of metabolic rate are utilized in fish energetic studies. Standard metabolism is the rate of energy expenditure by an unfed, resting fish, or the minimum energy required to sustain basic functions. Active metabolism is the energy required by a fish swimming aerobically at maximum sustainable speed. Finally, the amount of energy spent by an unfed fish maximum swimming activity is given by the difference between

active and standard metabolism, which is termed the scope for activity. Direct (measurement of heat production) and indirect (measurement of O₂ consumption or CO₂ production) methods are used to measure the metabolic rate (reviewed by Cech, 1990). However, the measurement of the oxygen consumption is considered to be more sensitive, is relatively easy to perform and is widely used to determine the metabolic rate in fishes (Beamish, 1978; Cech, 1990). However, such measurements are accurate only when the anaerobic contribution to metabolism is insignificant (Cech, 1990). The energy expenditure during aerobic swimming can also be measured in units of energy (e.g. cal or J) by applying an oxycalorific coefficient to rates of oxygen consumption (reviewed by Beamish, 1978). The range of the oxycalorific coefficients in teleosts are reviewed by Beamish (1978), and the energetic cost for locomotion, independent of swimming speed, is often expressed as the caloric expenditure required to transport 1 unit of body mass 1 km (Nielson, 1972).

1.7 Trade – off with Swimming

There is a close relationship between feeding, growth, and other key elements of fitness such as swimming performance (Gregory & Wood, 1999). In addition, under certain conditions, individual fish may be able to either optimize growth rate or swimming performance. Several factors are known to influence swimming performance (reviewed by Hammer, 1995), such as body size (Beamish, 1978), growth rate (Kolok, 1992), carotinoid pigment density (Nicoletto, 1991) and condition factor (Kodric-Brown & Nicoletto 1993). Given the numerous factors that influence swimming performance, it

is not surprising that the recent literature suggests a tradeoff between growth rate and aerobic swimming performance in several fish species (Kolok & Oris 1995; Farrell *et al.*, 1990; Gregory & Wood, 1999). Kolok & Oris (1995) found a significant negative correlation between specific growth rate and critical swimming speed in male fathead minnows *Pimephales promelas*. In a similar study with rainbow trout *Oncorhynchus mykiss*, Gregory and Wood (1998) found a negative correlation between critical swimming speed and specific growth rate.

In the Atlantic silverside *Menidia menidia*, despite the negative influence of low temperature and short growing season, the rapid intrinsic growth of northern fish results in an equal or slightly larger mean phenotypic size as compared with southern fish at the onset of winter (Conover, 1992). However, Billerbeck *et al.* (2001) in a common environment study involving Atlantic silverside, found that the higher growth and food consumption among northern latitudinal populations was a tradeoff against locomotory performance. They suggested that the allocation of energy to growth or to the metabolism of ingested food (specific dynamic action; SDA) might limit the energy available for active metabolism and thus diminish locomotor capacity.

The Atlantic cod *Gadus morhua* is distributed over a wide geographic area, has distinct life history characteristics and migration patterns (Ruzzante, *et al.*, 1996), and recent studies have described life history variation and genetic differences among geographically separated Atlantic cod stocks (Ruzzante *et al.*, 1999). Further, Svasand *et al.* (1996) and Purchase and Brown (2000a & b) have shown CnGV in growth and food conversion. Therefore, the Atlantic cod is an interesting species to study stock specific

variations in physiological performance. Several studies have determined the aerobic and anaerobic swimming performance of cod (Soofiani & Priede, 1985; Reidy *et al.*, 2000), its swimming endurance (He, 1991) and the effect of feeding (Soofiani & Hawkins, 1982), temperature, salinity, and oxygen consumption on swimming metabolism (Claireaux, 1995; Schurmann & Steffensen, 1997; Jordan *et al.*, 2001). However, studies that have examined the physiological variation between cod populations are very limited. Nelson *et al.* (1994) reported variations in exercise physiology and other biochemical aspects between Atlantic cod from Bras d'Or lake of Nova Scotia and the nearby Atlantic Ocean, with Bras-d'Or lake cod displaying higher metabolic, ventilatory and cardiac rates. Further, Bras-d'Or lake cod used a greater proportion of anaerobic metabolism in reaching its maximal performance with relatively greater metabolic acid base disturbance and higher lactate levels during recovery. Therefore, it would be interesting to examine the physiological differences and possible tradeoffs of latitudinally separated Atlantic cod populations.

The depletion of wild cod stocks has created enormous interest in cod aquaculture. However, identifying the population characteristics is important in selecting better performing populations for culture (Ruzzante *et al.*, 1997; Swain *et al.*, 2001; Beacham *et al.*, 2002; Smedbol & Stephenson, 2001). Several studies have measured different traits in Atlantic cod (Svasand *et al.*, 1996; Purchase & Brown, 2000a & b; Nelson *et al.*, 1994; Reidy *et al.*, 2000; He, 1991; Schurmann & Steffensen, 1997; Claireaux *et al.*, 1995), however, none of the studies have investigated differences in growth, food conversion efficiency, protein synthesis, and swimming performance or

tradeoffs between these parameters, in multiple populations subjected to common environments. Thus this thesis investigates the interactive effects of temperature and food level on growth rate, food conversion efficiency and energy allocation in different cod stocks. Further, it uses growth rate as a surrogate component of fitness, and thereby investigates whether capacity for growth is a tradeoff with swimming performance.

1.8 Research goals

The present study is part of an on-going project whose purpose is to describe the genetic basis of phenotypic variation among populations of Atlantic cod *Gadus morhua*, through out most of its range in the Northwest Atlantic. The scientific objective of the main project addresses the question of local adaptation in this widely distributed marine fish, and has three goals. First, spawning and rearing Atlantic cod larvae and juveniles from different areas under the same environmental conditions to determine the genetic and environmental basis of phenotypic variation. Second, using “common garden” experiments (Conover *et al.*, 1997), to test the hypothesis of Countergradient variation, which predicts that, northern populations have intrinsically faster growth rate and are energetically more efficient than southern populations. Third, to describe individual and population differences in spawning behavior and mate competition, and identify the phenotypic and genetic correlates of individual variation in Atlantic cod reproductive success.

I compared growth and swimming metabolism in two populations of Atlantic cod juveniles and the results are presented in this thesis. The Objectives of my study are two fold:

1) Determine the genetic and environmental basis of phenotypic variation among juveniles of two cod populations (Southern Gulf of St. Lawrence; Northumberland Strait, P. E. I.; 46°N; 64°W; NAFO Division 4T) and (Placentia Bay, Newfoundland; 48°N; 54°W; NAFO Division 3Ps), by conducting common garden experiments (Chapter 2.0).

2) Compare the critical swimming speeds (*U_{crit}*) of these populations and, determine whether a tradeoff between locomotory performances against growth exists (Chapter 3.0).

Chapter 2.0

Growth of juvenile Atlantic cod (*Gadus morhua*) from Placentia Bay, Newfoundland and Southern Gulf of St. Lawrence.

2.1 Introduction

The Atlantic cod (*Gadus morhua*) has historically been a significant resource in the North Atlantic Ocean, and considerable effort has been made in the past to elucidate the Atlantic cod population complex (Jonsdottir *et al.*, 2001). Understanding the population structure is fundamental to the assessment, conservation and management of this species. The importance of “clarifying the relationships among cod stocks” towards management of the species was addressed by Rice in 1997. Atlantic cod are found from Baffin Island (~63 °N) to Cape Hatteras (~35 °N) in the western north Atlantic (Scott and Scott 1988). Despite considerable study, the basic features of the population structure remain controversial, with conflicting data on population structure within northern cod (Bentzen, 1996). Geographic surveys (Hutchings *et al.* 1993), vertebral data (Templemen 1981; Lear & Wells 1984), and tag recovery data (Lear 1984; reviewed in Lear & Green 1984 and Taggart *et al.* 1995) suggest that northern cod are divided in several distinct offshore spawning units. Further, Bentzen *et al.*, (1996) and Ruzzante *et al.*, (1997) found genetic variation using micro satellite loci when comparing northern cod from inshore bays with those from offshore locations suggesting that separate stocks exist in the two areas (Ruzzante *et al.*, 1996; 1997). However, these observations provide no evidence of reproductive isolation among spawning units.

The theory underlying observed inter-population differences in growth was presented in Chapter 1.0. As mentioned in that chapter, few studies have addressed the relative contribution of genotypic and environmental influences on the phenotypic variation in northwest Atlantic cod. (Hunt von Herbing & Boutilier, 1996; Svasand *et al.*, 1996; Puvanendran & Brown, 1998; Purchase & Brown, 2000a & b; Otterlei, *et al.*, 1999). The study in this chapter was conducted to determine the effect of temperature and food level on growth rate, food conversion efficiency and energy allocation in two latitudinally separated cod populations (3Ps and 4T) in a “common garden” experiment to fulfill the objectives described in chapter 1.0. My working hypothesis for these studies is that at both temperatures (11 °C and 7 °C) and food levels (high and low), the more northern of the two populations (NAFO Division- 3Ps –48 °N; 54°W, Placentia Bay, Newfoundland) will display faster growth rates, better food conversion efficiencies and survival, than the southern population (NAFO Division 4T - 46°N; 64°W, Northumberland Strait, P. E. I., Southern Gulf of St. Lawrence).

2.2 Materials and Methods

2.2.1 Broodstock

The experiment was carried out at the Ocean Sciences Center (OSC), Memorial University of Newfoundland. Adult 3Ps (65 fish) and 4T (59 fish) cod were captured from the wild prior to spawning and kept in captivity at the OSC (3Ps), or Dalhousie University (4T) (Halifax, Nova Scotia), respectively. Fish from 3Ps were kept in two 12-m³ tanks and the temperature was gradually raised from 2 to 6 °C in 10 days. They were

fed with frozen fish (Herring) every 3 days, and gradually weaned onto a pelleted commercial feed (Surgain Feed). Once weaned, the broodstock was fed *ad-libitum* daily with 5 mm feed. Eight consecutive batches of eggs were collected after two weeks of spontaneous spawning. Adult Atlantic cod broodstock from 4T were kept at similar conditions as 3Ps, however, the holding tank for 4T was 680 m³. Eight consecutive batches of eggs were transported to OSC at 30-50 degree days (4-6 days at 6 - 8 °C).

2.2.2 Egg incubation and larval rearing

Fertilized eggs from both 3Ps and 4T were incubated at the OCS at 6 – 8 °C in 250 L circular tanks (8) with water flow (2 L min⁻¹) and aeration. Light intensity was 300-400 lux and photoperiod was 24hr. Dissolved oxygen and temperature were monitored daily and dead eggs were siphoned out. When nearly 100% of the eggs had hatched, larvae were transferred to eight 500 L-rearing tanks at 10 - 12 °C. During this period they were fed with live feed (*rotifers* and *Artemia*). Larvae were weaned to dry feed at 60 dph and were fed *ad-libitum* with pelleted feed (Dana commercial feed, Havnen 13, DK-8700 Horsens, Denmark) using auto feeders for 6 months, under these conditions. During this period they were size graded 4-5 times to reduce cannibalism using a standard grader.

2.2.3 Pre-experimental rearing and experimental set up

Juveniles were transferred to 500 L tanks (8 tanks for each population) at 10 to 12 °C two weeks prior to the experiment. The experiment for the 4T fish started first, as they

were 14 to 16 days older than juveniles in the 3Ps population. Ninety fish in total (total tank biomass avg. 1300 g) were placed in each tank. They were selected from graded stocks of small, medium and large fish in the proportion of 20:60:20, respectively. Similarly, the 3Ps population was moved to eight randomly selected 500 L tanks with each tank carrying 90 fish (total biomass of 1100 g). All 16 tanks were supplied with aerated seawater at a flow rate of 4 – 5 L min⁻¹.

The experimental fish were subjected to two different temperatures (High; 10-12 °C – HT and Low; 6 – 8 °C – LT) and two different food levels (High - 2% of body weight – HF; and Low 0.67% body weight - LF). Both 3Ps and 4T juveniles were acclimated to the low temperature for a period of two weeks before the start of the experiment. Both populations were randomly assigned two replicates for each the following combinations of treatments: High temperature and high food (HTHF), high temperature and low food (HTLF), low temperature and high food (LTHF) and low temperature and low food (LTLF).

All tanks were hand fed twice daily with formulated pelleted feed to satiation, or until the ration was finished. The amount of food eaten by the group of fish in each tank was recorded. The feed was delivered as 10 to 20 pellets at a time. Consumption of the pellets by fish in each tank was closely monitored. The point of satiation was determined when approximately half of the pellets fed sank to the bottom, uneaten by the fish. Thereafter, another 5 to 10 pellets were distributed to each tank to ensure satiation was achieved.

Broad spectrum fluorescent tubes provided lighting, and photoperiod was adjusted as 12D: 12L, with an artificial dawn and dusk at the start of the experiment. Twilight was simulated with an incandescent light for 0.5h before and after fluorescent lighting. Light intensity was measured at the water surface, and was 300 Lux.. The temperature, dissolved oxygen levels and mortalities were recorded daily for each tank.

2.3 Data collection and analyses

2.3.1 Growth measurements

Growth measurements (wet mass, standard length and total length) were taken at the start of the experiment, and then every 21 days during the 18-week experiment. Twenty-five fish from each replicate (50 fish per treatment) were sampled randomly at each time point. Wet mass (WM) (to the nearest 0.01 gram) and total biomass (TB) of all the fish in the tank (to the nearest 1gram) were measured using an electronic balance. Standard length (SL, nearest 0.1 cm), the distance from the tip of the mouth to the end of the vertebral column and total length (TL, nearest 0.1cm), the distance from the tip of the mouth to the end of the caudal fin were measured using a measuring board. All sampled fish were returned to the tanks after measurements. Fish were not fed 24 hours before sampling. Using wet mass, the mass specific growth rate (SGR) of each tank was determined using the following relationship:

$$\text{SGR} = ((\ln(W_t) - \ln(W_o))t^{-1}) \times 100$$

Where W_t mean final wet mass (g), W_o is the mean initial wet mass (g), and t is the duration between initial and final sampling (days) (Busacker, *et al.*, 1990).

Food conversion efficiency (FCE), was determined using the following relationship:

$$FCE = W_g W_{fe}^{-1}$$

Where W_g is the weight gain of fish in each tank and W_{fe} is the weight of food eaten by fish in each tank (Purchase & Brown, 2000a) over a specific time period.

Condition factor (K) was calculated using Fulton's condition factor;

$$K = 100 W L_t^{-3}$$

Where W is the wet mass (g) and L_t is the total length (cm) (Purchase & Brown, 2000b).

Hepatosomatic index (HSI) was calculated at the end of the experimental period. To do this, a total of 10 randomly selected fish per treatment were killed using 2-phenoxyethanol, and the fish body and liver masses were measured (to the nearest 0.01mg) for each fish using an electronic balance. HIS was calculated as:

$$HSI = \text{Liver weight}/\text{total weight} * 100 \text{ (Grant, et al., 1998)}$$

2.3.2 Data analyses.

Differences in SGR, FCE, SL, K, survival (%), and HSI between 3Ps and 4T populations were compared within each treatment. Data sets for each of the above variables were analyzed with general linier model using SPSS (SPSS 9.0 for Windows). A repeated measure, power analysis was performed to determine the differences in SGR, FCR and K between the two populations and to adjust for the growth of the fish over time. The initial mean wet mass was used as a covariable in the model to account for the differences in initial wet mass and length between the two populations. The test was performed with population, temperature, and feed level as explanatory variables in the

model to understand the effect of temperature and food level on differences between the 3Ps and 4T populations. Thereafter, the same model was used to test the differences within treatment for SGR, FCR, standard length, and K between 3Ps and 4T with initial mean mass as the covariable. The data for survival, and HSI were tested between populations at the end of the experiment. A three way ANOVA was performed initially to understand the effects of food level and temperature on survival, HIS and was compared between populations for a given temperature and food level. Residual plots were examined for compliance for normality, independency, and homogeneity (Sokal & Rohlf, 1995).

2.4 Results

2.4.1 Initial data

The age of 3Ps and 4T juvenile cod were the same at the start of the experiment. 4T juveniles had a significantly greater standard length (Fig. 2.1; a) ($F = 18.960$, $df = 1$, $p = 0.002$), total length (Fig. 2.1; b) ($F = 20.043$, $df = 1$, $p = 0.002$), and wet mass (Fig. 2.1; c) ($F = 47.290$, $df = 1$, $p = 0.000$). However, the condition factor was not significantly different at the start of the experiment (Fig. 2.1; d) ($F = 1.587$, $df = 1$, $p = 0.243$).

2.4.2 Specific growth rate

Total biomass data was used to calculate specific growth rate (SGR). SGR was not significantly different between 3Ps and 4T juveniles in all treatments HFHT (Figure 2.2; a) ($F = 7.629$, $df = 1$, $p = 0.221$), HTLF (Figure 2.2; b) ($F = 0.127$, $df = 1$, $p =$

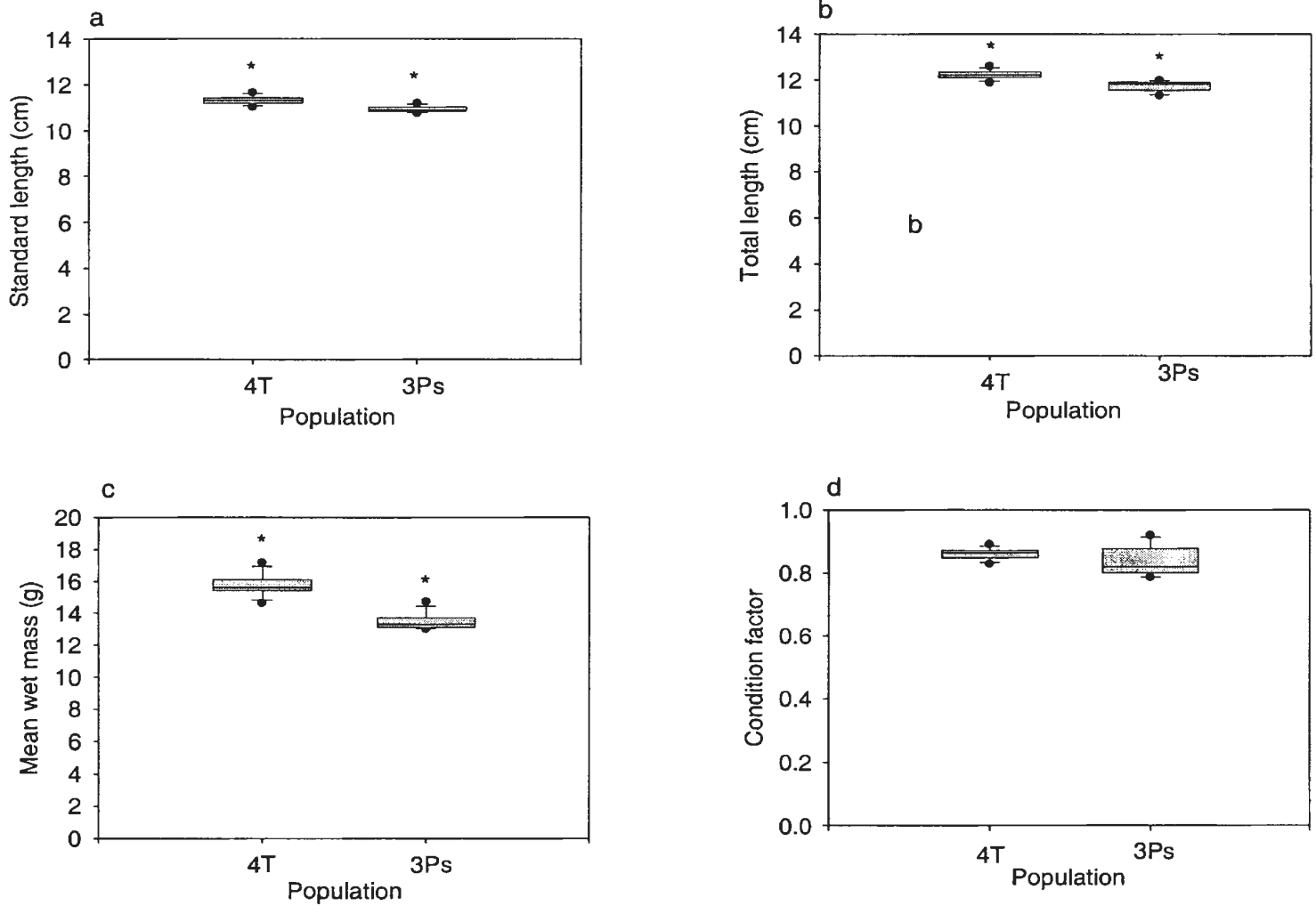


Figure 2.1 (a) Mean standard length (cm), (b) Mean total length (cm), (c) Mean wet mass (g), (d) Mean condition factor (\pm SD) of 0+ juvenile cod for populations 4T and 3Ps at the start of the experiment. N = 200 fish per population. (* = $p < 0.05$). The boundary of the box closest to zero indicates the 25th percentile, a line within the box marks the median, and the boundary of the box farthest from zero indicates the 75th percentile. Whiskers above and below the box indicate the 90th and 10th percentiles. The 5th and the 95th percentile are shown by a symbol (●).

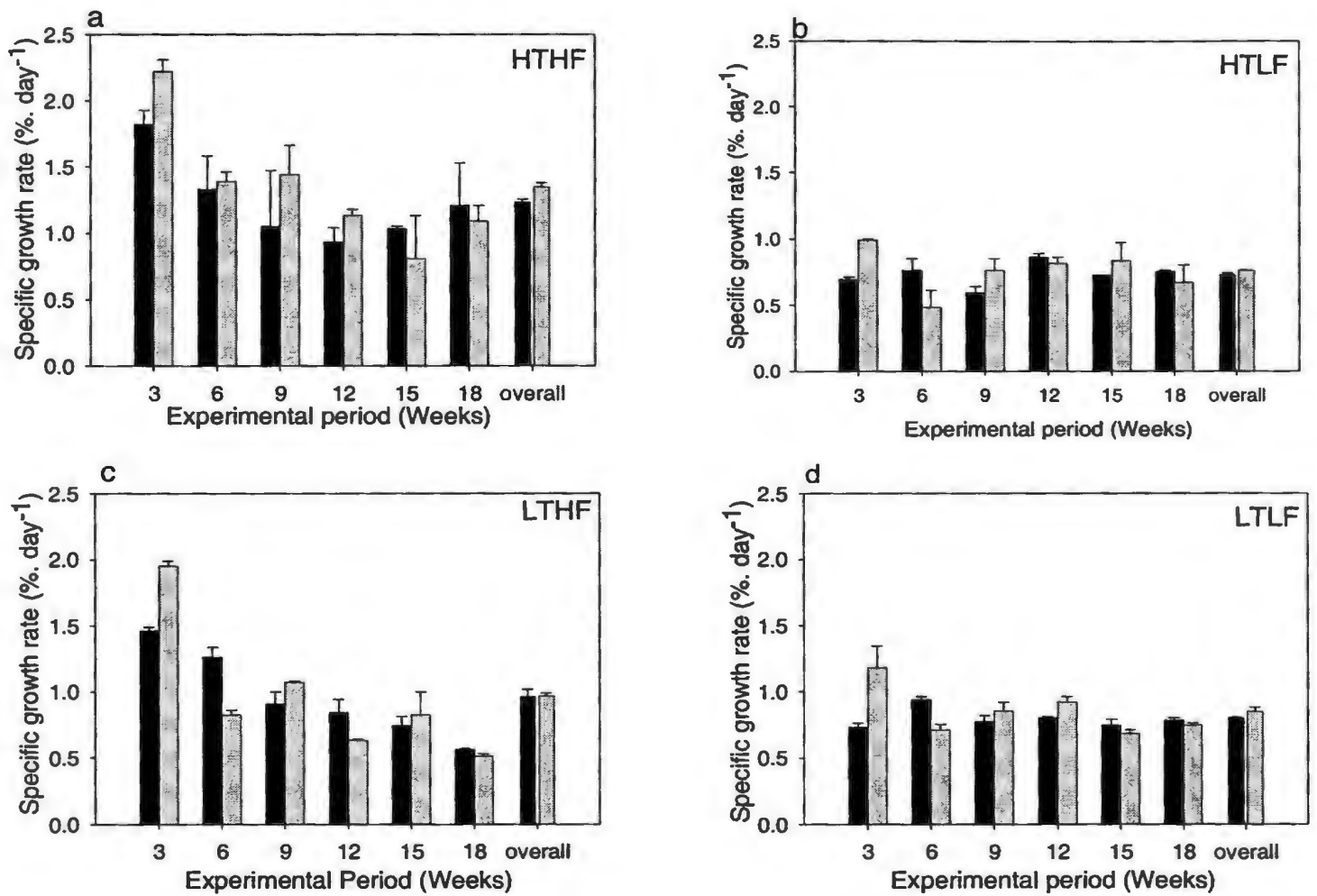


Figure 2.2 Specific growth rate (\pm SD) for 0+ cod juveniles from populations 4T (black bars) and 3Ps (grey bars) at (a) High temperature and high feed (HTHF), (b) High temperature and low feed (HTLF), (c) Low temperature and high feed (LTHF), (d) Low temperature and low feed (LTLF), during the 18-week experimental period. Data on overall specific growth rate during the 18-week experiment are also included for each treatment. (N=180 for each treatment at the start of the experiment).

0.782), LTHF (Figure 2.2; c) ($F = 0.483$, $df = 1$, $p = 0.613$), and LTLF (Figure 2.2; d) ($F = 41.005$, $df = 1$, $p = 0.099$). However, the SGR of both 3Ps and 4T juveniles were significantly higher in the HF treatments than the LF treatments in both HT ($F = 789.34$, $df = 1$, $p = 0.000$), and LT ($F = 45.24$, $df = 1$, $p = 0.007$). Similarly, the SGR of both 3Ps and 4T juveniles was significantly higher in HT than in the LT groups for both HF ($F = 121.299$, $df = 1$, $p = 0.002$), and LF ($F = 36.40$, $df = 1$, $p = 0.009$). The overall SGR's were calculated for each treatment group using the initial and the final mean wet mass and the overall SGR of HF 3Ps juveniles was 9% higher than 4T juveniles. The difference was close to significance ($p = 0.06$). However, the rest of the treatment groups showed no significant difference in SGR's.

2.4.3 Food conversion efficiency

Both 3Ps and 4T juveniles had similar food conversion efficiencies (FCE) in both HF ($F = 0.013$, $df = 1$, $p = 0.928$) and LF ($F = 0.005$, $df = 1$, $p = 0.953$) rations at HT, and HF ($F = 0.006$, $df = 1$, $p = 0.952$) and LF ($F = 1.807$, $df = 1$, $p = 0.407$) ration at LT (Figure 2.3), through out the experimental period. Similarly the overall FCE, calculated using the total amount of food eaten during the entire experimental period (18 weeks), was not significantly different for 3Ps and 4T juveniles for all treatment groups. However, both 3Ps and 4T juveniles had a significantly higher FCE with LF than with HF in the LT ($F = 32.699$, $df = 1$, $p = 0.011$), but the ration had no significant effect on the FCE's of both 3Ps and 4T juveniles in HT ($F = 1.86$, $df = 1$, $p = 0.266$). The temperature had no

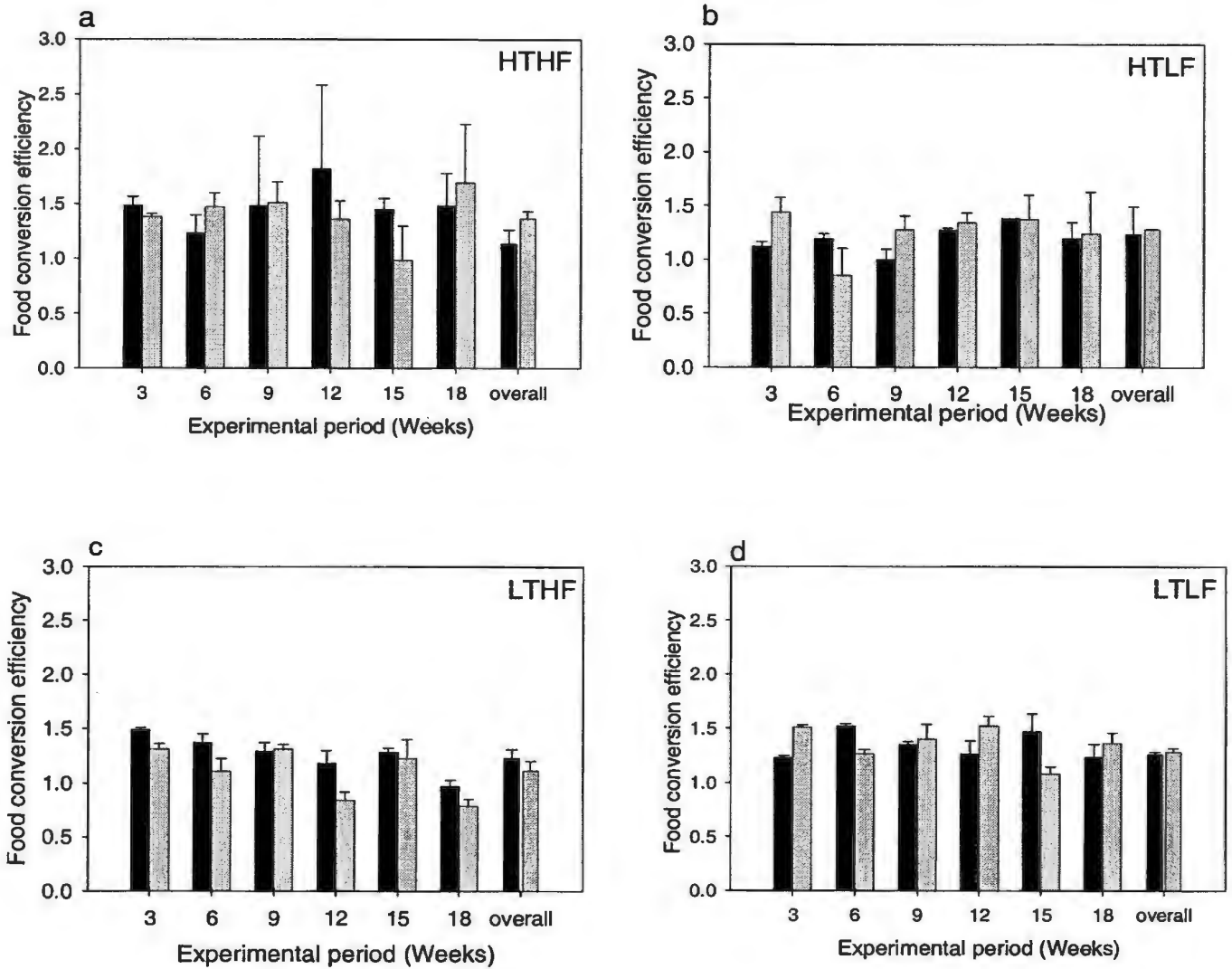


Figure 2.3 Mean food conversion efficiency (FCE) (\pm SD) for 0+ cod juveniles from populations 4T (■) and 3Ps (▒) at (a) HTHF, (b) HTLF, (c) LTHF, (d) LTLF, (See Fig; 2.2 for details) during the 18 week experimental period. Data on overall food conversion efficiency during the 18-week experiment are also included for each treatment (N=180 for each treatment at the start of the experiment).

significant effect on the FCE in both 3Ps and 4T juveniles with HF ($F = 7.76$, $df = 1$, $p = 0.069$), but both populations had a significantly higher FCE with the LF in the LT than in the HT.

2.4.4 Standard length

No significant differences were found between the two populations in standard length in any treatment, HTHF, ($F = 1.147$, $df = 1$, $p = 0.439$); HTLF, ($F = 1.057$, $df = 1$, $p = 0.491$); LTHF, ($F = 0.030$, $df = 1$, $p = 0.890$); and LTLF, ($F = 1.140$, $df = 1$, $p = 0.479$) (Figure 2.4).

Similarly, the overall increase in standard length between 4T and 3Ps juveniles during the experimental period was not significantly different. However, both 3Ps and 4T juveniles had a significantly higher standard length with HF, in both HT, ($F = 71.40$, $df = 1$, $p = 0.003$) and LT ($F = 41.92$, $df = 1$, $p = 0.007$), than the LF treatment. The temperature had no significant effect on the standard length for both 3Ps and 4T juveniles in the LF treatments ($F = 0.190$, $df = 1$, $p = 0.692$). However, both 3Ps and 4T juveniles fed with HF had a significantly higher standard length in the HT ($F = 48.57$, $df = 1$, $p = 0.006$), than the corresponding treatment in the LT.

2.4.5 Condition factor, Hepatosomatic index and Survival.

Condition factor was not significantly different between the two populations in any treatment, HTHF, ($df = 1$, $F = 2.52$, $p = 0.358$); HTLF, ($df = 1$, $F = 2.056$, $p = 0.388$); LTHF, ($df = 1$, $F = 8.22$, $p = 0.214$); LTLF, ($df = 1$, $F = 9.32$, $p = 0.196$) (Fig. 2.5).

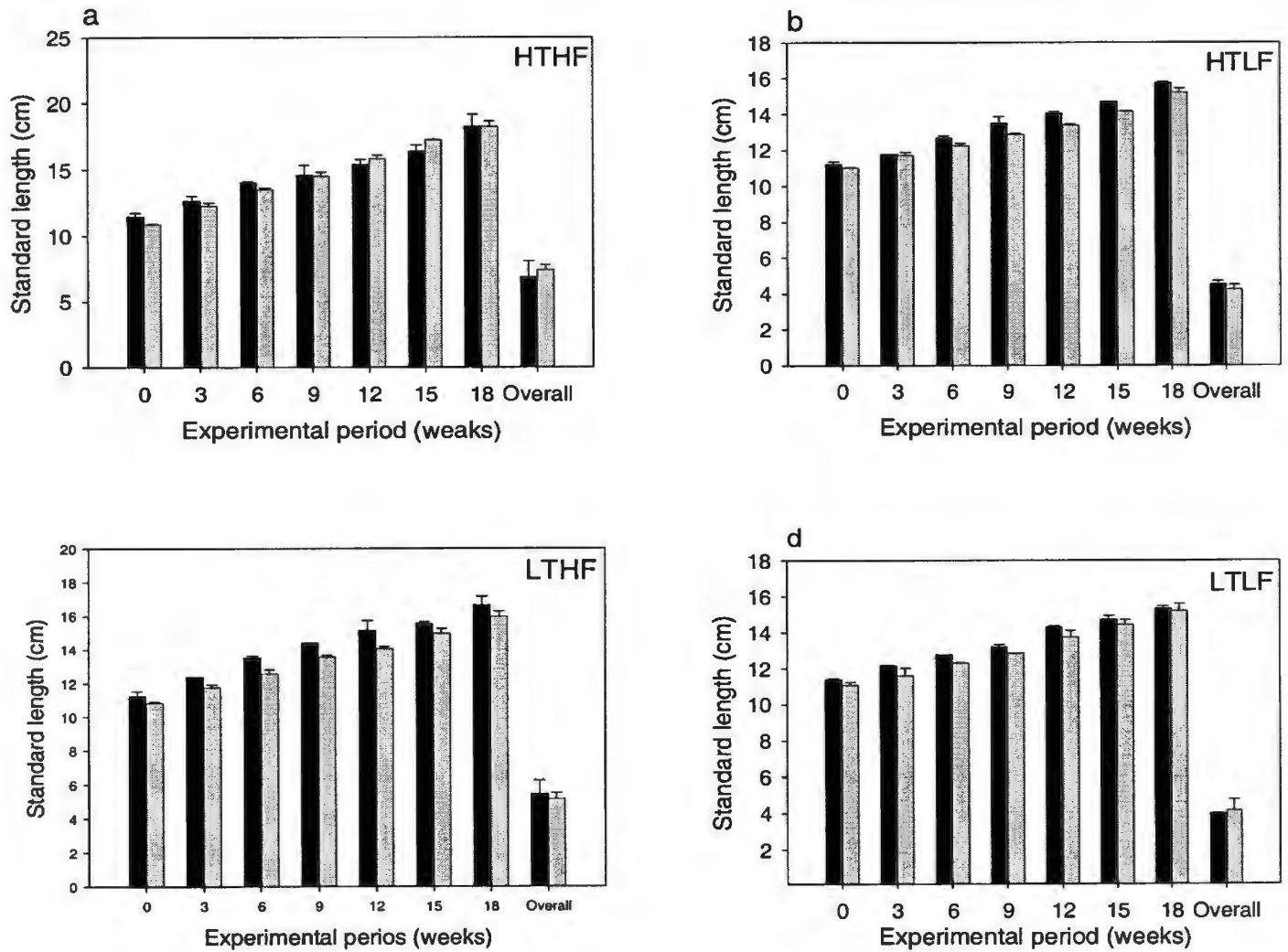


Figure 2.4 Mean standard length (SL)(\pm SD) for 0+ cod juveniles from populations 4T (black bars) and 3Ps (grey bars) at (a) HTHF, (b) HTLF, (c) LTHF, (d) LTLF, (See Fig; 2.2 for details) during the 18 week experimental period. Data on overall standard length during the 18 week experiment are also included for each treatment. (N=180 for each treatment at the start of the experiment). (N=180 for each treatment at the start of the experiment).

However, both 3Ps and 4T juveniles fed with HF had a significantly higher condition factor in both HT and LT, than the corresponding groups LF. Hepatosomatic index was not significantly different in cod fed with HF ration (2% of the body weight) at either temperature (HT, $F = 0.894$, $df = 1$, $p = 0.350$; and LT, $F = 0.168$, $df = 1$, $p = 0.685$) (Fig. 2.6) or those fed the low ration at LT ($F = 0.188$, $df = 1$, $p = 0.667$). However, population 3Ps had a significantly higher hepatosomatic index with low feed at HT ($F = 4.386$, $df = 1$, $p = 0.043$).

The 3Ps juveniles had a significantly higher overall percent survival than 4T juveniles at HT with HF, (Fig. 2.7.a) (97.22 ± 0.78 and 87.22 ± 2.35 , $F = 32.40$, $P = 0.030$ for 3Ps and 4T respectively). However, percent survival was similar in the rest of the treatments (3Ps and 4T respectively; Fig, 2.7): HTLF, (95.55 ± 3.14 and 88.88 ± 1.5 , $F = 7.2$, $P = 0.115$); LTHF, (98.33 ± 0.78 and 96.11 ± 0.78 , $F = 8.00$, $P = 0.106$); LTLF, (95.55 ± 1.57 and 96.11 ± 0.78 , $F = 0.200$, $P = 0.698$).

The specific growth rate (SGR) reaction norms for 3Ps juveniles were higher than 4T juveniles for both temperature and food level and they had slightly different slopes, even though the SGR was not statistically different (Fig 2.8). The reaction norm for FCE of 3Ps juveniles was also higher than 4T juveniles at HT, however the crossing reaction norms for FCE for food level at LT and temperature at HF (Fig. 2.8 c & d) is indicative of strong interaction between environment and the genotype. The crossing reaction norm for standard length for food level at HT (Fig, 2.9a) and temperature at HF (Fig. 2.9 b) indicates a strong interaction between the environment and the genotype. This suggests

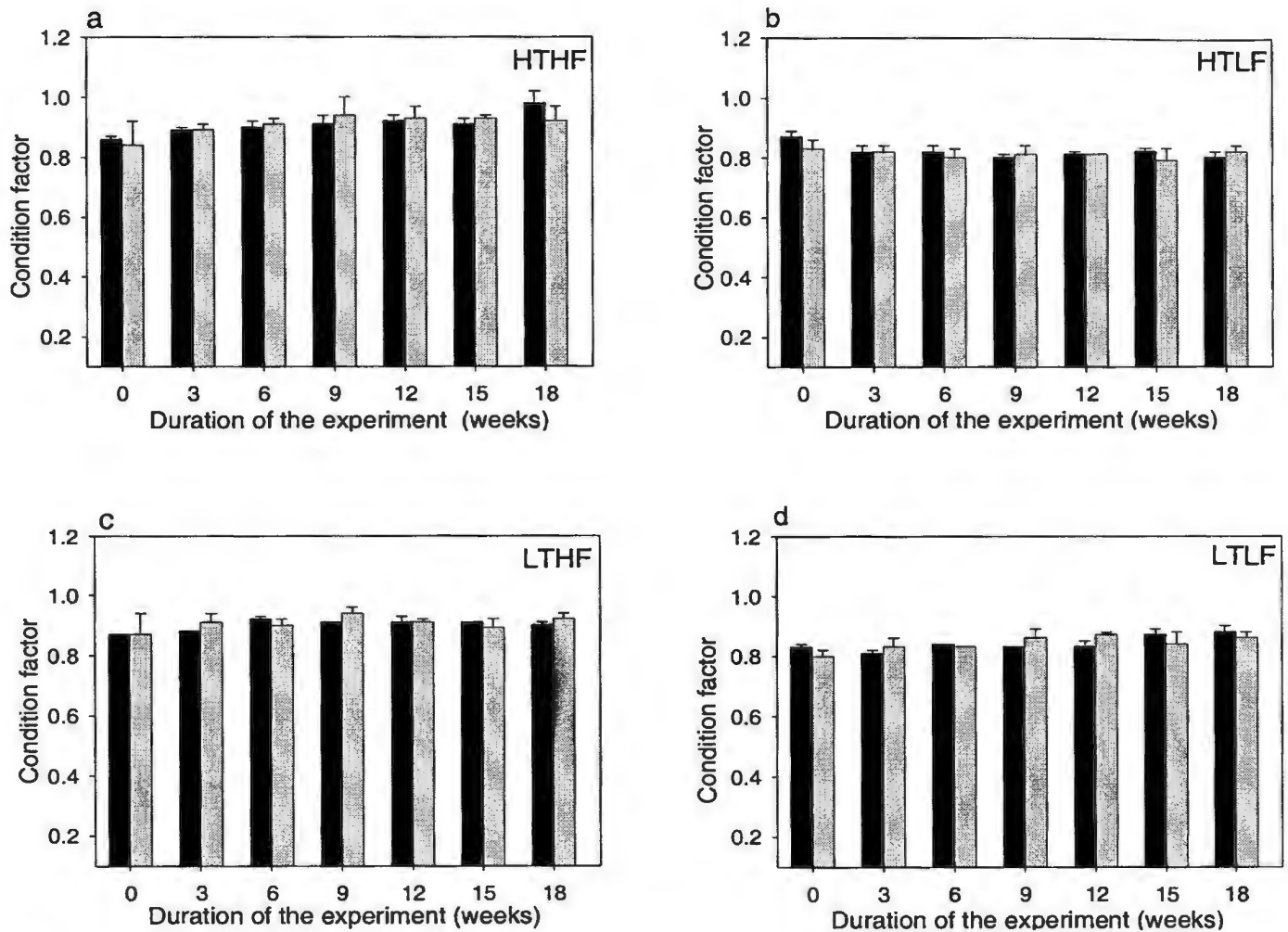


Figure 2.5. Mean Fulton's condition factor (K) (\pm SD) for 0+ cod juveniles from populations 4T \blacksquare and 3Ps \blacksquare at (a) HTHF, (b) HTLF, (c) LTHF, (d) LTLF, (See Fig; 2.2 for details) during the 18 week experimental period. Data on overall condition factor during the 18-week experiment are also included for each treatment. (N=180 for each treatment at the start of the experiment).

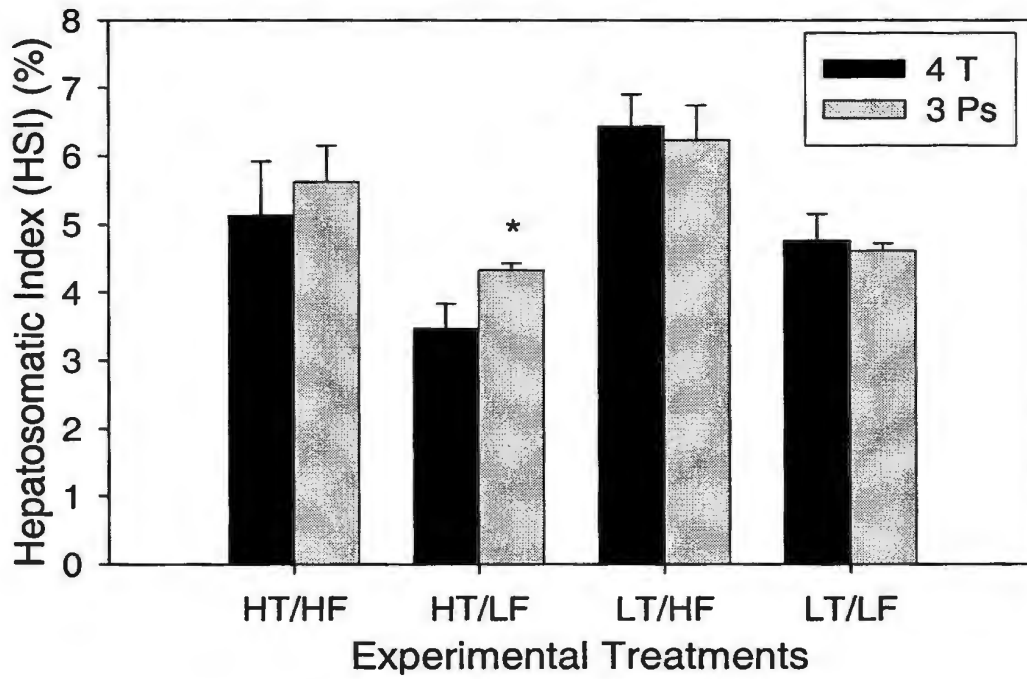


Figure 2.6 Mean Hepatosomatic Index (HSI) (\pm SD) for 0+ cod juveniles from populations 4T and 3Ps at HTHF, HTLF, LTHF, LTLF, (See Fig; 2.2 for details) at the end of the 18 week experimental period. (N=180 per treatment at the start of the experiment (* = $p < 0.05$)).

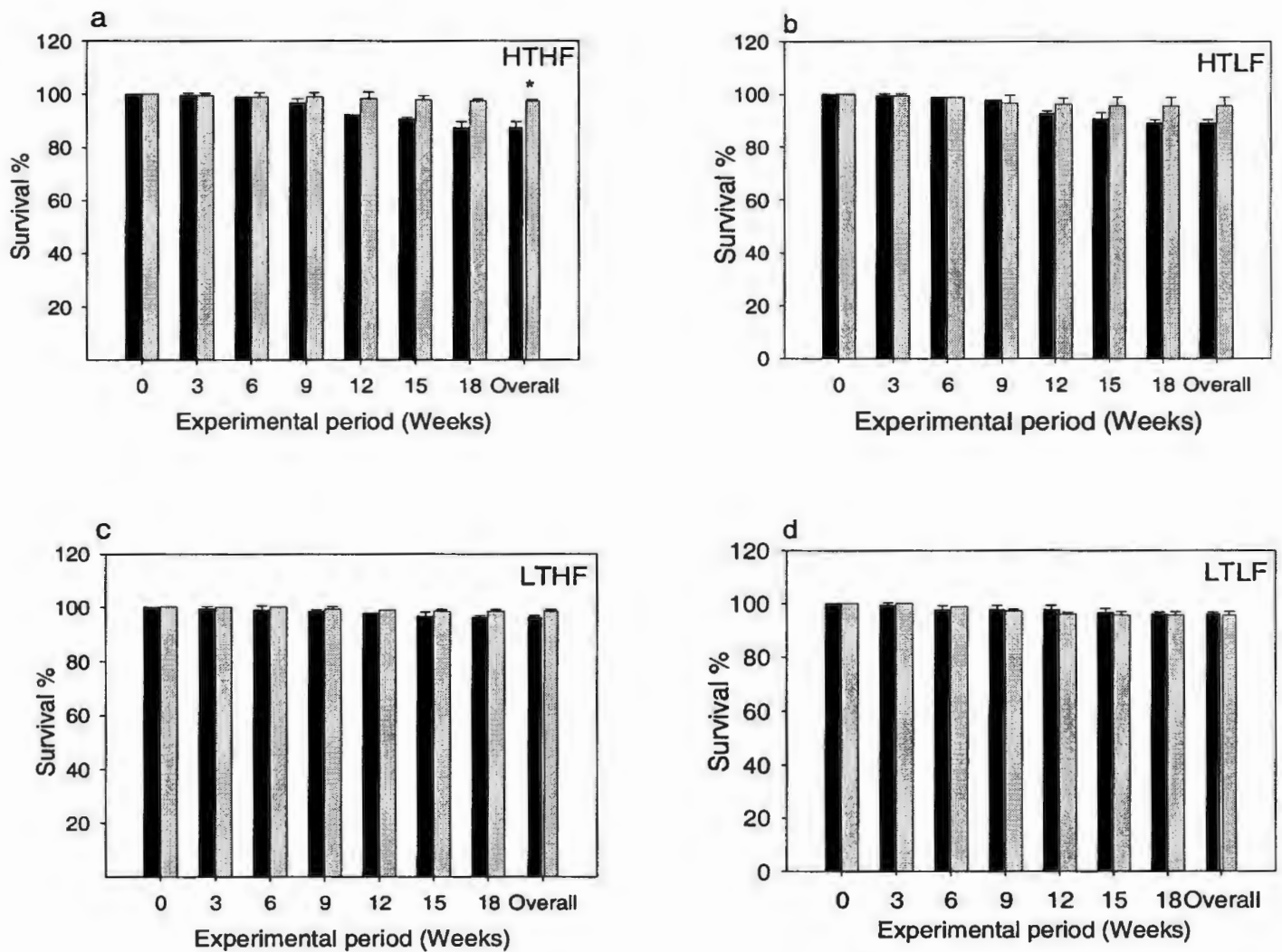


Figure 2.7 Mean survival (%) (\pm SD) for 0+ cod juveniles from populations 4T (■) and 3Ps (▒) at (a) HTHF, (b) HTLF, (c) LTHF, (d) LTLF, (See Fig; 2.2 for details) during the 18-week experimental period. Data on overall survival during the 18-week experiment are also included for each treatment (N=180 per treatment at the start of the experiment) (* = $p < 0.05$).

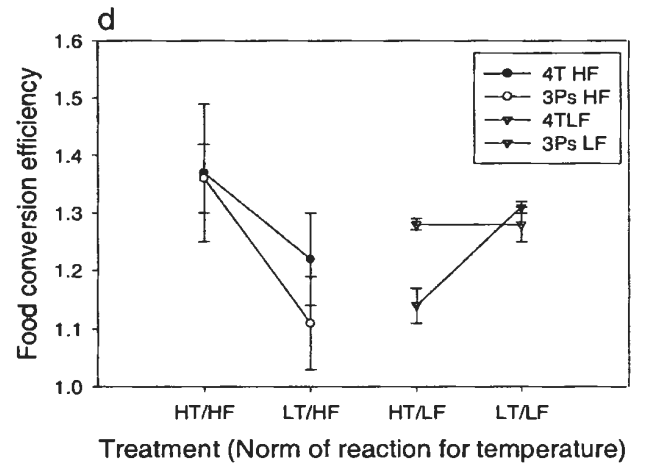
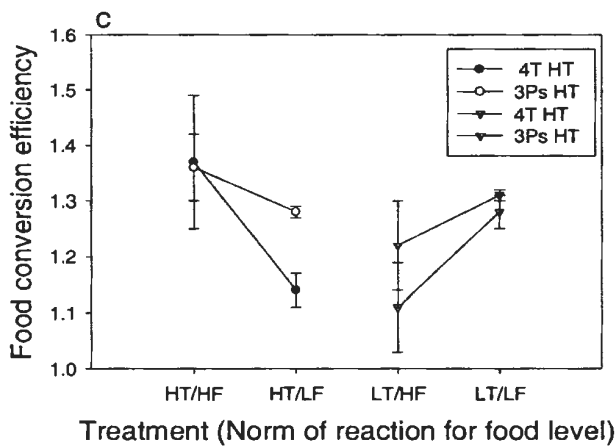
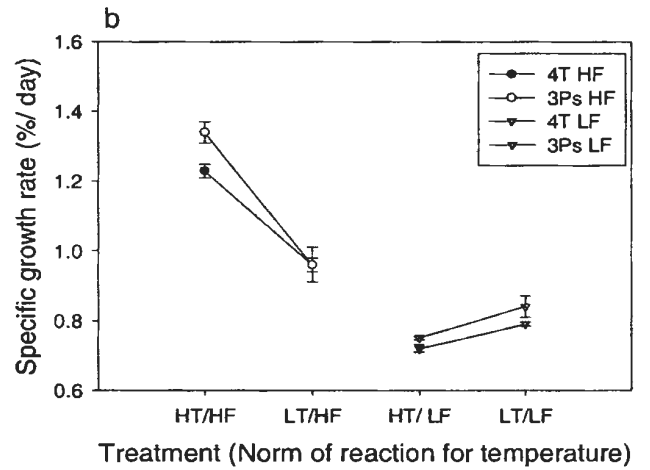
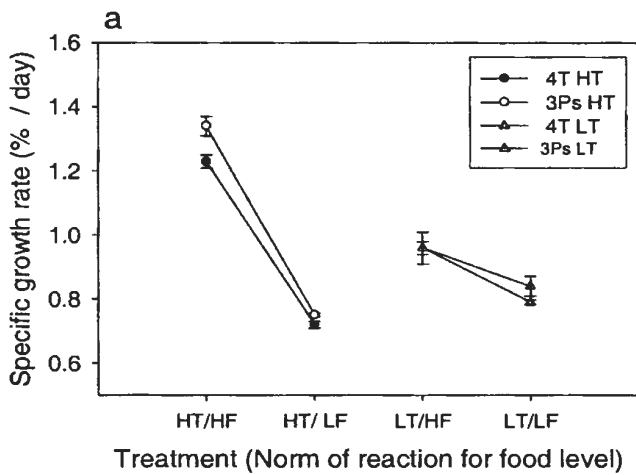


Figure 2.8. Reaction norms for 0+ cod juveniles from populations 4T and 3Ps at (a)

Specific growth rate at different food levels, (b) Specific growth rate at

different temperatures, (c) Food conversion efficiency at different food levels

and (d) Food conversion efficiency at different temperatures, (See Fig; 2.2 for

details) during the 18 week experimental period (Values are mean \pm SD).

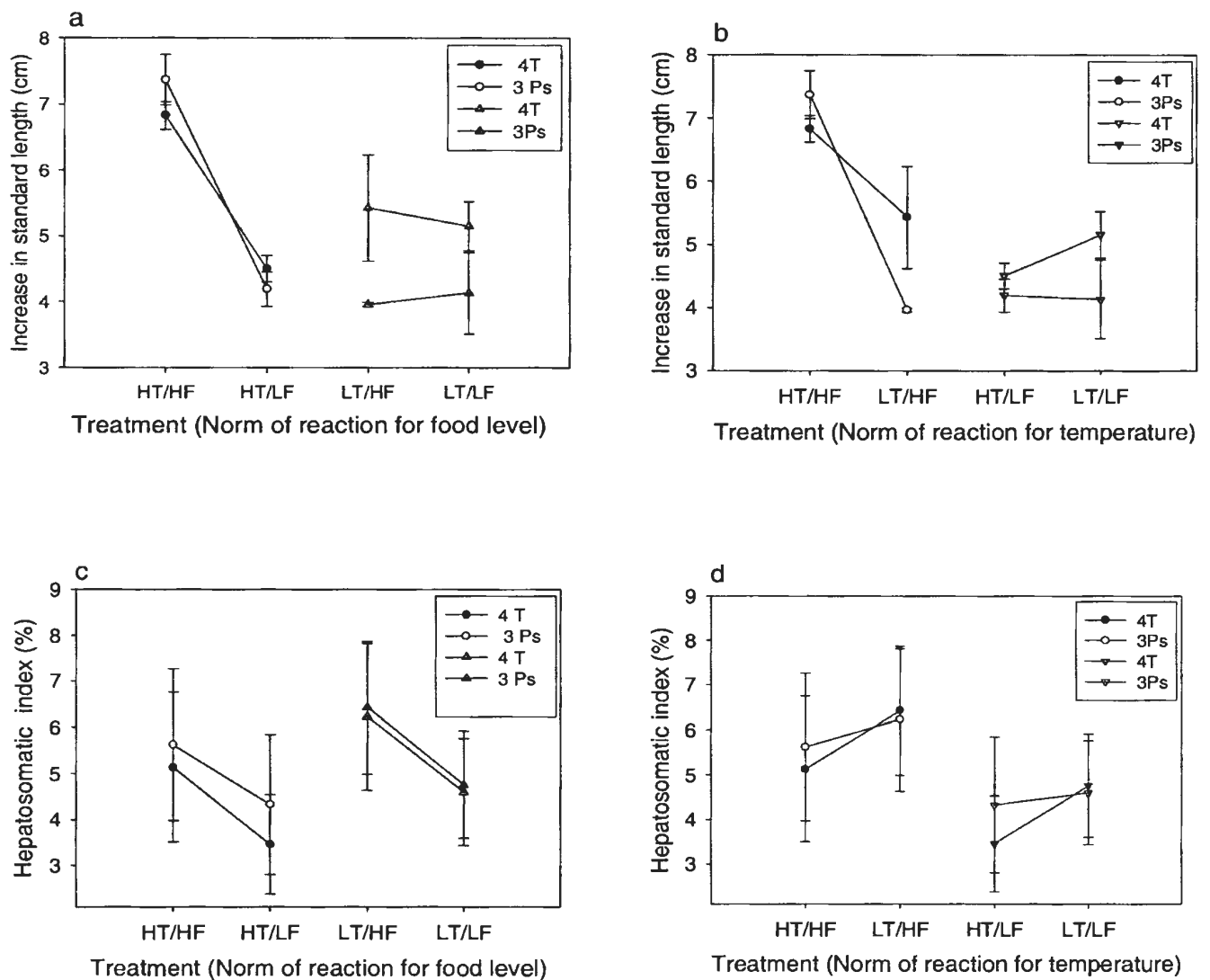


Figure 2.9 Reaction norms for 0+ cod juveniles from populations 4T and 3Ps at (a) Increase in standard length at different food levels, (b) Increase in standard length at different temperatures, (c) Hepatosomatic index at different food levels and (d) Hepatosomatic index at different temperatures, (See Fig; 2.2 for details) during the 18 week experimental period (Values are mean \pm SD).

that the rank order for performance (standard length) depends on the environment. However, 4T juveniles had a higher increase in standard length at LT and LF, while 3Ps juveniles had a higher reaction norm for HIS at HT for food level (Fig. 2.9a), however the rank order for HIS reaction norm switched at LT. The 3Ps and 4T juveniles had crossing reaction norms for temperature for both HF and LF (Fig. 2.9d).

2.5 Discussion

Both the 3Ps and 4T cod juveniles at HT showed a higher SGR over the juveniles in the corresponding treatments at LT. Faster growth of cod at higher temperatures is well documented (Campana & Hurley, 1989; Brander, 1995; Hunt von Herbing & Boutilier., 1996), and Brander (1994) found that over the first four years of life, each 1 °C increase in water temperature results in a 29% increase in size. Pederson and Jobling (1989) suggested that the optimal temperature for growth for small cod (50-1000 g) was 11-15°C. However, Bjornsson *et al.* (2001) found that optimal temperature for growth decreases substantially with increasing size of cod (from 17 °C for 2 g fish to 7 °C for 2000 g fish). Therefore, the high temperature used in my experiment was well within favorable limits and would not have hindered the capacity for growth.

No significant difference in SGR was found in my experiment between 4T juvenile cod (Gulf of St Lawrence) and 3Ps cod (Placentia Bay) reared at high food ration and high temperature (11 °C). These results are consistent with the results of other common garden experiments (Purchase & Brown, 2000b), where they found no significant differences in growth rate between Gulf of Maine and Grand Banks juvenile cod. However, the overall specific growth rate of 3Ps, the more northern of the two populations was 9.75% higher than the overall SGR of 4T juveniles. Even though it was not significant ($p = 0.06$), the 3Ps juveniles supported the trend in higher capacity for growth when provided with favorable temperatures. Results from other studies also suggest higher capacity for growth from higher latitudes, in adults (Brander, 1995), juvenile (Suthers & Sunby, 1996), and larval cod (Hunt von Herbing *et al.*, 1996;

Purchase & Brown, 2000a). In temperature-controlled studies, faster growth rates in northern populations have also been found in other species of fish; largemouth bass (Williamson & Carmichael, 1990), Atlantic salmon *Salmo salar* (Nicieza *et al.*, 1994), and striped bass *Morone saxatilis* (Conover *et al.*, 1997). However, 3Ps fish were significantly smaller in size than 4T juveniles at the start of the experiment, this may have contributed to the trend in faster growth.

Seasonality, as measured by the length of the growing season, has a potent evolutionary effect on growth rates (Schultz & Conover, 1997). This is the principal underlying the CnGV hypothesis. Laboratory experiments with larval striped bass *Morone saxatilis* (Walbaum), American shad *Alosa sapidissima*(L.), Atlantic silverside *Menidia menidia* (L.), and mummichog *Fundulus heteroclitus* (L.) (Conover, 1990; Present & Conover, 1992; Schultz *et al.*, 1996; Conover *et al.*, 1997) have shown that larval and juvenile fish from northern populations have a higher inherited capacity for growth than fish from southern populations. Although not significant, the more northern of my populations (3Ps) showed relatively higher SGR over 4T juveniles in HTHF treatment. The narrow latitudinal differences (2°) between the two populations may have contributed towards lowering the magnitude of difference in SGR's.

Both the 3Ps and 4T populations fed ad-lib (HF) in warm water (HT) had a substantially faster growth rates than juveniles kept at LT. The SGR of 3Ps juveniles in the HTHF treatment was 40.62% higher than its corresponding treatment in the low temperature, while the difference in SGR for 4T juveniles in the respective treatments was only 28.12%. The difference in SGR of both 3Ps and 4T juveniles between

temperatures with LF was lesser in magnitude (4T-7.59% and 3Ps-10.58% higher in warmer water as compared with juveniles in cold water). Brandt (1993) found similar results with Chinook salmon (*Oncorhynchus tshawytscha*) and striped bass (*Morone saxatilis*) where he evaluated growth rates across thermal fronts of different temperatures and prey concentrations. Both species had higher growth with sufficient prey availability at optimal temperatures, but lower temperatures were better for growth if prey availability was low. Despatie *et al.* (2001) discussed the thermal referendum for cod from southern Gulf of St Lawrence, where she found that fish fed with a lower ration and with a negative growth rate tend to select colder water. In other words, due to high cost of metabolism, fish raised in higher temperature with restricted food can display a negative growth rate. Temperature may be the single most important factor determining the growth rates of early life stages of fish (Houde, 1989, Blaxter 1992). The faster growth of cod at higher temperatures is well documented (Campana & Hurley, 1989; Brander, 1994; 1995, Otterlei *et al.*, 1999). Literature suggests that previous efforts to model age and temperature – dependant growth in the field have been influenced by co-varying temperature and food conditions. Restricted prey availability can possibly explain the relatively low optimum temperature estimated growth of cod larvae in the field given by Campana and Hurley (1989). For example, in a study with cod larvae, Otterlei *et al.* (1999) showed that the growth rates of larvae increase when the temperature ranged between 4 and 14 °C, resulting in a 17-fold increase in dry weight over that period from 6 to 12 °C. Near maximum growth with optimal temperature is attainable only when fish are fed close to maximum ration, since restricted food intake will have a marked

influenced on scope of growth at any given temperature (Brett and Groves, 1979; Jobling, 1994). In my study, the reduction in SGR of 3Ps and 4T in high temperature and low food treatments may have been due to restricted ration. Brett and Groves (1979) have shown that reducing the optimal temperature at lower rations could increase the scope of growth.

The SGRs of both the 3Ps and 4T populations (HF) in HT were higher compared to juveniles in LT. This suggests that the faster growth rates of southern populations in the wild (Brander, 1994) may not be due to a higher genetic capacity for growth. However, the difference in SGR between the two temperatures was greater in the 3Ps population, indicating a better response from the northern population. This supports the predictions of Conover and Present (1990) (i.e. CnGV) where larval and juvenile fish from northern populations have a higher capacity for growth than fish from southern populations (see also Isely *et al.*, 1987; Nicieza *et al.*, 1994; Purchase & Brown, 2000a; 2000b). In addition to the increase in the capacity of the northern juveniles to grow, it's important to consider the relationship between size at age and the opportunity to grow. The potential length of the growing season, as determined by temperature and hours of day-light (Thorp *et al.*, 1989), decreases with increase in latitude for the northern populations. Therefore when reared at the same temperature, high altitude individuals (3Ps) may grow faster than low –latitude conspecifics (4T). However, the difference in temperature experienced between these two populations in the wild is very narrow during the growing season. The average temperature of 3Ps and 4T during growing season is

about 1 °C and 2 °C respectively (Swain *et al.*, 1998), and therefore having similar growth rates.

The mean food conversion efficiency for 3Ps and 4T juveniles fed ad-lib in the HT was not significantly different, with 4T reporting only a marginal higher FCE (0.73%) over 3Ps. However, contrasting results were observed in a study (Purchase & Brown, 2000 a) involving juvenile cod from the Grand Banks (GB) and Gulf of Maine GOM). GB cod (northern population) had a higher FCE (14%) than GOM cod, but the growth rate of GB and GOM juveniles were not significantly different. High latitude populations may evolve improved food conversion efficiencies in order to better exploit the limited periods when temperatures allow for rapid growth (Nicieza *et al.*, 1994). Northern populations have increased FCE compared with southern populations in Atlantic silverside *Menidia menidia* L. (Present & Conover, 1992) and Atlantic salmon *Salmo salar* L. (Nicieza *et al.*, 1994). Further evidence in support of counter-gradient variation theory was reported in another two experiments involving juvenile turbot (Imsland *et al.*, 2000; 2001) and Atlantic halibut (Jonnsen *et al.*, 2000).

Mean food conversion efficiency between the 3Ps and 4T juveniles were not significantly different in the HT with HF, LF or between the two feed levels. However, both populations had a significantly higher FCE at LTLF than LTHF. However the FCE between the 3Ps and 4T juveniles within a treatment (LTHF or LTLF) was not significantly different. The temperature had no significant effect on the FCE for both 3Ps and 4T juveniles with the HF. However, both 3Ps and 4T Juveniles in the LTLF treatment had a significantly higher FCE than LTHF treatments. These results are

inconsistent with findings of Purchase and Brown (2000b), where they found a higher FCE at elevated temperature over ambient. However, Brown *et al.* (1989) found that relatively larger cod had higher food conversion efficiencies under colder temperatures.

The 3Ps juveniles were significantly smaller in standard length and total length than 4T at the start of the experiment. However, the two populations showed no significant difference in standard length at the end of the 18-week experimental period, indicating a trend in faster growth of northern population. However, conducting the same experiment for a longer duration could have resulted in more conclusive evidence.

The condition factor (K), the relationship between length and weight, provides an index frequently used by fisheries biologists to quantify the well being of a fish (Tesch, 1971). Condition factor and hepatosomatic index are good predictors of the nutritional status of fish (Lambert & Dutil, 1997; Grant *et al.*, 1998). Fish with a high K value are heavy for their length. The K value for a given fish can also be considered as its deviation from some hypothetical ideal fish of that species growing isometrically. The condition factor of fish of the same species, from different populations, can also be compared (Weatherley, 1972). However the condition factor between 3Ps and 4T were not significantly different at the end of the experiment, which suggests the increase in wet weight, and length in juveniles of the two populations occurred in similar proportion.

Much of the energy storage in cod is as lipids in the liver (Lambert & Dutil, 1997) and fish with higher hepato-somatic indices probably have more lipid reserves. The 3Ps juveniles had a significantly higher (25.19%) HSI in HTLF but with HF (9.55%) it was not significant. These results are contradictory to Purchase and Brown (2000b), where

they found that GOM (42° N; 70° W), cod had a better HIS than GB (48° N; 53° W), the more northern of the two populations. They argued that fish from warmer water are more adapted for lipid storage at warm water and the opposite for fish from cold water. This may be due to the narrow latitudinal (2 °N) and temperature difference (~1 °C) between the 4T and 3Ps populations (Swain *et al.*, 1998).

Reaction norms are presented for SGR, FCE, standard length and HSI. A reaction norm is a set of phenotypes that would be produced if a genotype were exposed to a defined set of environments (Via *et al.*, 1995). The non-parallel reaction norms for SGR are indicative of genetic and environmental influence on the trait (Conover & Schultz, 1995). However, the norm of reaction of 3Ps juveniles for SGR for food level (at HT), and reaction norm for temperature (for HF), was indicative of environmental influence on the phenotypic trait and genetic plasticity. A crossing reaction norm is a strong indication of environment and genotype interaction, where the rank order of performance for a given trait depends on the environment (Conover & Schultz, 1995). Similar reaction norms were observed in FCE for temperature (with LF) and increase in standard length (norm of reaction for feed at HT and for temperature at HF), where the difference in phenotypic traits (FCE, and standard length) observed in the respective temperatures are more likely due to the influence of the environment on the genotype. The non-parallel reaction norms observed in some traits (FCE, HSI, and standard length) constitute evidence of counter-gradient variation and genetic differences between 3Ps and 4T juveniles (Conover & Schultz, 1995).

Results of the present study did not support the hypothesis of Counter Gradient Variation in growth. However, the northern population (3Ps) did have a better survival in HFHT treatment. The survival was not significantly different between the two populations in rest of the treatments. The 3Ps juveniles had a significantly higher HSI with restricted feed at high temperature.

Information available on phenotypic variability in juvenile cod across natural environments is very limited. Therefore, the extent of the involvement of genotype and/or environment on phenotypic variation is unclear. Phenotypic plasticity is another way of explaining a phenotype as it's focused on the adaptive response to environmental heterogeneity (Conover & Schultz, 1995). On the other hand CnGV is a geographical pattern of genotypes (with respect to environment) in which the genetic influence on a trait opposes environmental influence, thereby minimizing phenotypic change along the gradient (Conover & Schultz, 1995). In the present study, I expected the more northern of the two populations (3Ps) to display a better performance in traits such as growth, feed conversion, and condition factor. However, the magnitude of the latitudinal difference between 3Ps (48° 70'N; 54° 20' W) and 4T (46° N; 64° 57'W) was small and the average temperature that the two populations are exposed to in the wild is likewise very similar (Swain, 1998; 1999). Further, no one has investigated the existence of CnGV in cod juveniles at narrow latitudinal differences. Therefore the exact cause (genetic or/and environment) for the trend for the slight better performance of 3Ps population is unclear. Imsland *et al.* (2000) pointed out that different ecosystems may result in adaptations similar to those induced by latitudinal variances (based on temperature and day length),

and cannot be categorized as CnGV. The interaction of a genotype with the environment can either inflate or reduce the phenotypic variance, and it could be detected only by testing individuals or genotypes from different locations in a series of common environments. Even though the present study did not fully support CnGV, investigating the norms of reaction gave a better understanding of the genetic and environmental influence on the phenotypic plasticity observed in this experiment. They indicated possible genetic variability between 3Ps and 4T populations and are consistent with previous findings (Purchase and Brown, 2000a; b).

The northern population did not show a statistically significant difference in capacity for faster growth. However, the better survival of 3Ps juveniles in warmer water with *ad-libitum* feed is a valuable character in selecting suitable stocks to be used in aquaculture. If the observed differences are genetic in origin and are representative of their respective populations, it could have significant implications for cod broodstock development.

Chapter 3.0

Swimming performance of juvenile Atlantic cod (*Gadus morhua*) from Placentia Bay, Newfoundland and the Southern Gulf of St. Lawrence.

3.1 Introduction

As reviewed in chapter 1.0 several studies have investigated the relationship between growth and swimming performance (Kolok & Oris, 1995; Gregory & Wood, 1999) in fish. Faster growth rates of juvenile fishes are believed to be positively associated with fitness (Conover, 1992), but the slower growth rate of southern fish at their natural temperatures is curious. Conover and Shultz (1995) pointed out that the possible ecotypic difference, which involves genotype and environmental interactions, where improved fitness in one environment can occur only at the expense of reduced performance in some other fitness trait. Stearns (1989) suggested possible tradeoffs, where faster growth rate may be negatively correlated with the ability to withstand other environmental challengers or reproductive performance (Roff, 1982; Stearns, 1992).

In this chapter, I investigated CnGV in growth and a possible trade off with critical swimming speed (U_{crit}) in Atlantic cod, *Gadus morhua*. Several studies have indicated that Atlantic cod exhibit CnGV in growth across latitudes, with northern populations exhibiting faster growth and improved food conversion efficiencies than southern populations (Svasand *et al.*, 1996; Purchase & Brown 2000a; 2000b), but none of them have investigated possible tradeoffs associated with faster growth.

Billerbeck *et al.* (2001) reported a tradeoff between growth rate and locomotor performance in Atlantic silverside *Menidia menidia*. They compared both prolonged and burst-swimming capacities between an intrinsically fast growing northern fish (Nova Scotia, NS) and an intrinsically slow growing southern fish (South Carolina, SC), and growth-manipulated phenotypes within each population. They found both prolonged and burst swimming speeds of NS fish were significantly lower than that of SC fish, and that in growth manipulated phenotypes the fast growing phenotypes had a slower swimming speed than the slow growing phenotype within a population. Lankford *et al.* (2001), studying the same two populations of Atlantic silverside *Menidia menidia* found that fast growing NS silversides suffered significantly higher predation mortality than once from SC. In a study involving rainbow trout *Oncorhynchus mykiss*, Gregory and Wood (1998) found a significant negative relationship between specific growth rate and U_{crit} with a full ration suggesting that there is a tradeoff between growth and swimming performance.

Both 3Ps (Placentia Bay) and 4T (Southern Gulf of St. Lawrence) populations of juvenile cod (Chapter 2.0) were used in this study. It was hypothesized that the capacity for faster growth would trade-off against swimming performance in the high latitude population (3Ps juveniles).

3.2 Materials and methods

All experiments were carried out at the Ocean Sciences Centre, and juvenile cod from the same two populations (3Ps and 4T) used in the growth (Chapter 2.0) experiment were tested for their swimming capability. Critical swimming speed (U_{crit}), the

maximum velocity attained by a fish over a set time period (Beamish 1978), was used as a measurement of their swimming performance. Critical swimming speeds (U_{crit}) were determined by swimming fish to exhaustion using incremental velocity steps in a Blazka respirometer (Blazka *et al.*, 1960) (Volume, 6.948L).

A 15-day difference was maintained between the two populations to account for the age difference, as 4T fish were hatched 15 to 16 days prior to 3Ps. The swim-tunnel respirometer was placed in the same room where the growth experiments were conducted to allow for easy access to the water sources from two temperatures (High, 11 ± 1 °C and Low, 7 ± 1 °C). The fish chamber was kept covered and activity in the room was minimized. A total number of 10 fish per population (5 fish per replicate) from the high feed (2% of body weight) tanks, from both temperatures (11 °C & 7 °C) were used in the experiment. Individual fish weighing 30 to 45 grams were captured using a six-inch net, and the wet mass was recorded using an electronic balance prior to the experiment. Fish were individually tested for their U_{crit} . A pre-experimental trial was conducted to determine the time duration required to pre-condition an experimental fish.

3.2.1 Pre-experimental trial

A total of six juveniles were used and each fish was forced to swim at a velocity of 75 cm s^{-1} (approx. 4 to 5 bl s^{-1}) for 5 minutes at 11 °C. Dissolved oxygen level was measured every 20 minutes until the oxygen drop was consistent. This experiment determined that the oxygen drop ($\text{mg O}_2 \text{ min}^{-1}$) of all the fish was stable around 80 to 90 minutes after the brief intense swimming period. Metabolic rates were calculated for each

fish and the average metabolic rates were plotted against the duration (time in min.) of the experiment to determine the time at which they achieve to a stable metabolic rate during the pre-experimental trial (Fig 3.0).

3.2.2 Incremental velocity swim test

The incremental velocity-swimming test (Brett, 1964) was performed on the 40 experimental fish from both 4T and 3Ps populations. According to the pre-experimental trial, a fish was placed in the respirometer 1 hour and 30 minutes before the experiment and pre- conditioned to a flow speed of 2 cm sec^{-1} at the test temperature. Then each fish was allowed to swim at increasing water velocities until they reached exhaustion. This was used to determine the swimming and metabolic capacity of individual fish. In this protocol, current velocity was increased by 7.5 cm s^{-1} every 20 min. until they could no longer swim. At each swimming speed, oxygen consumption was measured for 15 min., the period of oxygen measurement beginning 5 min. after the swimming speed was increased. For each fish, exhaustion was determined by the inability of the fish to separate itself from the rear grid of the respirometer. The time and speed at which the fish could no longer swim was noted for the calculation of critical swimming speed.

At the end of the *Ucrit* measurements, the fish was anesthetized (MS 222 0.1 g l^{-1}), and standard length, total length, body width (at the anterior base of the 1st dorsal fin) was recorded. Body width and depth (at the base of the pectoral fin attachment) and the width of the head anterior to the eyes were recorded using a caliper (to the nearest 0.01mm) (Hawkins and Quinn, 1996). A digital photograph of the lateral view of the fish was also

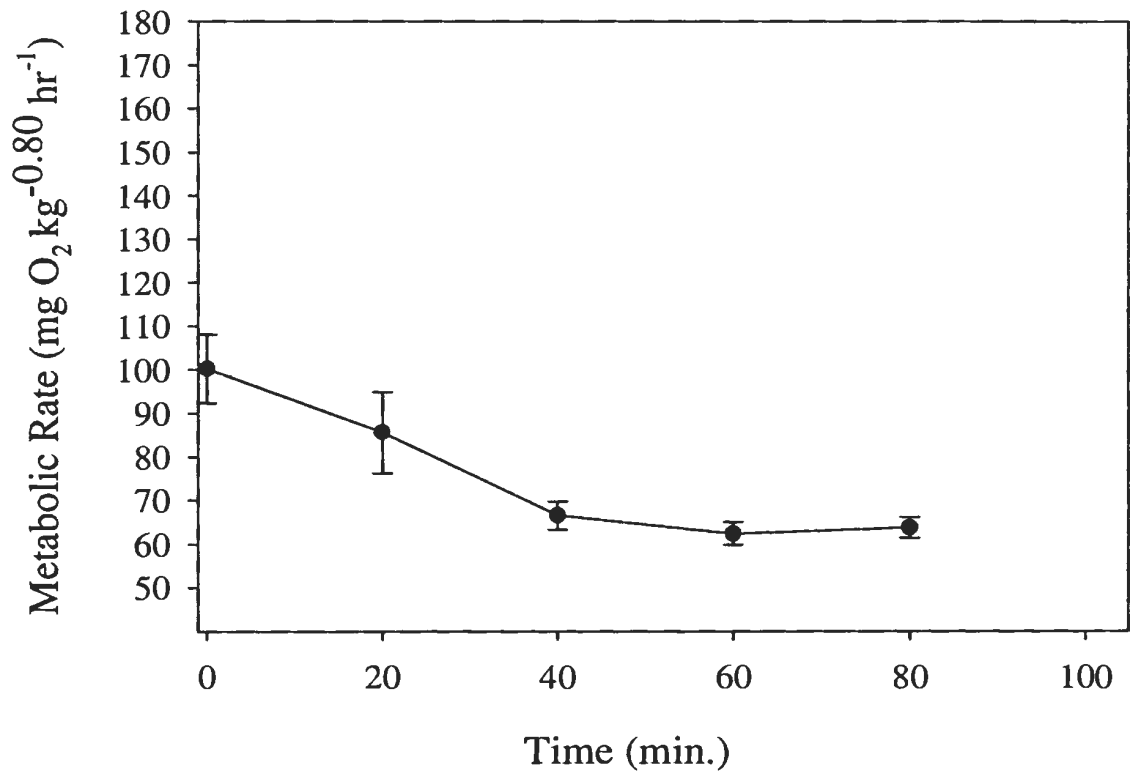


Fig 3.0 Mean metabolic rate (mg O₂ kg^{-0.80} hr⁻¹) (\pm SD) of *Gadus moruha* (3PS population) after a brief period of intense swimming. (n=6).

taken after spreading dorsal, pelvic, anal and caudal fins to determine if correlation existed between the fin areas and U_{crit} . A tiny fin clip on the 1st dorsal fin was made to avoid using the same fish twice.

3.2.3 Measurements and calculations

Water temperature and oxygen content within the swim tunnel were continuously measured by pumping water through an external circuit (at 50 ml min⁻¹) using a peristaltic pump (Masterflex L/S Model 77200-12, Cole Parmer). This circuit was constructed of tubing with low gas permeability (Masterflex, 6419-16, Tygon), and contained a customized flow chamber (WTW Inc., Germany) that housed an oxygen electrode with thermal sensor. This oxygen electrode was connected to an oxygen meter (Model Oxy 340, WTW Inc., Germany), which automatically measures temperature. The meter was corrected for the salinity level of the seawater (assumed as 33.6 ppt.).

Oxygen consumption was measured at the beginning of each experiment, and at all swimming speeds by stopping the flow of the water into the tunnel for 15 min. and recording the drop in water oxygen content. Metabolic rate (MO_2 ; mg O₂ kg^{-0.80} h⁻¹) was calculated for all fish as (Reidy *et al.*, 1995):

$$MO_2 = (((C_i - C_f) T^{-1}) \times (V_c - W_a) \times 60\text{min}) \times (W_a^{-0.8})$$

Where, C_i is the water oxygen content at the start of the measurement, C_f is the water oxygen content at the end of the experiment, V_c is the volume of the respirometer, T is the time required to make the MO_2 measurement, and W_a is the wet mass of the animal. To account for the variation in size among the fish, MO_2 was adjusted to a standard body

mass of 1 kg using a mass exponent of 0.80 (Saunders, 1963; Reidy *et al.*, 1995; Reidy *et al.*, 2000);

Critical swimming speed (U_{crit}) was calculated as (Brett, 1964);

$$U_{crit} = V + ((T_f) \times V_i) / T_i$$

Where V is the velocity at which the fish swam for the entire time increment; V_i is the velocity increment, T_f is the time elapsed from the last change in current velocity to fatigue, and T_i is the time increment (the time between steps).

Swimming efficiency for individual fish was measured as cost of transport (COT) (in $\text{cal kg}^{-0.8} \text{ km}^{-1}$) (Nielsen, 1972; Parsons & Sylvester, 1992) using an oxycaloric coefficient of $3.25 \text{ cal mg O}_2^{-1}$;

$$\text{Cost of Transport} = \frac{\text{Metabolic rate}}{\text{Swimming speed}} = \frac{\text{cal kg}^{-0.8} \text{ hr}^{-1}}{\text{km hr}^{-1}} = \text{cal kg}^{-0.8} \text{ km}^{-1}$$

A blank experiment (i.e. without a fish) indicated that water O_2 content in the respirometer (volume; 6.948 L) did not decrease during a 15 min. experimental period.

3.2.4 Statistical Analyses.

Metabolic rates were analyzed for each swimming speed using General linear model (SPSS 9.0) repeated measures, univariate analysis. Differences in metabolic rates and COT were compared between 3Ps and 4T juveniles at each swimming speed on a given temperature using one-way ANOVA. Standard metabolic rate (SMR) was calculated for each fish by log transforming the oxygen consumption data and regressing against swimming speed. The y intercept for this equation was used to calculate the SMR.

SMR, *Ucrit*, metabolic scope and maximum oxygen consumption were compared between the two temperatures and populations using two-way ANOVA.

Fish length, wet mass, total length, standard length and condition factor between 3Ps and 4T juveniles were compared using two-way ANOVA to test for population temperature interactions. Pearson correlation coefficients were calculated to determine if *Ucrit*, metabolic scope or COT were significantly correlated with the morphological data.

The effect of tank was tested initially with 2x2 ANOVA to test interactions between tank and population. Residual plots were examined for compliance of normality, independence, and homogeneity (Sokal & Rohlf, 1995).

3.3 Results

The age of 4T and 3Ps juvenile cod were the same at the start of the experiment and there was no significant difference in wet mass, total length or condition factor. (Table 3.1).

3.3.1 Metabolism

Standard metabolic rate (SMR) was not significantly different between 3Ps and 4T juvenile cod at both 11 °C (111.55 ± 17.82 and 106.69 ± 6.67 mg O₂ kg^{-0.8} hr⁻¹, respectively: F= 0.654, P= 0.429) and 7 °C (72.71 ± 8.41 and 72.41 ± 11.92 mg O₂ kg^{-0.8} hr⁻¹, respectively: F=0.017, p = 0.897). However, there was a significant difference in SMR for both populations between the two temperatures (F= 93.69, p = 0.000).

Table 3.1 Initial mean wet mass (g), total length (cm) and condition factor (\pm SD) of (0+) juvenile cod from population 3Ps and 4T. (n = 10 for each population at 11 °C and 7 °C).

	Population	Temp: °C	F – Value	P- value
Avg. wet mass (gm)				
39.9 \pm 2.92	3Ps	11	3.049	0.098
36.0 \pm 6.42	4T			
40.0 \pm 3.29	3Ps	7	0.121	0.732
39.4 \pm 4.35	4T			
Total length (cm)				
17.08 \pm 0.04	3Ps	11	2.48	0.132
16.63 \pm 0.66	4T			
17.20 \pm 0.73	3Ps	7	0.377	0.547
16.98 \pm 0.86	4T			
Condition factor				
0.80 \pm 0.06	3Ps	11	0.726	0.405
0.77 \pm 0.09	4T			
0.78 \pm 0.07	3Ps	7	0.267	0.611
0.80 \pm 0.06	4T			

The metabolic rate of 3Ps and 4T juveniles increased with swimming speed at both 11 °C and 7 °C and both populations had significantly higher metabolic rate at 11 °C. However, there was no significant difference in metabolic rates between 3Ps and 4T juvenile cod at a given temperature (at 11 °C or 7 °C; Figure 3.1 & Table 3.2). Further, The maximum oxygen consumption of 3Ps and 4T juveniles was similar at 11 °C (169.61 ± 15.26 and 173.38 ± 21.11 mg O₂ kg^{-0.8} hr⁻¹, respectively: F = 0.183, p = 0.674) and 7 °C (129.00 ± 22.20 and 127.75 ± 15.17 mg O₂ kg^{-0.8} hr⁻¹, respectively: F = 0.022, p = 0.885).

At 11 °C the 4 T juvenile cod had a 20.33% higher metabolic scope than the 3Ps juveniles, but this difference was not significant (F = 1.111, p = 0.306). Both 3 Ps and 4 T juveniles had a similar metabolic scope at 7 °C (F = 0.006, p = 0.940). The metabolic scope for activity remained the same in both groups between 11 °C and 7 °C (F = 0.612, p = 0.439; Table 3.2).

3.3.2 Critical swimming speed (*U_{crit}*) and Cost of transport

Both 3Ps and 4T juveniles had significantly higher critical swimming speeds (*U_{crit}*) at 11 °C (20.58 % and 9.56 %, respectively), as compared with corresponding groups at 7 °C (61.22 ± 0.48 cm s⁻¹ vs. 50.77 ± 1.0 and 58.10 ± 1.25 cm sec⁻¹ vs. 52.54 ± 3.53 cm s⁻¹ respectively), (F = 9.965, p = 0.003). However, the critical swimming speeds of 3Ps and 4T juveniles within 11 °C (F = 0.211, p = 0.651) and 7 °C (F = 0.600, p = 0.449) were not significantly different (Table 3.2).

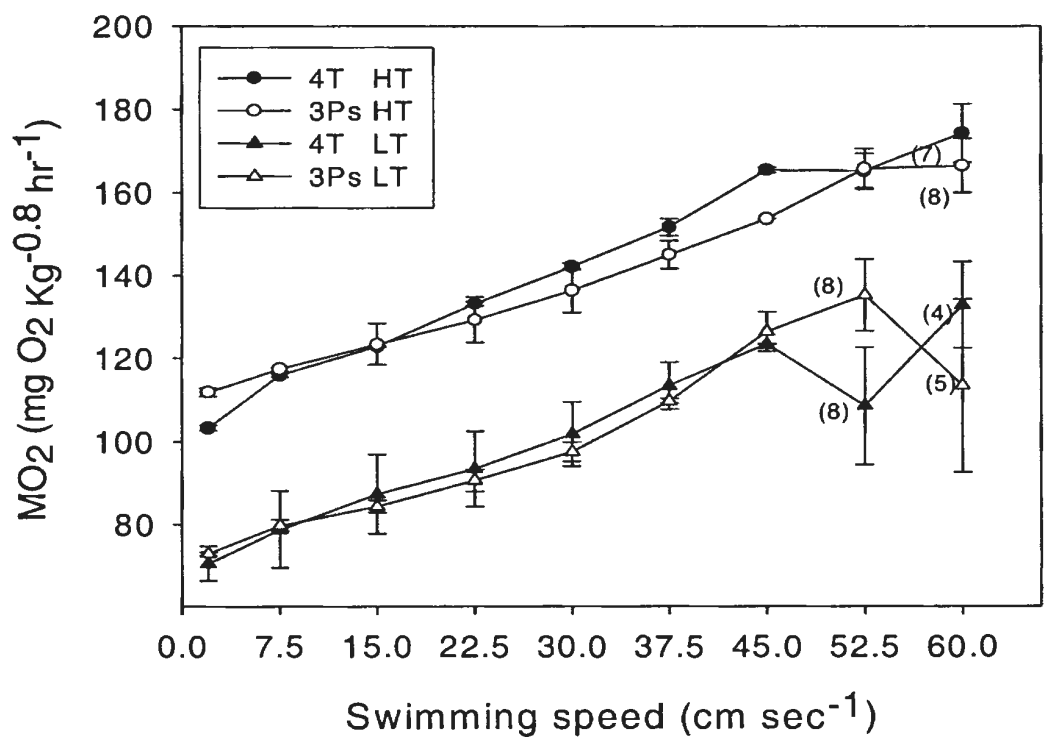


Figure 3.1 Relationship between mass adjusted oxygen consumption (MO_2) ($mg\ O_2\ kg^{-0.8}\ hr^{-1}$) (\pm SD) and swimming speed ($cm\ sec^{-1}$) for (0+) juvenile cod from 3Ps and 4T at 11 °C (HT) and 7 °C (LT). (Number of fish that swam at a given speed is indicated if $N < 10$).

Cost of transport (COT) decreased substantially as swimming speed was increased (Figure 3.2), with COT at maximum swimming speeds only approx. 20% of those at 7.5 cm s⁻¹. Swimming at 11 °C was significantly more costly for both 3 Ps and 4 T juveniles than at 7 °C. However, there was no significant difference in COT between populations within a given temperature (11 °C or 7 °C). Therefore a second order regression was fitted to the relationship between swimming speed (cm s⁻¹) and COT for both populations at 7 C° and 11 C°, and the minimum COT was determined by the derived relationship.

Fin surface area was positively correlated with standard ($r^2 = 0.726$, $p = 0.000$) and total length ($r^2 = 0.606$, $p = 0.000$), and body depth was correlated with fish length ($r^2 = 0.463$, $p = 0.003$ and $r^2 = 0.513$, $p = 0.001$ for standard and total lengths respectively) and condition factor ($r^2 = 0.470$, $p = 0.002$). However, morphological parameters were not significantly different between 3Ps and 4T juveniles. Body depth was positively correlated with U_{crit} ($r^2 = 0.331$, $p = 0.037$) and metabolic scope ($r^2 = 0.326$, $p = 0.040$) (Table 3.4), and standard lengths were negatively correlated with COT ($r^2 = -0.321$, $p = 0.043$) (Table 3.4). Metabolic scope for activity also had a strong positive correlation with U_{crit} ($r^2 = 0.687$, $p = 0.0$). Fin surface areas were significantly correlated with one another (Table 3.3); therefore the relationship between swimming performance and total fin surface area was tested (Reidy *et al.*, 2000) (Table 3.4).

Table 3.2 Temperature dependent differences in *Ucrit*, standard, and maximum oxygen consumption (MO_2), and metabolic scope between (0+) 3Ps and 4T juvenile cod at 11 °C and 7 °C.

Pop:	<i>Ucrit</i> (cm sec ⁻¹)	Standard MO_2 mg O ₂ kg ^{-0.8} hr ⁻¹	Maximum MO_2 mg O ₂ kg ^{-0.8} hr ⁻¹	Metabolic Scope mg O ₂ kg ^{-0.8} hr ⁻¹
11°C				
3Ps	61.22 ± 0.48	111.32 ± 0.33	166.55 ± 4.34	58.06 ± 4.00
4T	58.10 ± 1.25	106.69 ± 0.97	173.14 ± 0.76	66.45 ± 1.73
7°C				
3Ps	50.77 ± 1.00	72.72 ± 2.50	129.00 ± 0.47	56.29 ± 2.98
4T	52.54 ± 3.53	72.11 ± 7.80	127.74 ± 0.01	55.64 ± 7.81

Table 3.3 Pearson product –movement correlations (r^2) of total surface areas among the different groups of fins.

	Dorsal	Anal	Caudal
Dorsal	-	0.674**	0.481**
Anal	-	-	0.423**

** P < 0.01

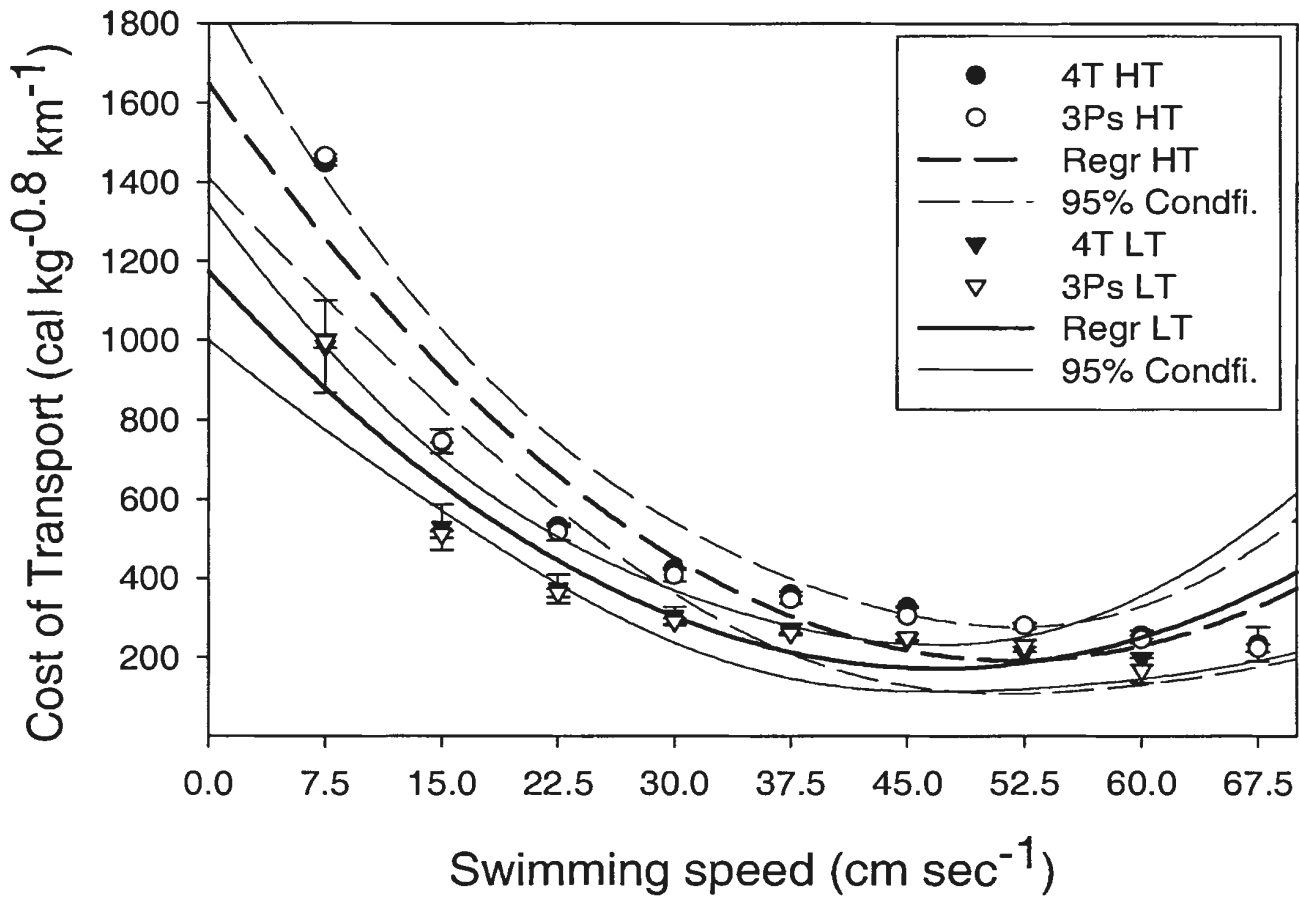


Figure 3.2 Relationship between cost of transport ($\text{cal kg}^{-0.8} \text{ km}^{-1}$) (COT) and swimming speed (cm sec^{-1}) for (0+) juvenile cod from populations 3Ps and 4T at 11 °C and 7 °C. All values are mean (\pm) SD. Fish per treatment ($n = 10$) and number of fish swam at each speed (if $N < 10$) is given in Figure 3.1. The fitted lines represent second order regression with 95% confidence intervals of swimming speed and COT.

The crossing reaction norm for metabolic scope and *Ucrit* (Fig. 3.3) indicates a strong interaction between the environment and the genotype. This suggests that the rank order for performance (*Ucrit* & metabolic scope) depends on the environment. However, 4T juveniles had a higher metabolic scope at 11 °C, while 3ps juveniles had a greater reaction norm for *Ucrit* at 11 °C (Fig. 3.3). The rank order for metabolic scope and *Ucrit* reaction norms switched at 7 °C.

Table 3.4 Pearson product –movement correlations (r^2) between *Ucrit*, metabolic scope, COT, morphology and morphological parameters.

	<i>Ucrit</i> (cm s ⁻¹)	Metabolic scope (mgO ₂ kg ^{-0.80} hr ⁻¹)	COT at <i>Ucrit</i> (mgO ₂ kg ^{-0.80} hr ⁻¹)
Total fin surface area (cm ²)	-0.115	0.009	-0.215
Standard length (cm)	-0.089	-0.053	-0.321*
Total length (cm)	-0.011	0.030	-0.288
Body depth (cm)	0.331*	0.326*	-0.274
Condition factor	0.287	0.277	0.015

*P <0.05

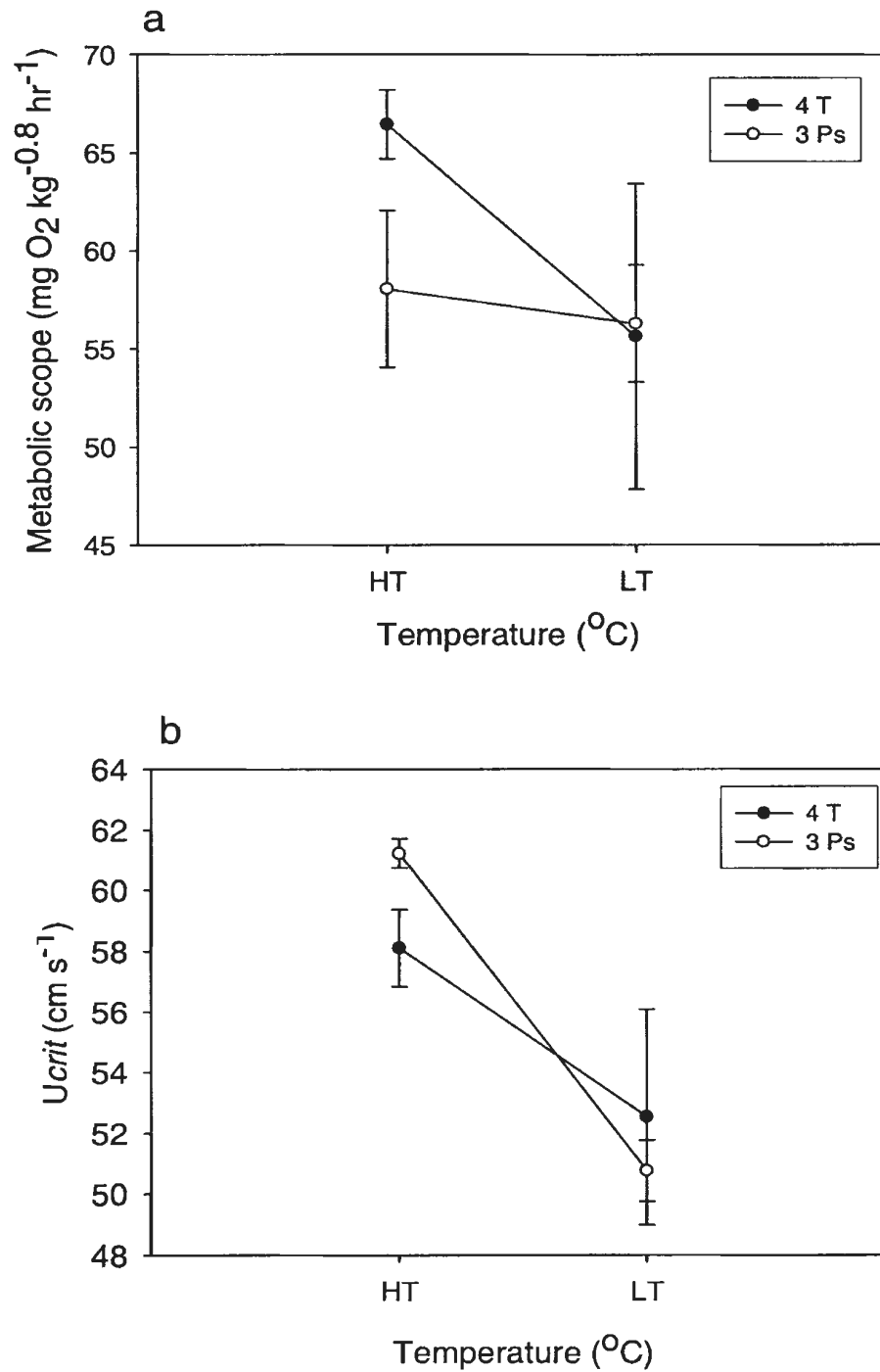


Figure 3.3 Reaction norms of (0+) juvenile cod from populations 4T and 3Ps reared under high temperature and high feed (HTHF), low temperature and low feed (LTHF) for (a) metabolic scope and (b) critical swimming speed (*U_{crit}*) for (\pm SD) during the 18 week experimental period.

3.4 Discussion

Calculated SMR (oxygen consumption of a non fed fish at rest) (Beamish & Moorkherjee, 1964; Fry, 1971; Brett, 1972) for both 3Ps and 4T juveniles was significantly different between 11°C and 7°C. However, there was a 34.8% and 32.42% reduction in SMR at 7 °C for 3 Ps and 4T, respectively. Reduced oxygen consumption at low temperature is well documented. Saunders (1963) found a significant increase in oxygen consumption for both starved and fed cod with an increase in temperature. The oxygen consumption of both large (>1kg) and small (<1kg) cod increased when the temperature was increased from 3 °C to 10 °C, with larger cod having a higher magnitude of increase. Hochachka and Somero (2001) suggest that low metabolic rates at low temperatures were due to a decrease in the rate of enzymatic activity. However, the oxygen consumption in larger cod leveled off when the temperature was further increased from 10 °C to 15 °C, but continued to rise for smaller cod. The effect of temperature on metabolic rate was also demonstrated for *Gadus morhua* (Hunt von Hurbing & Boutilier, 1996), Arctic cod *Boreogadus saida* (Hop & Graham, 1995), and European sea bass *Dicentrarchus labrax* (Koumoundouros *et al.*, 2002) (reviewed by Hunt von Hurbing & White, 2002).

In my study, the standard metabolic rate at 7 °C was similar for both 3Ps and 4 T juveniles (approx. 72 mg O₂ kg^{-0.80} hr⁻¹) and it was in the same range reported by Reidy, *et al.* (2000). Hunt von Hurbing and White (2002) reported similar SMR for small juvenile cod (Avg. wt. 1.9g – 3.2g) (96 mg O₂ kg^{-0.80} hr⁻¹). The average wet mass of 3Ps and 4T juveniles cod were 39g, however information available on oxygen consumption in

a similar weight class juvenile cod is very limited. Several studies have measured SMR in larger juvenile cod at an average temperature (5 °C): Saunders (1963), 0.43 kg (62.5 mg O₂ kg^{-0.8} hr⁻¹); Schurman and Steffensen (1997), 79 – 437 g (44.37 mg O₂ kg^{-0.8} hr⁻¹); Webber (2001), 1.58 – 3.7 kg (53.58 mg O₂ kg^{-0.8} hr⁻¹); Bushnell and Steffensen (1994), 152 g (82.75 mg O₂ kg^{-0.8} hr⁻¹); Claireaux *et al.* (2000), 950 – 1850 g (38.5 mg O₂ kg^{-0.8} hr⁻¹).

The standard metabolic rates (SMR) of 3Ps (111.55 mg O₂ kg^{-0.8} hr⁻¹) and 4T (106.69 mg O₂ kg^{-0.8} hr⁻¹) juveniles at 11°C were not significantly different. Soofiani and Priede (1985) and Saunders (1963) reported SMR values for cod with an average weight of 188g (122.5 mg O₂ kg^{-0.8} hr⁻¹ at 10 °C) and 150g (191.25 mg O₂ kg^{-0.8} hr⁻¹ at 15 °C) respectively. Saunders (1963) reported that smaller individuals consume oxygen at a greater rate per unit weight than larger individuals. Therefore, the comparatively higher SMR observed in 3Ps and 4T juveniles for their weight (avg. mass 39 g) at 11 °C are within the limits reported in the literature.

Maximum oxygen consumption for 3Ps (169.61 mg O₂ kg^{-0.8} hr⁻¹ at 11 °C & 129.0 mg O₂ kg^{-0.8} hr⁻¹ at 7 °C) and 4T (173.14 mg O₂ kg^{-0.8} hr⁻¹ at 11 °C & 127.75 mg O₂ kg^{-0.8} hr⁻¹ at 7 °C) cod juveniles and was not significantly different between the two populations at either given temperature. Similar values were reported by several other studies for larger cod. Webber *et al.* (1998) reported a maximum oxygen consumption of 232.8 mg O₂ kg^{-0.8} hr⁻¹ at 10 °C and 172.8 mg O₂ kg^{-0.8} hr⁻¹ at 5 °C for Atlantic cod (averaging 1.91 kg) from Eastern Passage, Nova Scotia. Reidy *et al.* (2000) reported maximum oxygen consumption for adult cod (6 years) at 206 mg O₂ kg^{-0.8} hr⁻¹ at 5 °C. Similarly, Schurmann

and Steffensen (1997) reported $183.25 \text{ mg O}_2 \text{ kg}^{-0.8} \text{ hr}^{-1}$ at $5 \text{ }^\circ\text{C}$ and $247.37 \text{ mg O}_2 \text{ kg}^{-0.8} \text{ hr}^{-1}$ for cod averaging $79 - 473 \text{ g}$. Soofiani and Priede (1985) suggested that cod in swim tunnels attain their maximum oxygen consumption during recovery but not at maximum swimming speed. He observed a 40% higher oxygen consumption during recovery than that observed during sustained swimming. However, results of my experiment contradict his findings where the maximum oxygen consumption was reported at maximum sustained swimming speed. Tang *et al.* (1994) and Reidy *et al.* (1995) had similar results, which support my findings.

The difference between the oxygen consumption at maximum swimming speed and at zero activity is used to determine the animal's metabolic scope for aerobic activity (Fry, 1971). Based on the CnGV hypothesis, I expected a higher metabolic scope for activity in the relatively slow growing (under common environmental conditions) southern population (4T), as compared with individuals from 3Ps. The metabolic scope for activity of 4T juveniles ($66.45 \text{ mg O}_2 \text{ kg}^{-0.8} \text{ hr}^{-1}$) was 20.33% higher than in 3Ps juveniles ($58.05 \text{ mg O}_2 \text{ kg}^{-0.8} \text{ hr}^{-1}$), however it was not significantly different. Nelson *et al.* (1994) compared two populations of cod, one from the Bras d'Or lakes of Nova Scotia (BDC) ($60^\circ 25' \text{W}$, $45^\circ 85' \text{N}$) and the other from the Atlantic Ocean off the Nova Scotian coast (SSC) ($64^\circ 25' \text{W}$ and $44^\circ 33' \text{N}$). These two populations were from similar latitude as 3Ps (48°N) and 4T fish (46°N), however BDC cod originated from a brackish water environment with lower salinity. The absolute metabolic scope between these two populations was not significantly different but it was higher than experienced in my experiment (BDC $121.77 \text{ mg O}_2 \text{ kg}^{-0.8} \text{ hr}^{-1}$ and SSC $124.5 \text{ mg O}_2 \text{ kg}^{-0.8} \text{ hr}^{-1}$). However, the

actual scope for activity (calculated by subtracting minimal MO_2 by the maximum MO_2) (SSC $78.4 \text{ mg O}_2 \text{ kg}^{-0.8} \text{ hr}^{-1}$ and BDC $91.72 \text{ mg O}_2 \text{ kg}^{-0.8} \text{ hr}^{-1}$) was close to the populations I tested. The higher absolute metabolic scope may be due to the use of larger size cod (average weight 0.8 to 1.22 kg). In another study in Scotland involving cod, Soofiani and Priede (1985) reported a higher value ($179.28 \text{ mg O}_2 \text{ kg}^{-0.8} \text{ hr}^{-1}$) for cod of similar weight to my 3Ps and 4T cod at 10°C .

The critical swimming speed was not significantly different between 3Ps and 4T juveniles at a give temperature (11°C or 7°C), even though it was hypothesized that the southern of the two populations (4T) would have a higher U_{crit} . Billerbeck *et al.* (2001) investigated the latitudinal effect of swimming performance in Atlantic silverside, (from Nova Scotia-NS, 44°N and South Carolina-SC, 33°N). He found that the rapid growth and the high level of food consumption in northern genotypes of Atlantic silverside traded-off against the aerobic and anaerobic swimming performance in a common environment experiment. Faster growth rates in relatively northern populations have been reported for several species under common environment studies. Purchase and Brown (2000a; 200b) found faster growth rates in Atlantic cod from Grand Banks (45°N) over Gulf of Maine (42°N), striped bass *Morone saxalite* from New York (41°C) had a faster growth rate than fish from Southern Carolina (33°N) (Conover *et al.*, 1997). Imsland *et al.* (2001) reported higher growth rates and food conversion efficiencies for higher latitude juvenile turbot *Scophthalmus maximus* (Norway, 59°N & Iceland, 63°N) over fish from southern latitudes (France, 45°N & Scotland, 55°N). However, the specific growth rate of 3Ps and 4T juveniles were not significantly different (Chapter 2.0).

Therefore lack of a difference in *Ucrit* (or tradeoff of aerobic swimming performance against growth) between these two populations is not surprising.

Conover (1990) and Conover and Present (1990) suggested that high latitude populations show CnGV in growth across latitudes. They also suggested that the faster growth rate reflects an adaptation to a shorter growing season with limitations in favorable temperatures and day length. However, ecosystems at the same latitudes may experience similar temperatures and day lengths, and growth variation (if any) between such populations cannot be categorized as CnGV, but rather local adaptations (Imsland *et al.*, 2000. Deniel (1990) found faster growth in southern populations (Bay of Douarnenez, Brittany, France) of plaice *Pleuronectes platessa* (L.) and dab *Limanda limanda* (L.) than in northern populations (English Channel and North sea), but no one has investigated the tradeoffs in swimming performance associated with growth differences between populations from similar latitudes. However, Billerbeck *et al.* (2001) provided evidence for a trade off in fitness with rapid growth in Atlantic silverside populations with substantial latitudinal difference. The narrow latitudinal difference (approx: 2° N) between 3 Ps and 4T juveniles may have been responsible for the similar growth rates and the lack of insignificant differences in critical swimming speeds (*Ucrit*).

Individual specific growth rates were not measured for the fish used in the swimming experiment. However, the overall specific growth rate of 3Ps and 4T juveniles at 11 °C and 7 °C was correlated with the average critical swimming speed of the respective populations. The *Ucrit* was negatively correlated with specific growth rate at 11 °C but it showed a positive correlation at 7 °C. Several studies have investigated the

relationship between specific growth rate and U_{crit} . Fathead minnows (*Pimephales promelas*) had a significantly negative relationship between U_{crit} and specific growth rate (Kolok & Oris 1995) and similar results were reported for juvenile rainbow trout (*Oncorhynchus mykiss*) (Gregory & Wood 1998). The relationship between specific growth rate and swimming performance is partially determined by life history and therefore may not be the same for all fish. Few studies have indicated a positive relationship between specific growth rate and swimming performance (Kolok, 1992; Farrell *et al.*, 1990; Young & Cech, 1993). The swimming performance of fish is dependant on water temperature (Brett, 1971; Beamish, 1978) where maximum velocity increases with increasing temperature. The effect of temperature on locomotory performance has been demonstrated in cod (Claireaux *et al.*, (1995); Schurmann & Steffensen, 1997; Castonguay & Cry, 1998; Claireaux *et al.*, 2000) and also it has been shown that cod have higher growth rates in warmer water (Brander, 1995). However, the cost of rapid growth in warmer temperatures results in a negative correlation with locomotory performance (Gregory & Wood, 1998; Kolok & Oris, 1995; Billerbeck *et al.*, 2001), which might explain the negative correlation between specific growth rate and U_{crit} at 11 °C for 3Ps and 4T populations. The reverse is true for the positive relationship at 7 °C, where energy available for activity is greater due to the slower growth rates and lower standard metabolic rates (SMR) (Claireaux *et al.*, 2000) at low temperatures.

The U_{crit} values for 3 Ps and 4 T juveniles were a little higher than what other studies have found. However, limited information is available on U_{crit} values for cod juveniles of similar mass (30 g – 45 g). Schurmann and Steffensen (1997) reported that

Ucrit increases with temperature to a maximum and then decreases at higher temperatures. They reported *Ucrit* values for cod averaging 242 g (1.6 bl s⁻¹ at 5°C and 1.7 bl s⁻¹ at 10 °C for 371 g cod). Soofiani and Priede (1985) reported values for cod averaging 150 g of 2.0 bl s⁻¹ at 10 °C. Bushnell *et al.*, (1994) reported metabolism of two cod populations, from northern range (*Gadus morhua*) and southern range of Greenland (*Gadus ogac*). The temperatures for the two types range from -0.5 °C to 13 °C and 0 °C to 10 °C respectively. Even though they had different geographical and temperature preferences the two populations had similar metabolic rates and swimming performances. My results were strikingly similar, where I found no difference in metabolic rate or swimming performances between the two populations, where both 3Ps and 4T juveniles had similar *Ucrit* values at 11 °C (3.58 bl s⁻¹ and 3.48 bl s⁻¹ respectively) and 7 °C (2.95 bl s⁻¹ and 3.09 bl s⁻¹ respectively).

The energy required to generate movement against the water current is considered the cost of transport (COT; Videler, 1993). The COT was not significantly different between 3Ps and 4T at 7 °C or 11 °C. However, the lowest COT was reported for both populations at 7 °C at 47.4 cm s⁻¹ and 11 °C at 51.9 cm s⁻¹. The performance of fish is dependent on water temperature (Brett, 1971; Beamish, 1978), and they exhibit a general trend of increasing performance with increasing water temperatures to an optimum (Brett, 1971; Gamperl *et al.*, 2002). The performance of the juvenile cod used in this experiment showed a similar trend by having higher maintenance metabolic rate, active metabolic rate, metabolic scope and *Ucrit* at 11 °C. Even though both populations had the lowest COT (highest efficiency) at 7 °C they swam much faster at 11 °C (more effective).

Gamperl *et al.* (2002) reported similar results for redband trout (*Oncorhynchus mykiss*) from two streams in Southeastern Oregon, where trout from both streams had the minimum COT at 12 C° as compared with 24 C°. Both populations showed a higher standard deviation in metabolic rates at high speeds (at 11 °C & 7 °C) indicating greater individual variation in energy expenditure, which is typical for Atlantic cod (Tang *et al.*, 1994; Reidy *et al.*, 2000). According to my hypothesis, 4T juveniles were expected to be more efficient and effective in swimming performance under common environment conditions but neither of the two populations showed a significant difference at a given temperature.

Standard length, total length, wet mass and condition factor were not significantly different between 3Ps and 4T juveniles. Condition factor was not correlated to the swimming performance of cod. Reidy *et al.* (2000) reported similar results for Scotian Shelf cod. However, Kolok (1992) found a significant positive correlation between condition factor and aerobic swimming performance of winter acclimated largemouth bass, but not in summer acclimated bass. He suggested a lower condition factor for bass during winter because they undergo periods of fasting.

The small standard deviations for all morphological measurements indicate little variation between 3Ps and 4T populations. Among different morphological measures, body depth was positively correlated with U_{crit} , metabolic scope and condition factor while standard length was negatively correlated with COT for both 3Ps and 4T juveniles. Trade offs between accumulation of energy reserves and locomotory efficiency are documented in small birds, where an increase in storage of energy reserves increases the

cost of flight because of the excess weight (Chai & Millard, 1997). Similarly Boily and Magnan (2002) suggested higher swimming cost for stout brook charr and yellow perch. However, the body depth of 3Ps and 4T juveniles was not significantly different. Total fin surface areas were not correlated to aerobic swimming performance in my study which supports the findings of Webb (1973) for sockeye salmon, Kolok (1992) in summer acclimated largemouth bass and Reidy et al. (2000) Atlantic cod.

A crossing reaction norm is a strong indication of environment and genotype interaction, where the rank order of performance for a given trait depends on the environment (Conover & Shultz, 1995). Similar reaction norms were observed in metabolic scope and *Ucrit* where the difference in phenotypic traits observed are more likely due to the influence of the environment (temperature) on the genotype.

None of the two groups showed counter-gradient variation in growth or a trade off of growth with swimming performance. Narrow latitudinal difference and similar temperature regimes between the two populations in the wild may have resulted in similar growing seasons for both groups. However, investigating the metabolism of different cod stocks is important for better understanding of the species and as a useful tool in selecting brood stocks for aquaculture purposes.

Chapter 4.0

Summary and suggestion for future research.

4.1 Summary

The depletion of many cod stocks has created enormous interest in culturing this species (Avault, 2001), and identifying populations, which possess good characteristics for culture, is important for a potential broodstock development. Variation in characteristics between cod stocks has suggest that genetic differentiation may exist between stocks (Ruzzante et al., 2001; Knutsen, 2003). However, such differences do not provide information on the phenotypic and life history variation among cod stocks (Brander, 1994).

Geographic variation in life history traits is well documented in many organisms including Atlantic cod (Brander, 1994). The counter-gradient variation hypothesis predicts that growth and other life history traits of fish can vary between latitudes with northern populations showing better growth performances. There's little information available on testing for CnGV on the effect of water temperature on different Atlantic cod stocks (Svasand *et al.*, 1996; Purchase & Brown, 2000a; 2000b).

Common environment experiments are often used to achieve a better understanding of genetically based phenotypic differences between populations and it further provides evidence for intra-specific adaptations. This approach was used in my study in order to make latitudinal comparisons between 3Ps and 4T juvenile cod kept under different temperature and food levels (Chapter Two). In the first experiment,

growth and food conversion efficiency of juveniles cod from Placentia Bay (3Ps) were compared to cod juveniles from Gulf of St. Lawrence (4T). The results did not support the CnGV hypothesis, as there was no significant difference in growth and food conversion efficiency between the two populations at a given temperature (7 °C or 11 °C) or food level (High or Low feed). The 3Ps fish had a significantly higher survival percentage over 4T at the end of the experiment even though other parameters tested were not significantly different.

To further investigate the trade-offs associated with swimming and growth of latitudinal populations, I looked at the swimming performance of the two populations. There are several benefits of faster growth, (i.e. reduced larval mortality, increased survival and fecundity) which are positively associated with fitness. However, improved fitness parameter in one environment is achieved at a reduced performance in another trait (Stern, 1989; Thompson, 1991). I expected 3Ps fish, the more northern of the two populations, to grow fast at the expense of critical swimming speed. However critical swimming speed, metabolic scope, and metabolic rates (resting, active and maximum) were not significantly different between the two populations.

Results of this experiment again did not support the CnGV hypothesis for growth and likewise no trade offs were associated between growth and critical swimming speed. However investigating the norms of reaction provides a better understanding of the genetic and environmental involvement in the phenotypic and genetic plasticity observed between the two populations, suggesting possible genetic variability between the 3Ps and 4T populations. The narrow latitudinal difference between the two populations and the

marginal temperature difference during the growing season may have contributed for the above results.

The lack of significant differences in SGR and size make it difficult to conclude which population is more suitable for aquaculture. However, a longer experimental period may have led to a positive result as I did see a slightly higher SGR for the 3Ps fish than the 4T juveniles during the 18-week experimental period. Thus, the 3Ps juveniles can be distinguished as a population displaying a trend of faster growth with significantly higher survival than 4T juveniles.

4.2 Future research

Investigating the growth, food conversion efficiency, survival and swimming performance of 3Ps and 4T was only one part of the large project. The project will further investigate populations for the same characteristics, which are latitudinally more distant. The primary objective of the overall project is to describe and determine the genetic basis of phenotypic variation among populations of Atlantic cod, through out its range in the Northwest Atlantic. The common garden experiments conducted in my thesis provided evidence of phenotypic and genotypic plasticity between 3Ps and 4T populations. The overall project will investigate the phenotypic and genetic correlates of meristic characters, spawning behavior and reproductive success. Upon completion of the entire study the results will provide insight into the selection of suitable broodstocks for aquaculture.

References:

- Abrams, P. A., Leimar, O., Nylin, S., and C. Wiklund, 1996. The effect of flexible growth rates on optimal sizes and development times in a seasonal environment. *Am. Nat.* 147: 381-395.
- Adams, S. R., and G. R., Parsons, 1998. Laboratory based measurements of swimming performance and related metabolic rates of field-sampled small mouth buffalo (*Ictiobus bubalus*) – a study of seasonal changes. *Physiol. Zool.* 71: 350-358.
- Adoff, G., Skjennum, F. C., and R. Enggelsen, 2002. Experience and prospects of Norwegian Cod farming. *Progress in Cod farming: Research to commercialization. Proceedings of Aquaculture Canada, Halifax. Bull. Aquacult. Assoc. Can.* 2001, 102-1: 8-11.
- Aiken, D., and Sinclair, 1995. From Capture to Culture; exploring the limits of Marine Production. *World Aquaculture Magazine*, September 26, (3): 21-34.
- Ali, M., and C. C. Lindsey, 1974. Heritable and temperature-induced meristic variation in the medaka *Oryzias latipes*. *Can. J. Zool.* 52: 959-976.
- Anon., 2000. Big marine hatchery planned. *Fish Farm. Int.*, March 27 (3): 20.
- Anonymous, 2000. *The State of World Fisheries and Aquaculture 1998*. United Nations Food and Agriculture Organization.
- Anonymous, 2002. *Progress in Cod Farming: Research to commercialization. Proceedings of Aquaculture Canada (2001)*. *Bull. Aquacult. Assoc. Can.* 102-140.
- Arendt, J. D., and D. A., Wilson, 1997. Optimistic growth: competition and an ontogenetic niche-shift select for rapid growth in pumpkinseed sunfish (*Lepomis*

- gibbosus*). *Evolution*, 51: 1946-1956.
- Avault, J. W. Jr., 2001. Selecting New Species for Commercial Aquaculture. *Aquaculture Magazine*, June 27 (3): 55-57.
- Beacham, T. D., Bratney, J., Miller, K. M., Le, K. D., and R. E. Whithler, 2002. Multiple stock structure of Atlantic cod (*Gadus morhua*) off Newfoundland and Labrador determined from genetic variation. *ICES. J. Mar. Sci.* 59: 650-665.
- Beamish, F. W. H., and P. S. Mookherjee, 1964. Respiration of fishes with special emphasis on standard oxygen consumption. I. Influence of weight and temperature on respiration of gold fish, *Carrassius auratus* L. *Can. J. Zool.* 42; 161-175.
- Beamish, F. W. H., 1966. Swimming endurance of some Northwest Atlantic fishes. *J. Fish. Res. Bd. Canada* 23: 341-347.
- Beamish, F. W. H., 1978. Swimming capacity. In: Hoar, W. S., Randall, J. D. (Eds.), *Fish Physiology*, and Vol 7. Academic Press Inc, New York, pp. 101-187.
- Bentzen, P., Taggart, C. T., Ruzzante, D. E., and D. Cook, 1996. Microsatellite polymorphism and the population structure of cod (*Gadus morhua*) in the Northwest Atlantic. *Can. J. Fish. Aquat. Sci.*, 53(12): 2706- 2721.
- Berven, K.A., Gill, D. E., and S. J. Smith-Gill, 1979. Countergradient selection of the green frog, *Rana clamitans*. *Evolution* 33:609-623.
- Berven, K.A. 1982. The genetic basis of altitudinal variation in the wood frog *Rana sylvatica*. I. An experimental analysis of life history traits. *Evolution* 36: 962-983.
- Billerbeck, J. M., Orti, G., and D. O. Conover, 1997. Latitudinal variation in vertebral

- number has a genetic basis in the Atlantic silverside, *Menidia menidia*. Can. J. Fish. Aquat. Sci., 54:1796-1801.
- Billerbeck, J. M., Schultz E. T., and D. O. Conover, 2000. Adaptive variation in energy acquisition and allocation among latitudinal populations of Atlantic silverside. *Oecologia* 122: 210-219.
- Billerbeck, J. M., Lankford, Jr., T. E. and D. O. Conover, 2001. Evolution of intrinsic growth and energy acquisition rates. I. Trade-offs with swimming performance in *Menidia menidia*. *Evolution* 55(9): 1863-1872.
- Bjornsson, B., 1993. Swimming speed and swimming metabolism of Atlantic cod (*Gadus morhua*) in relation to available food: A laboratory study. Can. J. Fish. Aquat. Sci. 50: 2542 - 2551.
- Bjornsson, B., Steinarsson, A., and M. Oddgeirsson, 2001. Optimal temperature for growth and feed conversion of immature cod (*Gadus morhua* L.). ICES. J. Mar. Sci., 58: 29-32.
- Blaxter, J. H. S., 1992. The effect of temperature on larval fishes. *Neth. J. Zool.*, 42: 336-357.
- Blazka, P., Volf, M., and M. Cepela, 1960. A new type of respirometer of the determination of the metabolism of the fish in an active state. *Physiol. Bohemoslov.*, 9: 553-558.
- Boje, J., 2002. Intermingling and seasonal migrations of Greenland halibut (*Reinhardtius hippoglossoides*) populations determined from tagging studies. *Fish. Bull.*, 100 (3): 414-422.

- Boily, P., and P. Magnan, 2002. Relationship between individual variations in morphological characters and swimming cost in brook charr (*Salvelinus fontinalis*) and yellow perch (*Perca flavescens*). *J. Exp. Biol.*, 205: 1031-1036.
- Brander, K. M., 1994. Patterns of distribution, spawning, and growth in north Atlantic cod: the utility of inter-regional comparisons. *International Council for the Exploration of the Sea, Marine Science Symposium 198*: 406-413.
- Brander, K. M., 1995. The effect of temperature on growth of Atlantic cod (*Gadus morhua* L.). *International Council for Exploration of the Sea, J. Mar. Sci.*, 52:1-10.
- Brandt, S. B., 1993. The effect of thermal fronts on fish growth: A bioenergetics evaluation of food and temperature. *Estuaries* 16 (1): 142-159.
- Brett, J. R., 1964. The respiratory metabolism and swimming performance of young sockeye salmon. *J. Fish. Res. Bd. Canada* 21: 1183-1226.
- Brett, J. R., 1967. Swimming performance of sockeye salmon (*Oncorhynchus nerka*) in relation to fatigue time and temperature. *J. Fish. Res. Bd. Canada* 24: 1731-1741.
- Brett, J. R., 1971. Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and fresh water ecology of sockeye salmon (*Oncorhynchus nerka*). *American Zoologist* 11: 99-113.
- Brett, J. R., 1972. The metabolic demand for oxygen in fish, particularly salmonids and a comparison with the other vertebrates. *Respir. Physiol.* 14; 151-170.
- Brett, J. R., and T. D. D. Groves, 1979. Physiological energetics in fish physiology, Vol. VIII (Eds. W. S. Hoar, D. J. Randall and J. R. Brett), Academic Press, London,

pp. 279-352.

Broomfield, K. 2002. Cod Farming come to surface. *Fish Farmer*, August 25 (4): 22.

Brown, J. A., Pepin, P., Methven, D. A., and D. C. Somerton, 1989. The feeding growth and behaviors of juvenile cod, *Gadus morhua*, L., in cold environments. *J. F. Biol.*, 35: 373-380.

Bundy, A., Lilly, G., and P. A. Shelton, 2000. A mass balance model of the Newfoundland-Labrador Shelf. *Can. Tech. Rep. Fish. Aquat. Sci.* No. 2310.

Busacker, G. P., Adelman, I. R., and E. M. Goolish, 1990. Growth. In: *Methods for fish biology* (Eds. Schreck, C. B., and P. B. Moyle). *Am. Fish. Soc. Bethesala, Maryland*. Pp. 363-386.

Bushnell, P. G., Steffenson, J. F., Schurmann, H., and D. R. Jones, 1994. Exercise metabolism in two species of cod in arctic waters. *Polar Biology*, 14; 43-48.

Campana, S. E. and P. C. F. Hurley, 1989. An age and temperature mediated growth model for cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) larvae in Gulf of Main. *Can. J. Fish. Aquat. Sci.* 46: 603-613.

Cao, W., Chan, Y., Wu, Y., and S. Zhu, 1981. Origin and evolution of Schizothoracine fishes in relation to the upheaval of Quinghai-Xizang Plateau. In *Geological and Ecological Studies of Quinghai-Xizang Plateau*, Gordon and Beach, New York, pp. 1053-1060.

Carr, S. M., Snellen, A. J., Howse, K. A., and J. S. Wroblewski, , 1995. Mitochondrial DNA sequence variation and genetic stock structure of Atlantic cod (*Gadus morhua*) from bay and off shore locations on ht e Newfoundland continental

shelf. *Mol. Ecol.* 4: 79-88.

Castonguay, M., and D. G. Cry, 1998. Effect of temperature on spontaneous and thyroxine-stimulated locomotor activity in Atlantic cod. *J. Fish. Biol.* 53: 303-313.

Cech, J. J., Jr. 1990. Respirometry. In *Methods for Fish Biology*, (Eds. Schreck, C. B., and P. B. Moyle). American Fisheries Society, Bethesda, Md.

Chai, P. and D. Millard, 1997. Flight and size constraints: hovering performance of large hummingbirds under maximum loading. *J. Exp. Biol.*, 200: 2757-2763.

Claireaux, G., Webber, D. M., Kerr, S. R. Kerr and R. G. Boutlier, 1995. Physiology and behavior of free-swimming Atlantic cod (*Gadus morhua*) facing fluctuating temperature conditions. *J. Exp. Biol.* 198: 49-60.

Claireaux, G, Webber, D. M., Lagardere, J. P., and S. R. Kerr, 2000. Influence of water temperature and oxygenation on the aerobic metabolic scope of the Atlantic cod (*Gadus morhua*). *J. Sea Res.*, 44:257-265.

Conover, D. O., 1990. The relation between capacity for growth and length of growing season: evidence for and implications of Counter-gradient variation. *Trans. Am. Fish. Soc.* 119:416-430.

Conover, D. O., and T. M. C. Present, 1990. Countergradient variation in growth rate: compensation for length of the growing season among Atlantic silversides from different latitudes. *Oecol.* 83: 316-324.

Conover, D. O., 1992. Seasonality and the scheduling of life history at different latitudes. *J. Fish. Biol.* 41(supplement B): 161-178.

- Conover, D. O., and E. T. Schultz, 1995. Phenotypic similarity and the evolutionary significance of counter-gradient variation. *Trends. Ecol. Evol.*10: 248-252.
- Conover, D. O., Brown, J. J. and A. Ehtisham, 1997. Counter-gradient variation in growth of young striped bass (*Morone saxatilis*) from different latitudes. *Can. J. Fish. Aquat. Sci.* 54: 2401-2409.
- Conover, D. O., and E. T. Schultz, 1997. Natural selection and evolution of growth rate in the early life history: What are the trade offs?. (Eds. R. C. Chambers and E. A. Trippel). *Early life history and recruitment in fish populations*. Chapman and Hall, London, UK. pp, 305-332.
- Conover, D. O., and E. T. Schultz, 1997. Phenotypic similarity and the evolutionary significance of counter-gradient variation. *Trends. Ecol. Evol.* 10:248-252.
- Conover, D. O., 1998. Local adaptation in Marine Fishes: evidence and implication for stock enhancement. *Bull. Mar. Sci.* 62: 477- 493.
- Conover, D., 2000. Darwinian fishery science. *Mar. Ecol. Prog. Ser.* 208:299-313.
- Cote, D. 1999. Swimming performance and growth rates of juvenile Atlantic cod intraperitoneally implanted with dummy acoustic transmitters. *N. Am. J. Fish.* 19: 1137-1141.
- Counihan, T. D., and C. N. Frost, 1999. Influence of externally attached transmitters on the swimming performance of juvenile white sturgeon. *Trans. Am. Fish. Soc.* 128: 965-970.
- Davidson, G. W., Sheehan, M. K., and P. S. Davie, 1999. The effect of tagging on the swimming performance of rainbow trout as a surrogate for kahawai *Arripis trutta*.

- Trans. A. Fish. Soc. 128: 971-973.
- Despatie, S. P., Castonguay, M., Chabot, D., and C. Audet, 2001. Final thermal preferendum of Atlantic cod: Effect of food ration. Trans. Am. Fish. Soc., 130: 263-275.
- Deniel, C., 1990. Comparative study of growth of flatfishes on the west coast of Brittany. J. F. Biol. 37: 149-166.
- Drucker, E. G., 1996. The use of gait transition speed in comparative studies of fish locomotion. Am. Zool. 36: 555-566.
- Drucker, P., 1999. Canada's developing aquaculture industry is poised to net big gains. In: Canadian Life Science (1999). Lab Business Biotechnology. Fall 1999 edition, Richmand hill, Ontario pp 1-5.
- Exadactylos, A., Geffen, A. I., and J. P. Thorpe. 1999. Growth and genetic variation in hatchery reared larval and juvenile Dover sole, *Solea solea* (L.) Aquaculture, 176: 209-226.
- Farrell, A. P., Johansen, J. A., Steffensen, J. F., Moyes, C. D., West, T. G., and R. K. Suarez, 1990. Effects of exercise and coronary ablation on swimming performance, heart size, and cardiac enzymes in rainbow trout, *Oncorhynchus mykiss*. Can. J. Zool. 68:1174-1179.
- Farlinger, S., and F. W. H. Beamish, 1977. Effects of time and velocity increments of the critical swimming speed of large mouth bass (*Micropterus salmoides*). Trans. Am. Fish. Soc. 106: 436-439.
- Fleming, I. A., and M. R. Gross, 1990. Latitudinal clines: A trade-off between egg

- number and size in pacific salmon. *Ecology*. 7: 1-11.
- Fry, F. E. J., 1971. The effect of environmental factors on the physiology of fish. In "Fish Physiology" (Eds. W. S. Hoar and D. J. Randall), Vol. 6; 1- 98. Academic Press New York.
- Gamperl, A. K., Rodnick, K. J., Faust, H. A., Venn, E. C., Bennett, M. T., Crawshaw, L. I., Keeley, E. R., Powel, M. S., and H. W. Li, 2002. Metabolism, swimming performance, and tissue biochemistry of high desert Redband trout (*Oncorhynchus mykiss* ssp.): Evidence for phenotypic differences in physiological function. *Phys. Bio. Zool.* 75(5):413-431.
- Grant, S. M., Brown, J. A., and D. L. Boyce, 1998. Enlarged fatty livers of small juvenile cod: a comparison of laboratory-cultured and wild juveniles. *J. Fish Biol.*, 52: 1105-1114.
- Gregory, T. R., and C. M. Wood, 1998, Individual variation and interrelationship between swimming performance, growth rate, and feeding in juvenile rainbow trout (*Oncorhynchus mykiss*). *Can. J. Fish. Aquat. Sci.* 56: 479-486.
- Gregory, T. R., and C. M. Wood, 1999. Interactions between individual feeding behavior, growth, and swimming performance in juvenile rainbow trout (*Oncorhynchus mykiss*) fed different rations. *Can. J. Aquat. Sci.* 56: 479-486.
- Haddon, M., and T. J. Willis, 1995. Morphometric and meristic comparison of orange roughy (*Hoplostethus atlanticus*: Trachichthyidae) from the Puysegur Bank and Lord Howe Rise, New Zealand, and its implications for stock structure. *Mar. Biol.* 123: 19-27.

- Halliday, R. G. and A. T. Pinhorn, 1990. The delimitation of fishing areas in the northwest Atlantic. *J. Northw. Atl. Fish. Sci.* 10:1-51.
- Hammer, C., 1995. Fatigue and exercise tests with fish. *Comp. Biochem. Physiol.*, 112(A): 1-20.
- Hawkins, D. K., and T. P. Quinn, 1996. Critical swimming velocity and associated morphology of juvenile coastal cutthroat trout (*Oncorhynchus clarki clarki*), steelhead trout (*Oncorhynchus mykiss*), and their hybrids. *Can. J. Fish. Aquat. Sci.* 53:1487-1496.
- He, P., 1991. Swimming endurance of the Atlantic cod, *Gadus morhua* L., at low temperatures. *Fish. Res.* 12: 65-73.
- Heisler N. 1984. Acid-Base regulations in fishes in fish physiology, Vol. X Part A (Eds. W. S. Hoar and D. J. Randall), Academic Press, London, pp. 315-401.
- Hop, H. and M. Graham, 1995. Respiration of juvenile Arctic cod (*Boreogadussaida*): affects of acclimation, temperature and food intake. *Polar Biol.* 5; 359-367.
- Houde, E. D., 1989. Comparative growth, mortality and energetics of marine fish larvae: temperature and latitudinal effects. *Fish. Bull. U. S.*, 87: 471-495.
- Hunt von Hurbing and R. G. Boutilier, 1996. Activity and metabolism of larval Atlantic cod (*Gadus morhua*) from Scotian Shelf and Newfoundland source populations. *Mar. Biol.* 124: 607-617.
- Hunt von Hurbing and L. White, 2002. The effects of body mass and feeding on metabolic rate in small juvenile cod. *J. Fish. Biol.* 61: 945-958.
- Hurlbut, T., and Clay, D. (1998). Morphometric and meristic differences between

- shallow and deep water populations of white hake (*Urophycis tenuis*) in the southern Gulf of St. Lawrence. *Can. J. Fish. Aquat. Sci.*, 55: 2274-2282.
- Hutchings, J. A., Myers, R. A., and G. R., Lilly, 1993. Geographic variation in the spawning of Atlantic cod, *Gadus morhua*, in the northwest Atlantic. *Can. J. Fish. Aquat. Sci.*, 50:2457-2467.
- Hutchings, J. A., 1996. Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. *Can. J. Fish. Aquat. Sci.* 53: 943-962.
- Isely, J. J., Noble, R. L., Koppelman, J. B., and D. P., Philip, 1987. Spawning period and first year growth of northern, Florida, an intergraded stocks of largemouth bass. *Trans. Am. Fish. Soci.*, 116: 757-762.
- Imsland, A. K., Foss, A., Sveinsbo, B., Jonassen, T. M. & S. O. Stefansson, 2001. Intra-specific differences in RNA/DNA ratios and metabolism of juvenile turbot. (*Scophthalmus maximus*). *J. World Aqua. Soc.* 32: 1-10.
- Imsland, A. K., Foss, A., Nævdal, G., Cross, T., Bonga, S. W., van Ham, e. & S. O. Stefansson, 2000. Counter-gradient variation in growth and food conversion efficiency of juvenile turbot. *J. Fish Biol.* 57: 1216-1226.
- Jeffrey, D. A., and D. S. Wilson, 1999. Population differences in the onset of cranial ossification in pumpkinseed (*Lepomis gibbosus*), a potential cost of rapid growth. *Can. J. Fish. Aquat. Sci.*, 57: 351-356.
- Jerry, D. R., and S. C. Cairns, 1998. Morphological variation in the catadromous Australian bass, from seven geographically distinct riverine drainages. *J. F.*

Biol. 52: 829-843.

Jobling, M., 1994. Fish bioenergetics. Chapman Hall, London, U. K.

Jonassen, T. M., Imsland, A. K., Fitzgerald, R., Bonga, S. W., Ham, E.V., Nevdal, G., Stefansson, M. O., and S. O., Stefansson, 2000. Geographic variation in growth and food conversion efficiency of juvenile Atlantic Halibut related to latitude. J. Fish. Biol. 56: 279-294.

Jonsdottir, O. D. B., Danielsdottir, A. K., and G. Naevdal, 2001. Genetic differentiation among Atlantic cod (*Gadus morhua* L.) in Icelandic waters: temporal stability. ICES. J. M. Sci. 58: 114-122.

Jordan, A. D., Jungersen, M., and J. F. Steffensen, 2001. Oxygen consumption of East Siberian cod: no support for metabolic cold adaptation theory. J. Fish. Biol. 59: 818-823.

Kaufmann, R., and W. Wieser, 1992. Influence of temperature and ambient oxygen on the swimming energetic of cyprinid larvae and juveniles. Env. Biol. Fishes 33: 67-95 .

Kennedy, C. J., Sweeting, R. M., Johansen, J. A, Farrell, A. P., and B. A., McKeown, 1995. Acute effects of chlorinated resin acid exposure on juvenile rainbow trout *Oncorhynchus mykiss*. Environ. Toxicol. Chem. 14: 977-982.

Kieffer, J. D., Aslop, D., and C. M., Wood, 1998. A respirometric analysis of fuel use during aerobic swimming at different temperatures in rainbow trout (*Oncorhynchus mykiss*). J. Exp. Biol. 201: 3123-3133.

Kinsey, S.T., Orsoy, T., Bert, T. M., and B. Mahamoudi, 1994. Population structure of

the Spanish sardine *Sardinella aurita*: natural morphological variation in a genetically homogeneous population. *Mar. Biol.* 118: 309-317.

Knutsen, K., Jorde, P. E., Andre, C. and CHR. N. Stenseth, 2003. Fine-scaled geographical population structuring in highly mobile marine species: the Atlantic Cod. *Molecular Ecology*, 12: 385-394.

Kodric-Brown, A., and P. F. Nicoletto, 1993. The relationship between physical condition and social status in pupfish *Cyprinodon pecosensis*. *Anim. Behav.* 46: 1234-1236.

Koljonen, M., Tahtiinen, J., Saisa, M., and J. Koskiniemi, 2002. Maintenance of genetic diversity of Atlantic salmon (*Salmo salar*) by captive breeding programs and the geographic distribution of microsatellite variation. *Aquaculture*, Vol. 212, no. 1-4, pp. 69-92.

Kolok, A. S., 1991. Photoperiod alters the critical swimming speed of juvenile large mouth bass, *Micropterus salmoides*, acclimated to cold water. *Copeia* 1991: 1085-1090.

Kolok, A. S., 1992. Morphological and physiological correlates with swimming performance in juvenile large mouth bass. *Am. J. Phys.* 263: R1042-R1048.

Kolok, A. S., and T. J. Oris, 1995. The relationship between specific growth rate and swimming performances in male fathead minnows (*Pimephales promelas*). *Can. J. Zool.* 73: 2165-2167.

Kolok, A. S., 1999. Inter-individual variation in the prolonged locomotor performance of ectothermic vertebrates: a comparison of fish and herpetofaunal methodologies

- and a brief review of the recent fish literature. *Can. J. Fish. Aquat. Sci.* 56, 700-710.
- Koumoundouros, G., Sfakianakis, D. G., Divanach, P. and M. Kentoury, 2002. Effect of temperature on swimming performance of sea bass juveniles. *J. Fish. Biol.*, 60: 923-932.
- Lambert, Y., and J. D. Dutil, 1997. Can simple indices be used to monitor and quantify seasonal changes in the energy reserves of cod (*Gadus morhua*)? *Can. J. Fish. Aquat. Sci.*, 54 (Suppl. 1): 104-112.
- Lankford, Jr. T. E., Billerbeck, J. M., and D. O. Conover, 2001. Evolution of intrinsic growth and energy acquisition rates. II. Trade-offs with vulnerability to predation in *Menidia menidia*. *Evolution*, 55(9): 1873-1881.
- Larsen, L-H., Pederson, T., Danielssen, D. S., and E. Moksness, 1993. The International Symposium sea ranching of cod and other marine species, Arendal, Norway, Program and abstracts, IMR, Bergan (Norway), 1993, pp.35.
- Larsen, L-H., Pederson, T., 2002. Migration, Growth and Mortality of released reared and wild cod (*Gadus morhua* L.) in Malangen, northern Norway. *Sarsia*, 87, 97-109.
- Lear, W. H., and R. Wells, 1984. Vertebral averages of juvenile cod, *Gadus morhua*, from coastal waters of eastern Newfoundland and Labrador as indicators of stock origin. *J. Northw. Atl. Fish. Sci.*5: 23-31.
- Lear, W. H., 1989. Atlantic cod, Underwater world, Pp. 2. Published by Department of Fisheries and Ocean Canada.

- Lear, W. H., and J. M. Green, 1984. Migration of the northern Atlantic cod and the mechanisms involved. In *Mechanisms of migration in fishes*. (Eds. J. D. McCleave, G. P. Arnold, J. J. Dodson and W. W. Neil. Plenum), New York. Pp. 309-315.
- Leary, R. F., Allendorf, F. W., and K. L. Knudsen, 1985. Inheritance of meristic variation and evolution of developmental stability in rainbow trout. *Evolution*, 39: 308-314.
- Levins, R., 1968. *Evolution in changing environments*. Princeton University Press.
- Levinton, J. S., 1983. The Latitudinal compensation hypothesis: growth data and a model of latitudinal growth differentiation based upon energy budgets. I. interspecific comparison of Ophryotrocha (*Polychaeta: Dorvilleidae*). *Biological Bulletin (Woods Hole)* 165: 686-689.
- Lewontin, R. C., 1965. Selection for colonizing ability. (Eds. H. G. Baker and G. L. Stebbins), *The genetics of colonizing species*. Academic Press, New York. Pp.79-94.
- Lindsey, C. C., 1978. Form function and locomotory habits in fish in *Fish Physiology*, Vol. VII (Eds. W. S. Hoar and D. J Randall), Academic Press, London, Pp. 1-100.
- Lindsey, C. C., 1988. Factors controlling variation In *Fish Physiology*. (Eds. W. S. Hoar, and D. J Randall), Academic Press, New York.
- Lonsdale, D. J., and J. S. Levinton, 1985. Latitudinal difference in copepod growth: an adaptation to temperature. *Ecology* 66: 1397-1407.
- Low-McConnel, R. M., 1987. *Ecological studies in Tropical fish communities*,

Cambridge University Press, Princeton, NJ.

- Malloy, K., and T. E., Targett, 1994. Effects of ration limitation and low temperature on growth, biochemical condition, and survival of juvenile summer flounder from two Atlantic coast nurseries. *Trans. Am. Fish. Society.* 123: 182-193.
- Minkoff, E. C., 1983. *Evolutionary Biology.* Addison-Wesley Publishing Company, Inc. pp (171).
- Mohn, R., and W. D. Bowen, 1996. Grey Seal predation on the eastern Scotian Shelf: Modeling the impact on Atlantic Cod. *Can. J. Fish. Aquat. Sci.* 53: 2722-2738.
- Myers, R. A., Mertz, G., and P. S., Fowlow, 1997. Maximum population growth rates and recovery times for Atlantic cod, *Gadus morhua*. *Fish. Bull.* 95: 762-772.
- Nelson, J. S., 1984. *Fishes of the World*, 2nd edition, J. Willey, New York.
- Nelson, J. A., Tang, Y., and R. G. Boutilier, 1994. Differences in exercise physiology between two Atlantic cod (*Gadus morhua*) populations inhabiting different environments. *Physiol. Zool.* 67: 330-354.
- Nelson, J. A., Tang, Y., and R. G. Boutilier, 1996. The effects of salinity change on the exercise performance of two Atlantic cod (*Gadus morhua*) populations inhabiting different environments. *J. Exp. Biol.* 199: 1295-1309.
- Nelson, J. A., Gotwalt, P. S., Reidy, S. P., and D. M. Webber, 2002. Beyond *Ucrit*: matching swimming performance tests to the physiological ecology of the animal, including a new fish 'drag strip'. *Comp. Biochem. Physiol.(A)*, 133: 289-302.
- Nicieza, A. G., Reiriz, L., and F. Brana, 1994. Variation in digestive performance between geographically disjunct populations of Atlantic salmon: Countergradient

- in passage time and digestive rate. *Oecologia*, 99: 243-251.
- Nicoletto, P. F., 1991. The relationship between male ornamentation and swimming performance in the guppy, *Poecilia reticulata*. *Behav. Ecol. Sociobiol.* 28:365-370.
- Nielsen, K. S., 1972. Locomotion: Energy cost of swimming, flying, and running. *Science*, 41:222-229.
- Otterlei, E., Nyhammer, G., Folkvord, A and S. O. Steffansson, 1999. Temperature and size dependant growth of larval and juvenile Atlantic cod (*Gadus morhua*): a comparative study of Norwegian coastal cod and northeast arctic cod. *Can. J. Fish. Aquat. Sci.* 56: 2099-2111.
- Parson, G. R., and J. L. Sylvester, Jr. 1992. Swimming efficiency of the white crappie, *Pomoxis annularis*. *Copeia*, 4: 1033-1038.
- Peake, S., Barth, C., and R. S. Mckinley, 1997. Effect of recovery parameters on critical swimming speed of juvenile rainbow trout (*Oncorhynchus mykiss*). *Can. J. Zool.* 75: 1724-1727.
- Pederson, T., and M. Jobling, 1989. Growth rate of large sexually mature cod, *Gadus morhua*, in relation to condition and temperature during an annual cycle. *Aquaculture*, 81:161-168.
- Pepin, P., and S. M. Carr, 1993. Morphological, meristic, and genetic analysis of stock structure in juvenile Atlantic cod (*Gadus morhua*) from the Newfoundland shelf. *Can. J. Fish. Aquat. Sci.*, 50:1924-1934.
- Petrell, R. J., and R. E., Jones, 2000. Power requirement of swimming in Chinook salmon

and Atlantic salmon and implications for food conversion and growth performance. *Aqua. Eng.*22: 225-239.

Pigliucci, M and C. D. Schlichting. 2002. Reaction norms of *Arabidopsis*. III. Response to nutrients in 26 populations from a worldwide collection. (http://weedworld.arabidopsis.org.uk/vol2/pigliucci_1.html).

Plaut, I., 2000. Resting metabolic rate, critical swimming speed and routine activity of the euryhaline cyprinodontid, *Aphanius dispar*, acclimated to wide range of salinities. *Physiol. Biochem. Zool.* 73: 590-596.

Plaut, I. 2001. Critical swimming speed: its ecological relevance. *Comp. Biochem. Physiol. (Part A)* 131, 41-50.

Pogson, G. H., Taggart, C. T., Mesa, K. A. and R. G. Boutilier, (2001). Isolation by distance in the Atlantic Cod, *Gadus morhua*, at large and small geographic scales. *Evolution*, 55(1): 131-146.

Present, T. M. C. and D. O. Conover, 1992. Physiological basis of latitudinal growth differences in *Menidia menidia*: variation in consumption of efficiency? *Func. Ecol.*6: 23-31.

Price, L. W. 1981. *Mountains and Man: A Study of Process and Environment*, University of California Press, California.

Purchase, C. F., and J. A. Brown, 2000a. Interpopulation differences in growth rates and food conversion efficiencies of young Grand Banks and Gulf of Main Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* 57: 2223-2229.

Purchase, C. F., and J. A., Brown, 2000b. Stock-specific changes in specific growth

- rates, food conversion efficiencies, and energy allocation in response to temperature change in juvenile Atlantic cod. *J. Fish. Biol.* 56: 36-52.
- Puvanendran, V., and J. A. Brown, 1998. Effect of light intensity on the foraging and the growth of Atlantic cod larvae: Interpopulation difference? *Mar. Ecol.: Prog. Ser.* 167: 207-214.
- Randall, D. J., and C. Brauner, 1991. Effects of environmental factors on exercise in fish. *P. Biol.* 160: 113-126.
- Reidy, S. P., Nelson, J. A., Tang, Y., and S. R. Kerr, 1995. Post exercise metabolic rate in Atlantic cod (*Gadus morhua*) and its dependence upon the method of exhaustion. *J. Fish. Biol.* 47: 377-386.
- Reidy, S. P., Kerr, S. R., and J. A. Nelson, 2000. Aerobic and anaerobic swimming performance of individual Atlantic cod. *J. Exp. Biol.* 203: 347-357.
- Rice, J. R. (Editor), 1997. Proceedings of the workshop on cod stock component, March 3-5, St. John's, Newfoundland. *Can. Stock Asses. Proc. Ser.*, 97/06.
- Ricklefs, R. E., and M. Wikelski, 2002. The physiology/life history nexus. *Trends Ecol. Evol.* 17: 462- 468.
- Riget, F., Boje, J., and V. Simonsen, 1992. Analysis of meristic characters and genetic differentiation in Greenland Halibut (*Reinhardtius hippoglossoides*) in the northwest Atlantic. *J. North.Atl.Fish.Sci.* 12: 7-14.
- Roff, D. A. 1982. Reproductive strategies in flat fish: a first synthesis. *Can. J. Fish. Aquat. Sci.* 39: 1686-1698.
- Rose, G. A., Atkinson, D. B., Baird, J., Bishop, C. A., and D. W., Kulka., 1994.

- Changers in distribution of Atlantic cod and thermal variations in Newfoundland water 1980- 1992. ICES Mar. Sci. Symp. 198:542-554.
- Ruzzante, D. E., Taggart, C. T., Cook, D., and S. Goddard, 1996. Genetic differentiation between inshore and off shore Atlantic cod (*Gadus morhua*) off Newfoundland: microsatellite DNA variation and antifreeze level. Can. J. Fish. Aquat. Sci. 53: 634-645.
- Ruzzante, D. E., Taggart, C. T., Cook, D., and S. V. Goddard, 1997. Genetic differentiation between inshore and off shore Atlantic cod (*Gadus morhua*) off Newfoundland: a test and evidence of temporal stability. Can. J. Fish. Aquat. Sci. 54: 2700-2708.
- Ruzzante, D. E., Taggart, C. T., and D. Cook, 1999. A review of the evidence for genetic structure of cod (*Gadus morhua*) populations in the Northwest Atlantic and population affinities of larval cod off Newfoundland and the Gulf of St Lawrence. Fish. Res. 43: 79-97.
- Ruzzante, D. E., Taggart, C. T., Doyle, R. W. and D. Cook, (2001). Stability in the historical pattern of the genetic structure of Newfoundland Cod (*Gadus morhua*) despite the catastrophic decline in population size from 1964 to 1994.
- Saunders, R. L., 1963. Respiration of Atlantic cod. J. Fish. Res. Bd. Canada, 20(2): 373-386.
- Schluter, D., 1995. Adaptive radiation in sticklebacks: Trade-off in feeding performance and growth. Ecology, 76(1): 82-90.
- Schultz, E.T., Reynolds, K. E., D. O. Conover, 1996. Countergradient variation growth

among newly hatched *Fundulus heteroclitus*: geographic differences revealed by common –environment experiments. *Func. Ecol.*, 10: 366-374.

Schultz, E.T., and D. O. Conover, 1997. Latitudinal difference in somatic energy storage: adaptive responses to seasonality in a estuarine fish. (Atherinidae: *Menidia menidia*). *Oecologia*, 109: 516-529.

Schurmann, H., and J. F. Steffensen, 1997. Effect of temperature, and activity on the metabolism of juvenile Atlantic cod. *J. Fish. Biol.* 50: 1166-1180.

Scott, W. B., and M. G. Scott, 1988. Atlantic fishes of Canada. *Can. Bull. Fish. Aquat. Sci. No.* 219.

Soofiani, N.M., and A. D. Hawkins, 1982. Energetic cost at different levels of feeding in juvenile cod, *Gadus morhua* L. *J Fish. Biol.* 21: 577-592.

Soofiani, N. M., and I. G. Priede, 1985. Aerobic metabolic scope and swimming performance in juvenile cod, *Gadus morhua* L. *J. Fish. Biol.* 26: 127-138.

Sokal, R.R., and J. J. Rohlf, 1995. *Biometry: the principles and practice of statistics in biological research.* 3rd Edition, Freeman, New York.

Starck, J. M. 1994. Quantitative design of the skeleton in in bird hatchlings: does tissue compartmentalization limit post hatching growth rates? *J. Morphol.* 222: 113-131.

Stearns, S. C., 1989. The evolutionary significance of phenotypic plasticity. *Bioscience*, 39: 436-445.

Stearns, S. C. 1992. *The Evolution of Life Histories*, Oxford University Press.

Stenson, G. B., Hammill, M. O., and J. W. Lawson, 1997. Predation by Harp Seals in Atlantic Canada: Preliminary consumption estimates for Arctic Cod, Capelin and

- Atlantic Cod. J. Northw. Atl. Fish. Sci., Vol. 22: 137-154.
- Sibly, R. M., Calow, P. and N. Nichols, 1985. Are patterns of growth adaptive? J. Theor. Biol. 112:553-574.
- Smedbol, R. K., and J. S. Wroblewski, 2002. Metapopulation theory and northern cod population structure: interdependency of subpopulations in recovery of a ground fish population. Fish. Res.55: 161-174.
- Svasand, T., Jorstad, K. E., and O. S. Kjesbu., 1996. Differences in growth performance between Arcto- Norwegian and coastal cod reared under identical conditions. J. Fish Biol. 49: 108-119.
- Suthers, I. M., and S. Sundby, 1996. Role of midnight sun: comparative growth of pelagic juvenile cod (*Gadus morhua*) from Arcto-Norwegian and a Nova Scotian stock. ICES. J. Mar. Sci., 53: 827-836.
- Swain, D. P., Chouinard, G. A., Morin, R., and K. F. Drinkwater, 1998. Seasonal variation in the habitat association of Atlantic cod (*Gadus morhua*) and American plaice (*Hippoglossoides platessoides*) from the southern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. 55.
- Swain, D. P., 1999. Changes in the distribution of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence- effects of environmental change or environmental preferences? Fish. Oceanogr., 8;1: 1-17.
- Swain, D. P., Frank, K. T., and G. Maillet, 2001. Delineating stocks of Atlantic cod (*Gadus morhua*) in the Gulf of St Lawrence and Cabot Strait areas using vertebral number. ICES J. Mar. Sci., 58: 253-269.

- Swain, D. P., and K. T. Frank, 2000. Depth – dependent vertebral number of Atlantic cod (*Gadus morhua*) on the Magdalen shallows and Scotian Shelf: stocks mixing or microgeographic trends within populations. *Can. J. Fish. Aquat. Sci.*, 57: 2393-2401.
- Swain, D. P. 1992. Selective predation in vertebral phenotype in *Gasterosteus aculeatus*: Reversal in direction of selection at different larval sizes. *Evolution*, 46: 998-1013.
- Swanson, C., Young, P. S., and J. J. Cech, 1998. Swimming performance of delta smelt: maximum performance, and behavioral and kinematic limitations on swimming at sub-maximal velocities. *J. Exp. Biol.* 201:333-345.
- Taggart, C. T., Penny, P., Barrowman, N., and C. George, 1995. The 1954-1993 Newfoundland cod tagging database: statistical summaries and spatial-temporal distributions. *Can. Tech. Report. Fish. Aquat. Sci.*, 2042.
- Tang, Y., Nelson, J. A., Reidy, S.P., Kerr, S. R., and R. G. Boutilier, 1994. A reappraisal of activity metabolism in Atlantic cod (*Gadus morhua*). *J. Fish Biol.*, 44: 1-10.
- Tave, D. 1984. Quantitative genetics of vertebral number and position of dorsal fin spines in the velvet belly shark, *Etmopterus spinax*. *Copeia*, 1984: 794-797.
- Taylor, E. B., Egginton, S., and E. W., Taylor, 1996. Seasonal temperature acclimatization of rainbow trout: Cardiovascular and morphometric influences on maximal sustainable exercise level. *J. Exp. Biol.* 199: 835-845.
- Templeman, W. 1981. Vertebral numbers in Atlantic cod, *Gadus morhua*, of the

- Newfoundland and adjacent area, 1947-71, and their use for delineating cod stocks. *J. Northw. Atl. Fish. Sci.* 2: 21-45.
- Tesch, F. W., 1971. Age and growth in Fish Production in Fresh Waters. (Eds. W. E. Ricker), Blackwell, Oxford, Pp. 98-130.
- Thompson, J. D., 1991. Phenotypic plasticity as a component of evolutionary change. *Trends Ecol. Evol.*, 6: 246-249.
- Thorpe, R. S., 1989. Geographic variation: multivariate analysis of six character systems in snakes in relation to character number. *Copeia* 1989: 63-70.
- Tudela, S. 1999. Morphological variability in a Mediterranean, genetically homogenous population of the European ancovy, *Engraulis encrasicolus*. *Fish. Res.*, 42: 229-243.
- Via, S., Gomulkiewicz, R., De Jong, G., Scheiner, S. M., Schlichting, C. D., and V. P. H. Tienderen, 1995. Adaptive phenotypic plasticity: consensus and controversy. *Tree*, 10: 212-217.
- Videler, J. J., 1993. *Fish Swimming*. Chapman & Hall, London. Pp. 207.
- Watkins, T. B., 1996. Predator-mediated selection of burst swimming performance in tadpoles of the Pacific tree frog, *Pseudacris regilla*. *Physiol. Zool.* 69: 154-167.
- Weatherley, A. H., 1972. *Growth and Ecology of Fish Populations*, Academic Press, London.
- Webb, P. W., 1973. The effects of partial caudal fin amputation on the kinematics and the metabolic rate of under yearling sockeye salmon (*Oncorhynchus nerka*) at steady swimming speeds. *J. Exp. Biol.*, 59: 565-581.

- Webb, P. W., 2002. Kinematics of plaice, *Pleuronectes platessa*, and cod, *Gadus morhua*, swimming near bottom. *J. Exp. Biol.* 205: 2125-2134.
- Webber, D. M., Boutilier, R. G., and S. R., Kerr, 1998. Cardiac output as a predictor of metabolic rate in cod *Gadus morhua*. *J. Exp. Biol.* 201: 2779-2789.
- Webber, D. M., Boutilier, R. G., Kerr, S. R., and M. J. Smale. 2001. Caudal differential pressure as a predictor of swimming speed of cod (*Gadus morhua*). *J. Exp. Biol.* 204: 3561-3570.
- Williamson, J. H., and G. J., Carmichael, 1990. An aquaculture evaluation of Florida, northern, and hybrid largemouth bass, *Micropterus salmoides*. *Aquaculture*, 85: 247-258.
- Winger, P. D., He, P., and S. J. Walsh, 2000. Factors affecting the swimming endurance and catchability of Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* 57, 1200-1207.
- Wootton, R. J., 1990. *Ecology of Teleost Fishes*. Chapman & Hall, London, UK.
- Yamahira, K., and D. O. Conover, 2002. Intra-vs Interspecific latitudinal variation in growth : Adaptation to temperature or seasonality?. *Ecology* 83(5): 1252-1262.
- Young, P. S., and J. J. Cech Jr., 1993. Improved growth, Swimming performance, and muscular development in exercise conditions young of the year striped bass (*Morone saxatilis*). *Can. J. Fish. Aquat. Sci.* 50: 703-707.

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