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## Growth Potential of Young Black Sea Bass, *Centropristis Striata*, in Artificial Environments

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GROWTH POTENTIAL OF YOUNG BLACK SEA BASS,  
CENTROPRISTIS STRIATA, IN ARTIFICIAL ENVIRONMENTS.

by

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Approved by:

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Anthony J. Provenzano (Director)

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DEDICATION

To My Parents;

To My Wife, Moonshin Kim;

To My Daughters, Sungmin Kim;

Hyomin Kim.

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## ABSTRACT

### GROWTH POTENTIAL OF YOUNG BLACK SEA BASS CENTROPRISTIS STRIATA, IN ARTIFICIAL ENVIRONMENTS

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Old Dominion University, 1987  
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The commercially important marine finfish, black sea bass (Centropristis striata), was evaluated for aquaculture potential by examining growth under controlled conditions in the laboratory. To investigate the effect of food and weight on growth, juveniles and young black sea bass were cultured in a closed system with a natural diet and a commercial diet at various feeding levels.

Growth was affected by type of food, food consumption rate, and fish body weight. For fish having positive weight gain, absolute growth rate (gram per day) increased exponentially as food consumption rate (percent of body weight per day) and/or mean body weight increased. Instantaneous growth rate (percent of body weight per day) of the fish also increased exponentially as food consumption rate (percent of body weight per day) increased but decreased as mean body weight increased. The starved fish also showed the same pattern in weight loss: absolute weight loss (grams per day) increased exponentially and instantaneous weight loss (percent of body weight per day) decreased exponentially as mean body weight of the fish increased.

The natural diet, which had a lower caloric value than the commercial diet, was significantly inferior to the commercial diet in terms of growth rate produced and food conversion efficiency. Fish fed

the natural diet had significantly higher food consumption rates than those fed the commercial diet.

For fish fed the commercial diet two generalized equations were developed to predict instantaneous and absolute growth rates in relation to mean body weight and food consumption rate. Estimated growth rates using these equations showed a good fit to observed growth rates.

Cultured black sea bass were not significantly different from the natural population in weight-length ratio according to relative condition index and a weight-length relationship.

Total energy consumption (cal per day) for standard metabolism of the individual fish increased exponentially with body weight but energy consumed per unit body weight decreased exponentially as body weight increased. Energy consumption for maintenance in relation to body weight showed the same pattern.

The energetics of the black sea bass related to maximum food consumption rate were estimated using the experimental results and reference values in the literatures.

Overall results show that cultured black sea bass can grow four to five times faster than natural populations and that the species is a good candidate for aquaculture.

## CHAPTER I

### INTRODUCTION

Aquaculture is of worldwide interest as a tool for producing desirable aquatic resources. Rapid advancements in technology have enabled culture of numerous aquatic organisms commercially for public and private purposes.

Marine finfishes are traditionally important food resources in many countries. For decades, various commercial landings of marine finfishes have indicated the shortage of these natural food resources on a global scale. Overfishing has been regarded as the dominant factor resulting in devastation of many species of marine finfishes (Bardach et al., 1972). Since fisheries can not satisfy demand, mariculture of marine finfishes has received great attention worldwide to produce the commercially important food resources (Girin, 1979).

The technology for culturing marine finfishes is relatively underdeveloped compared to that for freshwater counterparts or other marine organisms. Several factors contributed to slow development of the technology in marine finfish culture: (1) overestimating the magnitude of natural stocks, (2) lack of essential information for culture, (3) geographic limitation of seawater supply, (4) difficulties in obtaining seed stocks due to complicated and expensive nutritional requirements during the larval development, and (5) the requirements for sophisticated and expensive equipment, facilities and labor (Korringa, 1976; Girin, 1983).

Black sea bass, Centropristis striata L., is a common bottom

dwelling fish in coastal water of the east coast. It has been a desirable target of commercial fisheries for several decades. However, landings dropped drastically in the 1960's because of overfishing (Musik and Mercer, 1976; Cupka et al., 1977; Kendall, 1977). At present, sport fishing contributes the main fishing mortality of black sea bass in the middle and south Atlantic regions (Mercer, 1978). Due to restricted habitat on hard bottom and reduced population, sport fishing alone may be enough to exclude the population from other commercial fisheries. No particular management or restriction has been enforced to preserve the population. Little research has been attempted to find the potential of black sea bass for mariculture despite its recognizable scarcity in nature and inability of commercial fishing to satisfy market demands.

Southern black sea bass, C. melana, was tested for cultural potential by Hoff (1970), Roberts et al., (1977), and Harpster et al., (1977). They indicated that Centropristis species were good candidates for mariculture because of their hardy ecological and physiological characteristics: strong tolerance to low temperature, pH, and oxygen level, and high nitrogen compound levels, little space and food requirements for growth. The global popularity of serranid fishes in aquaculture as well as the feasibility of spawning induction of this species (Tucker, 1983) supports the idea that black sea bass has great potential for mariculture.

Successful commercial mariculture largely depends on development of inexpensive foods that promote optimal growth and survival. Because feeding represents a substantial cost in intensive fish farming, developing adequate commercial foods is a major concern of fish culture.

Growth is the net outcome of total physiological and behavioral processes influenced by the surrounding environmental conditions. At the individual physiological level the processes of digestion, absorption, assimilation, and metabolic expenditure all interplay to affect this growth. To define the potential growth of a fish, these growth-related physiological processes and the nature of the intake energy sources influencing those processes should be properly understood.

The purpose of this study was to investigate the potential of black sea bass for aquaculture by determining (1) growth in natural and commercial diets under laboratory conditions and (2) theoretical growth potential based on the experimental outputs.

Since no information on culturing black sea bass under laboratory environments was available, the following hypotheses were established to examine the potential of the black sea bass for artificial cultivation:

- (1) Natural environment is superior to an artificial environment in growth and condition.
- (2) Food consumption rates (feeding level) and the weight of the fish do not affect growth rates of the black sea bass.
- (3) A commercial diet is not superior to a representative natural diet of black sea bass for growth.

By relating food consumption, growth, and metabolic rate, an energy budget can be determined, providing a measure of the efficiency of food conversion and energy utilization.



## CHAPTER 11

### MATERIALS AND METHODS

#### Sampling and Conditioning

A total of 412 juvenile and young individuals of the black sea bass were collected by hook and line or traps at Rudee Inlet and Chesapeake Bay Bridge Tunnel pier, Virginia Beach, Virginia, in August, September, and November 1985 and May 1986. To minimize sampling injury, Number six short neck hooks were used in hook and line catches while modified round minnow traps were used with squid bait for trap sampling. The collected fish were then placed in 100 liter plastic coolers under low temperature (10 - 15° C) and supplementary aeration was provided with battery operated aerators. If the fish showed swimbladder inflation caused by an abrupt pressure change, air was taken from the swimbladder with a syringe. Upon arrival at the laboratory, the fish were stocked in an approximately 2000 liter closed system culture facility equipped with a series of various filtration and sterilization units.

After a two or three day starvation period to evacuate guts, the fish were anesthetized with 100 ppm MS-222 for measurement and tagging. The fish were rolled on paper towels to remove excess water and measured for standard length (SL, mm), total length (TL, mm) and live weight (or wet weight; W, g). To identify the fish, customized thread tags were individually placed in tissues surrounding the second dorsal spine or the tenth dorsal fin ray. If no damage or shock due to the tagging or measuring procedures was observed after a day, the fish were placed in rearing tanks for acclimation.

To avoid experimental bias due to the social and physiological stresses found in the preliminary observations, the fish were sorted roughly by size and placed in separate rearing tanks during the acclimation periods.

To acclimate the fish to laboratory feeding they were starved until about half of the fish in each tank showed active feeding or foraging movements in response to seminatural diets such as chopped squid, shrimp or mole crabs. The feeding of a natural diet always preceded commercial diet feeding because fish failed to respond to commercial foods during short acclimation periods. After the feeding response was stabilized, the fish were fed commercial foods of about one percent of live body weight daily.

#### Rearing Environments

A closed system was designed and built to provide an intensive culture facility for the study. The culture system consisted of three 300 liter rectangular rearing tanks, one 200 liter round starvation tank, one 600 liter rearing tank, one settling chamber, three mechanical filters, two chemical filters, two biological filters, two foam fractioners, and one ultra-violet sterilization unit. The details of the system were described in Appendix A.

The system was conditioned for more than four months to establish a proper bacterial population so that the biological filters could function efficiently in removing nitrogen compounds, especially ammonia. The loading capacity of the system was tested with large black sea bass between November 1984 and July 1985. Approximately 30 kg of black sea bass

could be maintained under satiation feeding regimes without the ammonia level exceeding 0.02 ppm.

The temperature, salinity, and photoperiod were maintained at  $21 \pm 2$  °C,  $25 \pm 2$  o/oo, 12 hour light : 12 hour dark respectively. The temperature was monitored with continuous temperature recorders (Taylor Instrument Co., Asheville, N.C.). Salinity was measured daily with a refractometer (American Optical Co.). In addition to twelve 40 watt fluorescent light bulbs three meters above the culture system, four 40 watt full-spectrum fluorescent light bulbs were set one meter above the water surface of rearing tanks to provide extra lighting during daytime and the photoperiod of the fluorescent light was controlled by an automatic timer. Natural light was reflected on the culture system from two 45 x 85 cm windows providing normal photoperiod during the experimental period.

The water quality of the culture system was monitored daily by measuring pH, nitrate, nitrite, and ammonia with a SeaTest Multi-Kit (Aquarium System Co.). Normally, the nitrate, nitrite, and ammonia levels did not exceed 40 mg/l, 0.01 mg/l, and 0.04 ppm respectively.

Seawater provided for the culture system was collected near Chesapeake Light Tower by the research vessel, R/V Linwood Holton. The salinity of collected sea water was about 31 o/oo. Due to shortage of sea water supply, synthetic salts (Forty Fathoms Inc.) were used to provide additional saline water for the culture system. Saline water of 100 o/oo was prepared initially by mixing synthetic salts and tap water. After aging one day with vigorous aeration, the water was filtered with 128 um meshed screen to remove detritus and later diluted to 25 o/oo with aged

tap water.

The flow rate in each rearing tank was maintained in a range of 3 - 6 liters per minute depending on the water quality. The turnover rate was about 10 - 24 times per day. Each day 2 - 5 % of water in the system was changed while siphoning out feces and excess foods. When the ammonia level of the system exceeded 0.06 ppm, a sufficient volume of water was changed to bring the ammonia level below 0.04 ppm.

Each 300 liter rearing tank was divided into eight compartments with plastic egg crates ( 1.2 cm x 1.2 cm lattice structure) and 2 mm meshed filter screen, which did not allow any particulates bigger than 2 mm in diameter to pass. The compartments of the rearing tanks were prepared to allow separate feeding for each group of black sea bass sorted by length or weight class. A feces collector (10 cm x 10 cm x 3 cm height) was placed on the bottom of each compartment. Supplementary aeration was provided for each compartment to achieve saturated dissolved oxygen levels. The total weight in each compartment did not exceed 1800 g live weight.

The fish involved in starvation tests were isolated from the fed fish in the starvation tank to prevent extra energy loss due to behavioral excitement evoked by feeding behavior of the other fish. A number of cylindrical ceramic pipes (12 cm diameter x 30 cm long) were installed in the starvation tank as shelters to reduce energy expenditure caused by active foraging movements and behavioral stress between the fish during starvation periods.

### Food Preparation

The black sea bass is an opportunistic carnivorous feeder. The major dietary items in nature are crustaceans, fish, and molluscs (Chee, 1977). To select test diets for the fish, the following factors were considered; (1) properly balanced nutritional quality which caused no acute or chronic nutritional diseases, (2) adequate feeding response of cultured fish, and (3) feasibility of food provision and feeding operation.

As a natural diet the mole crab, Emerita talpoida (Family Hippidae), was selected due to its abundance in the fish sampling area, frequent occurrence in the diets of captured samples, and homogeneous energetic value. According to the preliminary tests, black sea bass stocked in the culture system for three to eight months revealed normal development of male gonads and a few female gonads when mole crabs were fed as a sole dietary source. This indicated that the nutritional and energetic quality and quantity of mole crabs exceeded the minimal requirements for growth of the black sea bass.

Harpster et al. (1977) noted that high protein diets, especially trout chows, were desirable for culturing young southern black sea bass, C. melana. However, commercial dry diets frequently showed low feeding responses by cultured salmonoid fishes while commercial wet diets having high moisture contents (60 - 70 %) showed difficulties in feeding operation due to leaching of essential nutrients (i.e., vitamins, minerals, etc.) into the water before being consumed by cultured fish. Therefore, Rangen-Zeigler Soft-moist diet (Oregon moisture pellet type, Rangen-Zeigler Co., Gardners, PA), which had approximately 15 % of

moisture content, was selected as the commercial diet for this study among various commercial trout chows.

Mole crabs, E. talpoida, were collected at Rudee Inlet with screen nets in September 1985, and April and May 1986, and rinsed with tap water at the laboratory. Egg bearing individuals were discarded to reduce variation in the dietary energy of the mole crabs. Two layers of rectangular meshed screens (0.62 cm and 1.25 cm respectively) were used to sort the mole crabs into three size classes. Mole crabs which did not pass through 1.25 cm mesh screen were discarded while small mole crabs which passed through 0.62 cm mesh screen were normally provided to groups of small fish less than 125 mm in standard length or 50 g in average live weight. Mole crabs of intermediate size were provided to the rest of the cultured fish. Sorted mole crabs were rolled on paper towels to remove excess water, packed in 250 g units and frozen.

Two sizes of pellets of the commercial diet (0.275 cm and 0.55 cm in diameter) were utilized in the experiments. As with natural diets, small fish were fed the small size pellets. Both size pellets were screened to remove powdered portion (about 5 % of total weight) which otherwise would cause serious water quality deterioration and overestimation of intake energy for the experimental fish. To feed the juveniles of less than 20 g, the small size pellets were chopped and screened with 0.1 cm and 0.2 cm mesh screens. Only intermediate size particles were provided to those fish.

## Experimentation

### Growth

A series of experiments was undertaken to determine weight-specific growth patterns related to diet types and food consumption rate under laboratory conditions. The feeding conditions, food types and general experimental procedures are summarized in Table 1. All weight measurements of fish and foods used during the growth experiments were expressed in wet weight (live weight).

Applied feeding levels could be categorized into three regimes: (1) no feeding, (2) reduced feeding level, and (3) satiation feeding. The fish were considered satiated when they would no longer accept any food, in the presence of excess, after a period of active feeding. All excess foods were removed immediately. To ensure the satiated condition extra foods were provided 20 - 30 minutes after initial feeding. For natural diet feeding all excess foods were collected with nets, rolled on paper towels, and then weighed. Each value of the 'consumed foods' represents the wet weight difference between the amount of food presented and the amount of collected post feeding.

When the commercial diet was applied in satiation feeding, the uneaten excess foods soaked with water changed their weights. Despite that no partially consumed foods had been found in the commercial diet feeding, the pellets were easily crushed by the collecting procedure at post-feeding phase. This could result in underestimation of the quantity of excess. To minimize the errors in estimating the weight of excess foods, the number of pellets in the excess foods was counted and converted to weight by multiplying by the average weight of a pellet. The selected pellets screened during the preparation were relatively homogeneous in weight (range of 0.28 - 0.36 g with the average weight of 0.30 g). The

Table 1. Summary of growth experimentation

| experiment number  | experimental date (period in days) | no. of fish (mortal.) | no. of group & replica. | total mean body weight of fish (g) | total amount of food consumed (g) |
|--|------------------------------------|-----------------------|-------------------------|------------------------------------|-----------------------------------|
| <u>I. Starvation Experiments</u>                             |                                    |                       |                         |                                    |                                   |
| 9a   | 05/15-05/28 (14)                   | 72 (0)                | 1-1 (1)*                | 6975.8                             | 0                                 |
| 10a  | 05/30-06/09 (11)                   | 56 (0)                | 1-1 (1)                 | 7607.3                             | 0                                 |
| 11   | 06/10-07/22 (43)                   | 76 (0)                | 1-1 (1)                 | 11708.0                            | 0                                 |
| <hr/>  |                                    |                       |                         |                                    |                                   |
| <u>II. Natural Diet Experiments (Satiated feeding only)</u>  |                                    |                       |                         |                                    |                                   |
| <u>A. No size-sorting and single daily feeding frequency</u> |                                    |                       |                         |                                    |                                   |
| 1  | 10/09-12/07 (60)                   | 79 (4)                | 1-1 (1)                 | 4793.4                             | 14600.0                           |
| 2  | 12/09-01/17 (40)                   | 74 (0)                | 1-1 (1)                 | 5742.2                             | 9651.4                            |
| 3  | 01/20-02/04 (15)                   | 76 (2)                | 1-1 (1)                 | 6312.0                             | 3687.0                            |
| <u>B. Size-sorting and double daily feeding frequency</u>    |                                    |                       |                         |                                    |                                   |
| 9b   | 05/15-05/28 (14)                   | 53 (0)                | 7-7 (1)                 | 7135.6                             | 2512.3                            |
| 10b  | 05/30-06/09 (11)                   | 54 (1)                | 7-7 (1)                 | 7720.1                             | 1672.1                            |
| <hr/>  |                                    |                       |                         |                                    |                                   |
| <u>III. Commercial Diet Feeding Experiments**</u>            |                                    |                       |                         |                                    |                                   |
| <u>A. Satiated and single daily feeding frequency</u>        |                                    |                       |                         |                                    |                                   |
| 5  | 02/09-03/05 (25)                   | 180 (0)               | 6-12 (2)                | 16141.7                            | 6572.4                            |
| 6  | 03/11-03/25 (15)                   | 177 (0)               | 6-22 (3-4)              | 19345.3                            | 3159.9                            |
| 7  | 04/08-04/20 (13)                   | 187 (0)               | 6-25 (4-5)              | 22484.4                            | 2761.1                            |
| 8  | 04/21-05/09 (18)                   | 189 (3)               | 7-24 (2-4)              | 24744.0                            | 4096.8                            |
| <u>B. Satiated and double daily feeding frequency</u>        |                                    |                       |                         |                                    |                                   |
| 9c   | 05/15-05/28 (14)                   | 70 (2)                | 9-9 (1)                 | 8080.8                             | 1407.3                            |
| 10c  | 05/30-06/09 (11)                   | 80 (1)                | 10-10 (1)               | 7861.4                             | 793.2                             |
| <u>C. Reduced and single daily feeding frequency</u>         |                                    |                       |                         |                                    |                                   |
| 9d   | 05/15-05/28 (14)                   | 65 (0)                | 8-8 (1)                 | 7657.0                             | 903.4                             |
| 10d  | 05/30-06/09 (11)                   | 59 (0)                | 8-8 (1)                 | 7288.6                             | 402.6                             |
| <u>D. Reduced and half daily feeding frequency</u>           |                                    |                       |                         |                                    |                                   |
| 12   | 09/01-09/25 (25)                   | 62 (8)                | 8-8 (1)                 | 5347.0                             | 974.5                             |
| <u>E. Reduced and single daily feeding (no size-sorting)</u> |                                    |                       |                         |                                    |                                   |
| 4  | 01/20-02/04 (15)                   | 103 (0)               | 1-1 (1)                 | 6552.8                             | 978.0                             |

\* Group and replicate: numbers indicate 'number of size class' - 'total number of group' ' (number of replicate in each size class) '

\*\* Size-sorting of fish was applied in all except for experiment 4.



average weight of the small pellets was 0.12 g (range of 0.06 - 0.15 g).

In four preliminary experiments 74 - 103 fish weighing approximately 10 g to 150 g in initial body weight were reared in one 300 liter rearing tank to find the overall food conversion efficiency and growth rate under different feeding conditions. In the first preliminary experiment mole crabs were fed once daily at satiation level. In the second and third experiments 250 g of mole crabs (approximately 5 % of initial body weight per day) were provided daily to the fish as natural diet source. To reduce the size hierarchy effect in growth observed in the first preliminary experiment, a divider was set in the middle of the tank and several large fish were isolated from the remaining fish for the second through the fourth preliminary experiment.

Commercial diet, Rangen-Zeigler Soft-moist diet (hereafter, Rangen-Zeigler Soft-moist diets and mole crabs are referred to as the commercial diet and natural diet respectively for this study), was first introduced in the fourth preliminary experiment. Due to high energetic value and relatively low food consumption rate of the fish fed the commercial diet, only 70 g of the commercial diet was provided to 103 fish (approximately one percent of the mean body weight per day) for 15 days.

Based on information from the four preliminary experiments, a series of experiments was conducted to determine the growth rates of fish related to feeding levels, diet types, and size of the fish. Size sorting of the fish by length or weight was applied to all fed fish based on pre-experimental measurements. The fish grouped in size classes with two to five replicates for each size class were placed in individual compartments of four rearing tanks. The commercial diet was provided separately to

each group of fish.

Satiation feeding levels with single daily feeding frequency were applied in experiments 5, 6, 7, and 8 using the commercial diet (see Table 1 and 3). In experiments 9 and 10 two types of diets and three feeding regimes (0 %, 50 %, and 100 % of satiated feeding levels) were applied respectively to each of four size replicate groups of fish: (1) starvation, (2) satiation with the commercial diet, (3) satiation with the natural diet, and (4) reduced feeding with half the amount of the satiation feeding of the commercial diet. The fish in the satiated feeding experiments were fed twice daily and the groups of fish under reduced feeding level were fed once daily.

In addition to experiments 9a and 10a, a total of 76 fish were starved for various periods (11 - 43 days) in experiment 11. In experiment 12 a total of 62 fish having been involved in a starvation experiment (experiment 11) were sorted by weight and tested for 25 days under reduced feeding with the commercial diet. The food was provided every other day until no active feeding response was detected. All environmental factors were maintained constant during the experimental period as previously described.

A total of 1703 observations were made in all growth experiments. The number of fish involved in each experiment ranged from 53 - 187. Most individuals were used repeatedly in several experiments when normal growth was observed. Those individuals were mostly tested under the same feeding condition in each experiment to avoid behavioral and physiological changes in food intake patterns, which possibly could result in sequential changes in growth.

Measurements were undertaken one day prior to each experiment and after one day of starvation at the end of each experiment. Dead fish were not replaced during the experiments. The fish were regrouped by size between each experiment to maintain groups of uniform size.

The initial preliminary experiment started on October 9, 1985 and the last experiment ended on September 20, 1986. Including 13 months for the periods of culture system conditioning and testing, about 24 months were spent in experimentation.

#### Respiration in standard metabolism

To obtain the basic energy expenditure of black sea bass, the standard metabolic rate was estimated by measuring respiration rates of fish. A semi-open circuit respirometer was designed to measure the oxygen consumption rate of black sea bass (the detail of the design is shown in Appendix B). To reduce the overall acclimation time of tested fish, the respirometer was designed to test three fish simultaneously. The respirometer consisted of four units; temperature control unit, ultra-violet sterilizer, reservoir, and measurement chamber. The measurement chamber consisted of three functional units; water leveling compartment, compartmented fish chamber, and oxygen meter probe housing equipped with four multi-direction gate valves.

Two 100 liter polyethylene coolers were modified for the reservoir and the measurement chamber. To maintain the constant temperature regime ( $21 \pm 0.1^\circ \text{C}$ ), a batch circulator (Model 2095 Bath & Circulator, Forma-Scientific) was connected to the reservoir with a customized submerged heat exchange unit. The dissolved oxygen of the reservoir and the

measurement chamber was fully saturated with double outlet aerators (Fritz Chemical Products). To remove particulates and excreta produced by test fish, a customized submersible activated carbon filter was placed in the reservoir. To prevent bacterial proliferation in the respirometer which could cause overestimation of consumed oxygen of tested organisms, two 30 watt ultra-violet light bulbs were placed on the top of the reservoir unit.

A highly sensitive oxygen meter (model 781, Strathkelvin Instruments) was used to measure the initial and final dissolved oxygen level of the fish chamber, and the continuous recorder (model 85217-5, Houston Instruments) was connected to the oxygen meter for continuously monitoring the chamber. The oxygen probe was set in the probe holder in the housing and four multi-direction gate valves were installed in the probe holder to select the pathway of the water for measurement.

The fish chamber was divided into three compartments. Each elongate rectangular compartment was effective in limiting fish movement without inducing stress. When the volume ratio between the compartment and fish was large enough to allow the fish to move in the compartment, additional side walls were installed to reduce the space.

The measurement chamber was located at a higher level than the reservoir. Water was continuously circulated between measurement chamber and the reservoir by a submerged pump and gravity. Water pumped from the reservoir filled the surrounding space of the fish chamber and then entered into the leveling compartment by air-lifted pathway. The water continuously flowed into the three compartments of the fish chamber and one bypass tube through separate pathways, and returned to the reservoir

by gravity. When the respirometer was in operation, the water which passed through a fish chamber or the bypass tube was directed into the probe housing by the gate valve to measure the dissolved oxygen concentration, and was collected in a graduated cylinder for measurement of volume. The water flow rate was gravitationally controlled by adjusting the difference of height between the chamber and the endpoint of tube directed to the graduated cylinder. In a preliminary experiment to ensure the reliability of the respirometer, precise duplicated results were acquired. A minimum acclimation period of two hours was required for good results.

In measuring the oxygen consumption rates, the fish were starved relatively long periods (15 - 30 days) because feeding was not possible due to the limited culture facility during the experimental period. Three starved fish were individually placed in each compartment of the fish chamber. After allowing 2 - 12 hours in the dark for acclimation with continuous monitoring, the dissolved oxygen concentrations of the water before and after the chamber were measured in ml/l. The difference between the two measurements represented consumed oxygen at the standard metabolic level for starved fish. The amount of oxygen consumed per minute (ml-oxygen/min) was calculated by multiplying the difference by the volume of water (liters) passing the chamber per minute. The value was later converted into calorific equivalent using the oxycalorific equivalent value (4.63 Kcal/liter oxygen) suggested by Brett and Groves (1979) for carnivorous fish.

Each measurement was continued for 10 - 15 minutes with three replicate measurements for each fish. The test fish were killed with 200

ppm MS-222, measured for weight and length, and frozen for further analysis. The water used for the respiration experiment was synthetic seawater used in the growth experiment. The salinity of the water was  $25 \pm 1$  o/oo and 1.0 um glass fiber filters were used to filter the water before use in the experiment.

#### Excretion

Since the culture system for the growth study did not allow measurement of the excretion rates, a separate series of experiments was conducted in non-circulated water using 32 fish. A 35-liter rectangular glass aquarium was filled with 15 liter synthetic seawater double-filtered by using 1 um glass fiber filter. Fish starved for two or three days were placed individually. After one hour acclimation, the water was sampled to determine the initial concentration of ammonia. Water was sampled 24 hours later to determine the daily excretion rate by difference. Three measurements were done for each fish using 3 sub-samples of water. The test fish were killed, measured, and frozen along with water samples for further analysis.

The environmental conditions in excretion experiments were similar to the culture conditions and a total of 96 measurements were undertaken for ammonia analysis.

#### Feces Production

The feces collectors were placed on the lower bottom of each compartment of the rearing tanks. Normally, feces were collected twice a day with a low pressure vacuum pump (1/6 HP, General Electric) before

feeding. Feces were siphoned from the collectors with debris and excess food, and filtered through double layer filters which consisted of an upper 10 um meshed screen layer and a lower regular 1 um glass fiber filter. Most feces were collected on the upper 10um meshed screen which allowed easy removal of the feces after drying. The feces and other materials collected on the collectors were air-dried. Under a microscope the feces were separated by color difference from detritus and uneaten food. After measurement of dry weight they were preserved in dessicators for calorific analysis. Feces collections were done in experiment 10 and a total of 112 samples were collected from 22 groups of fish, which were exposed to various food types and feeding levels. The feces production rate was expressed as percent of dry weight of the food consumed daily by a group of fish.

## Analysis

### Growth and Condition

#### 1. Growth rates

Since each experiment of this study was conducted for relatively short periods (11 - 60 days), it was assumed that the growth rate of the black sea bass, like that of most fishes, followed a typical exponential pattern for the duration of each experiment. Therefore, the equation of growth was represented by:

$$W_t = W_o(e^{gt}) \quad (1)$$

where 'Wo' and 'Wt' are the live weight at the beginning and the end of the experiment respectively, the exponent, 'g', is the instantaneous

relative rate of growth, and 't' is experimental period in days. For the practical purpose of estimating growth rate by linear regression analysis, this equation was transformed to:

$$\ln W_t = \ln W_o + gt$$

or (2)

$$g = ( \ln W_t - \ln W_o ) / t$$

For the convenience of calculation, the instantaneous growth rate of the fish was expressed :

$$G = 100g$$

or (3)

$$G = \frac{(\ln W_t - \ln W_o)}{t} \times 100$$

where G is the instantaneous growth rate expressed as percent of the body weight per day (hereafter, G will be simply described as 'instantaneous growth rate').

The average daily weight gain in gram live weight was calculated by the equation:

$$GW = ( W_t - W_o ) / t \quad (4)$$

where 'GW' is referred as 'absolute growth rate (g/day)'.

Mean body weight (W) in grams is the arithmetic mean of the initial and the final weights of an individual fish during an experiment. When growth rate of an individual fish is expressed in relation to weight of the fish, mean body weight (W) represents the weight of the fish resulting



in the weight-specific instantaneous and the absolute growth rates. Mean standard length in mm is also the arithmetic mean of the initial and the final standard length of a fish in an experiment.

## 2. Length-weight relationship

The length-weight relationship of the cultured black sea bass in this study is expressed by the equation:

$$\ln W = \ln a + b(\ln SL) \quad (5)$$

where 'W' is mean body weight in grams, 'SL' is mean standard length in mm, and 'a' and 'b' are constants. The regression lines were calculated by the methods of least squares. To evaluate the condition of the cultured fish, the length-weight relationships obtained from each experiment and different feeding condition within an experiment were compared with that of natural populations (Cupka et al., 1977; Mercer, 1978) by analysis of covariance. The length and weight of black sea bass described in this study represent mean body weight (W) in grams and mean standard length (SL) in mm respectively unless otherwise noted.

## 3. Condition indices

The condition index (K) is a value indicating the relative 'robustness' or 'heaviness' of a fish in relation to length. It is commonly used to compare conditions of a fish during a short-term period while the length-weight relationship is normally used to describe the long-term isometric growth (Ricker, 1979). To evaluate growth of the cultured fish in relation to feeding conditions, the condition index of

individual fish was calculated based on length and weight measurements at the beginning and the end of each experiment using the equation described by Cupka et al. (1977) for the southern population of the black sea bass:

$$K = (W/SL^3) 10^5 \quad (6)$$

where 'K' is the condition index expressed without units, and 'W' and 'SL' are the mean body weight in grams and mean standard length in millimeters respectively.

The relative condition index (RK) is the comparative value of weight between the cultured fish and the natural population at a given length. Mercer (1978) obtained the following weight-length relationship for the northern population of the black sea bass:

$$W_n = 0.00001 (SL_n)^{3.1798}$$

where 'W<sub>n</sub>' is the calculated weight in grams at standard length 'SL<sub>n</sub>' in millimeters from the fish of natural northern population. Relative condition index (RK) was obtained by comparing the weight of the cultured fish (W, g) to the calculated weight of fish in the natural population (W<sub>n</sub>, g) using the Mercer's equation at a given standard length (SL, mm):

$$RK = W / (0.00001 (SL)^{3.1798}) \quad (7)$$

Both condition index and relative condition index were used to compare the condition of the fish between groups exposed to different feeding conditions and with natural populations by analysis of covariance and Student's T-test.

#### Food Consumption

# 1) Average food consumption rates (RCm and Cm)

The rate of food intake of individual fish was defined in two ways in this study; (1) amount of food consumed daily (C) in grams per day, and (2) food consumption rate (RC) as percent of mean body weight per day.

During the experiments food was provided to a group of fish in each compartment of the culture tank rather than to individual fish because isolated individuals showed no feeding response. The average mean daily food consumption rate of a fish in a group was calculated as:

$$RC_m = \frac{(C_t)}{(W_m)(n)(t)} \times 100 \quad (8)$$

and

$$C_m = C_t / (nt) \quad (9)$$

and

$$F_m = WG_m / C_m \quad (10)$$

RC<sub>m</sub> : average daily food consumption rate (% of body weight/day)  
of an individual in a group

C<sub>m</sub> : average amount of food consumed daily (g/day) by an individual  
in a group

F<sub>m</sub> : average food conversion rate (gross growth efficiency) of  
an individual in a group

C<sub>t</sub> : total amount of food (g) given to a group for t days

W<sub>m</sub> : average mean body weight (W) of individuals in a group

WG<sub>m</sub> : average absolute growth rate of individuals in a group

n : number of individuals in a group

t : experimental period in days

The relationship between food consumption rates and growth rates of the fish was verified by correlation analysis and analysis of covariance using the average food consumption rate ( $RC_m$ ) and the average of mean body weight ( $W_m$ ).

## 2) Estimated individual food consumption rates ( $RC_{est}$ and $C_{est}$ )

The growth rates of individuals in a size group frequently showed large variation even in satiation feeding. The variation was frequently larger than that of average growth rates of groups ( $WG_m$ ) in different feeding conditions. Since the number of group observations for food consumption was not large enough for mathematical modeling, estimated individual food consumption rates were used to establish the food-growth relationship at an individual level. To estimate the actual amount of food consumed by a fish in a group, an experimental equation was derived from the following simplified theoretical background and assumption.

Under the laws of thermodynamics all energy ingested ( $I$ ) by a fish must turn up in one form or another through metabolism ( $R$ ), Growth ( $P$ ), excretion ( $U$ ), and feces ( $F$ ), where

$$I = F + U + R + P \quad (11-1)$$

The assimilation efficiency can be expressed as

$$a = (I - F) / I \quad (11-2)$$

Total metabolism ( $R$ ) can be divided into a variety of levels; standard metabolism ( $R_s$ ), feeding metabolism ( $R_f$ ), and active metabolism ( $R_a$ ). If the additional energy demand explicit in each is considered to be additive

as Brett and Groves (1979) suggested, then the total metabolism can be expressed as

$$R = R_s + b(R_r - R_s) + c(R_f - R_s) + d(R_a - R_s) \quad (11-3)$$

where the constants (b, c, and d) apply to estimates of the fraction of time each day that routine, feeding and active metabolism occur. Since the space provided for fish in the laboratory culture system is normally limited, active metabolism ( $R_a$ ) can be neglected.

When no external food energy is supplied ( $I=0$ ), the energy expenditure for routine metabolism ( $R_r$ ) results in endogenous energy consumption which causes weight loss ( $P_n$ ). Excretory energy loss ( $U$ ) is primarily caused by incomplete catabolic process of protein substrates. Since protein is commonly used for metabolic energy in starved fish (Gerking, 1955a, 1971; Elliott, 1975c; Brett and Groves, 1979), the weight loss ( $P_n$ ) of a starved fish for routine metabolism can be expressed in terms of energy as follows:

$$P_n = R_s + b(R_r - R_s) + U \quad (11-4)$$

When external energy intake results in positive growth ( $P_g$ ) of a fish, the growth ( $P_g$ ) can be expressed as:

$$P_g = I - F - U - R \quad \text{or} \quad (11-5)$$

$$P_g = I - F - U - (R_s + b(R_r - R_s) + c(R_f - R_s)) \quad \text{or} \quad (11-6)$$

$$P_g + P_n = I - F - c(R_f - R_s) \quad \text{or} \quad (11-7)$$

$$P_g + P_n = aI - c(R_f - R_s) \quad (11-8)$$

If the additional energy requirement for feeding,  $c(R_f - R_s)$  is less than 7 % of total energy input ( $I$ ) as Brett and Groves (1979) suggested for

carnivorous fish, assimilated intake energy by a fish can be approximated by weight gain and the weight loss during starvation for routine metabolism. The metabolic energy expenditure is normally regarded to be a function of weight of fish in constant environment (Elliott, 1975a, 1975b; Brett, 1979). Thus, the weight losses by the energy expenditures for routine metabolism of starved fish are primarily equal for fish having same weights at non-reproductive life stages and can be calculated from starvation experiments.

If we assume that the assimilation efficiencies (a) of individuals in a group are the same and the individual differences of energy expenditure for feeding,  $c(R_f - R_s)$  are negligible, the amount of food allocated for each fish ( $C_{est}$ ) in a weight group depends on the ratio between ' $P_g + P_n$ ' of individuals (see equation 11-8).

Since the temperature and other environmental factors were regarded to be constant in the experiments, the actual amount of food consumed by a fish in a group can be estimated from the amount of food given to the group, the absolute growth rate of individuals in the group of fish, and the calculated weight loss of the individual from starvation experiments (see equation 21). These terms can be simplified by the following expression:

$$C_{est} = \frac{WGi + WGstv}{\sum_{i=1}^N WGi + \sum_{i=1}^N WGstv} \times (Ct/t) \quad (12)$$

$$RC_{est} = (C_{est}/W_i) \times 100 \quad (13)$$

where

$C_{est}$  : estimated amounts of food consumed daily by an individual  
(g/day) in a size group

$R_{Cest}$ : estimated mean daily food consumption rate (% of body weight/day) of an individual in a group  
 $C_t$  : total consumed food (g) of a group for t days  
 $WG_i$  : mean daily weight gain (g/day) of an individual in the group  
 $WG_{stv}$ : calculated average daily weight loss of a fish in grams at a given weight during starvation (see eq. 21)  
 $W_i$  : mean body weight of an individual in grams  
 $n$  : number of fish in the group  
 $t$  : experimental period in days

Estimated food conversion rate (or gross growth efficiency,  $F_{est}$ ) of a fish is expressed as the ratio between the daily positive weight gain of a fish ( $WG$ , g/day) and the estimated amount food consumed daily ( $C_{est}$ ) by the fish :  $F_{est} = WG/C_{est}$ .

### 3) Maximum growth rate and food consumption rate

Maximum growth expressed as absolute growth rate or instantaneous growth rate is defined as the maximum daily growth potential of fish at a given mean body weight. The weight-specific maximum growth rate of fish was calculated from the satiation feeding experiments ( $n=1076$ ) except for experiments 10b and 10c.

The distribution of weights of the fish observed in the satiation feeding experiments was normal distribution over the range (4.3 - 295.2 g). Since the frequencies of the observations were concentrated in the middle weight range instead of spreading evenly over the observed weight range (independent variable), the equations derived by regression analysis using the data from individual fish would be biased. To correct this,

'group arrangement' were performed by grouping independent variables by given intervals.

The weights of fish were grouped into given weight intervals. The highest 10 % of values of the individual growth rates found in each weight interval were regarded as representing maximum growth rates for that interval. The regression analysis was performed using the mean maximum growth rates (representative value) and corresponding mean body weights in all weight intervals to obtain the equation for the maximum weight-specific growth rates at given weights. For the convenience of description, grouping the data by a given unit of independent variables is noted as 'group presentation' or 'group arrangement' hereafter. In the group arrangement of weights, seven weight intervals (10-30, 30-60, 60-90, 90-120, 120-150, 150-180, 180-300 g) were set for the commercial diet feeding while four weight intervals (10-50, 50-100, 100-150, 150-300 g) were used for the natural diet feeding due to the difference of the number of observations in different diet feeding experiments (n=800 for the commercial diet and n=276 for the natural diet feeding).

The maximum food consumption rate was calculated from the estimated food consumption rate of individuals (RCest), using the same method. The largest (upper 10 %) values of estimated individual food consumption rates (RCest) in each weight interval were selected. The average of the selected food consumption rates and the average of corresponding mean body weights of fish in each weight interval were regarded as representative values of maximum food consumption rate and mean body weight in the weight interval respectively. Regression analysis was performed by least squares method using the representative food consumption rates and mean body



weights in all weight intervals (n=7 for the commercial diet feeding and n=4 for the natural diet feeding).

#### 4) Maintenance food consumption rate

The food consumption rate for maintenance (RC<sub>man</sub>, % of body weight/day) refers to the level of food consumption rate at which no weight change occurs for a fish in normal feeding and locomotion activities. Fish which revealed a weight change of less than 1 % of body weight during an experiment were regarded as having consumed the food at maintenance level. A total of 129 fish fed the commercial diet showed a weight change of less than 1 % in experiments 5 through 8 and 9c. A total of 38 fish fed the natural diet had the weight change less than 1 % in experiments 1, 2, 3, and 9b. Group arrangement was performed using the same method and the weight intervals described in the previous section. Regression analysis was performed using the representative values in all weight intervals to find the weight-specific maintenance food consumption rate.

#### Multivariate analyses for growth modeling

To find the growth rate related to the combined effects of weight and food consumption, multivariate analysis was performed using a series of simple linear regression analysis and the method of group arrangement. Food and weight were regarded as two major independent variables affecting growth rate for the fish. Since both independent variables were continuous variables, group arrangement was performed for each variable by given intervals for simplification. The weights of the fish were grouped

by given intervals. A weight group was then divided into sub-groups by given intervals of estimated food consumption rate (RCest, 0.3 % for the commercial diet and 1.0 % for the natural diet according to the differences in observation frequencies and food consumption rates between the natural and the commercial diet). The means of the growth rates, weights, and food consumption rates of fish in each sub-group (each component of a matrix consisted of food and weight intervals) are regarded as the representative values of the sub-group. For example, if ten fish weighing 30 - 60 g have 0.3 - 0.6 % food consumption rates, the arithmetic means of growth rates, food consumption rates, and weights of the fish represent the growth rate, the food consumption rate, and the weight of a sub-group having the range of 30 - 60 g weight and 0.3 - 0.6 % food consumption rate. Fish of the same weight range but having different food consumption rates then belong to another sub-group in the weight group.

The regression analyses were performed using the representative values of each sub-group. Since simple regression analysis was used for this multivariable situation, only one independent variable was related to the dependent variable and the rest of the variables were fixed as constant values. If the equation obtained from each fixed variable showed a consistent relationship, the results were reanalyzed to find common equations expressed by both variables.

The matrix of grouping to derive the equations using these methods were: (two food types; commercial and natural diets) x (eight weight intervals; 4.3-30, 30-60, 60-90, 90-120, 120-150, 150-180, 180-210, 210-300 g) vs (estimated food consumption rate as continuous independent variable) or (two food types; commercial and natural diets) x (seven

intervals of estimated food consumption rate for the commercial diet; 0.0-0.3, 0.3-0.6, 0.6-0.9, 0.9-1.2, 1.2-1.5, 1.5-1.8, 1.8-2.1 % or five intervals of estimated food consumption rate for the natural diet; 0.0-1.0, 1.0-2.0, 2.0-3.0, 3.0-4.0, 4.0-11.0 %) vs (mean body weight of fish as continuous independent variable).

All equations developed in the analyses were primarily derived using regression analysis with least squares method and covariance analysis (F-test) was performed to evaluate the significant difference between regression lines in different experimental conditions. The slopes of equations calculated using regression analysis were subjected to significance probability test using student's T-test with the null hypothesis that slope was zero and the result was expressed as 'p(T)'. When experimental conditions were similar in size of fish and feeding conditions, overall measurements of experiments were used to develop equations after analysis of variance.

Correlation analyses were performed to examine the relationships between growth and weight of fish or between growth and food consumption using Pearson correlation analysis. Hoeffding's measure of dependance, 'D' was used to verify the significance probability of correlation using null hypothesis that correlation coefficient was zero and the result was expressed as 'p(D)'

The symbols used for this study are summarized in Table 2. For the convenience of description, the results of statistical analyses were also expressed by abbreviations such as 'n', (number), 'se', (standard error), 'WG-W', (absolute growth rate versus mean body weight, 'G-W', (instantaneous growth rate versus mean body weight), 'r(WG-G)',

(correlation coefficient in absolute growth rate and mean body weight relationship', 'p(F)' (significance probability in covariance analysis; F-test), 'r<sup>2</sup>' (coefficient of determination for equations), etc.

All calculations for statistical analysis for the growth study were performed on an IBM 4381 computer utilizing SAS softwares and programs from the computer library of Old Dominion University.

#### Waste Production

Since ammonia is the principal excretory product in most fishes (Brafield and Solomon, 1972; Elliott and Davison, 1975), it was assumed that black sea bass also produce ammonia as its major excretory product. The analytical method for ammonia used for the study was originally reported by Strickland and Parsons (1972) and modified by Cutter (1985). The measured values were converted to energy equivalent assuming that the nitrogenous substrates involved in the catabolic processes were standard protein including 16 % nitrogen. Thus, 4.89 Kcal/g ammonia was used for calorific equivalent of ammonia as suggested by Elliott and Davison (1975).

### Calorific analysis

To establish a general energy budget for black sea bass, the caloric values of foods, fish, and feces were measured using a direct measurement method. All samples prepared for calorific analysis were previously dried in an oven at  $60 \pm 2^\circ \text{C}$  for 2 - 5 days to constant weight. Each sample of the commercial diet for the analyzed (range of 1.0 - 1.5 g) was prepared by pelletizing 3 - 4 dried commercial diet pellets using a customized pelletizer. Two to ten dried mole crabs were ground with a mortar for homogenizing before pelletizing to a 0.5 - 1.5 g dry weight sample. More than five replicates were prepared in each size of commercial and natural diets. The variation in caloric value due to season was also considered for mole crabs and thus the samples were separately prepared by seasonal catch as well as size. Since daily production of feces of each group of fish was too small to quantify, all feces produced under same diet type were ground together and pelletized to 0.5 - 1.1 g samples to obtain average energetic value.

To measure calorific value of fish, two preparation methods were used. In the first method each frozen fish was descaled, minced in a small hand mincer with apertures of 4 mm diameter (model 303/2, Rival MGF., Kansas City, Mo.), and homogenized in a mortar. Three sub-samples weighing approximately 20 g were then dried in an oven to constant weight. After the dry weight was measured, three replicates were prepared from the three subsamples and the caloric values measured without pelletization. The scales were separately measured in caloric value since they could not be homogenized with the mortar. In the second method, a whole fish was directly dried in the oven after dissection into two pieces and later

ground by a mortar to homogenize.

The first method produced more homogeneous samples but caused underestimation of water content by losing moisture in the samples due to long preparation time for homogenizing and vice-versa in the second method. Therefore, the caloric values were measured using the samples prepared by the first method (n=22). The second method was additionally used to calibrate the water content measured by using the first method (n=6). A total of 66 samples were prepared from 22 fish in this caloric analysis. No attempt was made to compare the caloric differences between the fish exposed to different feeding conditions and only average caloric value of fish was measured. The caloric value of fish meat was also measured from three other fish for energy content in meat portion of the fish and compared to that of the whole body.

The caloric values of diets and fish were expressed in both dry and wet weight. In estimating water content, 3.0 % (n=34) was added to the values obtained from the frozen mole crabs and fish since the differences of weight before and after freezing were 2.2 - 4.1 % with the mean of 3.0 %. The caloric values of live weight or wet weight of the fish and diets were estimated from the caloric values of dry weights and water contents.

The caloric values of all samples were determined with an adiabatic bomb calorimeter (Plain bomb calorimeter, Model 1341, Parr Instrument Co.). The method used to operate the calorimeter has been described by the American Society of Testing Material (1966). The standardization was done with benzoic acid and 2436 cal/°C was obtained. Titration was undertaken with sodium carbonate solution (0.0709 N). Sulfur content of samples was not analyzed but estimated from the volume of sodium carbonate

used in titration based on the data described on the American Society of Testing Material (1966). Twenty milli-liter of sodium carbonate solution was considered to be equivalent to 1.0 % sulfur contents in the sample. The error from this estimation was assumed to be less than 0.01 % of the total caloric value.

Table 2 summary of symbols

| symbol                               | unit    | description   |
|--------------------------------------|---------|---|
| <u>1. Weight and length</u>          |         |   |
| W <sub>0</sub>                       | grams   | pre-experimental or initial body weight of a fish   |
| W <sub>t</sub>                       | grams   | post-experimental or final body weight of a fish  |
| W                                    | grams   | mean body weight of a fish (arithmetic mean of initial and final body weight)               |
| W <sub>m</sub>                       | grams   | average of mean body weight of fish in a group  |
| W <sub>i</sub>                       | grams   | mean body weight (W) of a fish in a group   |
| W <sub>n</sub>                       | grams   | calculated body weight of a fish in the natural population by Mercer (1978)                 |
| SL                                   | mm      | mean standard length of a fish (arithmetic mean of initial and final standard length)       |
| SL <sub>n</sub>                      | mm      | standard length of fish in the natural population (Mercer, 1978)                            |
| <u>2. Growth rates</u>               |         |   |
| WG                                   | g/day   | absolute growth rate (average daily growth rate) of a fish during an experiment (see eq. 4) |
| WG <sub>m</sub>                      | g/day   | average absolute growth rate of fish in a group   |
| WG <sub>i</sub>                      | g/day   | absolute growth rate (WG) of a fish in a group  |
| WG <sub>max</sub>                    | g/day   | calculated maximum WG at a given W (see eq. 15)   |
| WG <sub>n-max</sub>                  | g/day   | calculated maximum WG at a given W in the natural diet feeding condition (see equation 17)  |
| WG <sub>c-max</sub>                  | g/day   | calculated maximum WG at a given W in the commercial diet feeding condition (see eq. 19)    |
| WG <sub>stv</sub>                    | g/day   | calculated daily weight loss of a fish at a given mean body weight during starvation        |
| G                                    | % bw/d* | instantaneous growth rate (see equation 3)  |
| * % bw/d : % of body weight per day. |         |   |



Table 2 Continued

| symbol                                     | unit   | description  |
|--|--------|--|
| Gm   | % bw/d | average instantaneous growth of fish in a group  |
| Gmax                                       | % bw/d | calculated maximum G at a given W (see eq. 16)   |
| Gn-max                                     | % bw/d | calculated maximum G at a given W in the natural diet feeding condition (see eq. 18)       |
| Gc-max                                     | % bw/d | calculated maximum G at a given W in the commercial diet feeding condition (see eq. 20)    |
| Gstv                                       | % bw/d | calculated instantaneous rate of weight loss of a fish at a given weight during starvation |
| <u>3. Food and feeding related factors</u> |        |  |
| RCm  | % bw/d | average daily food consumption rate of a fish in a group during an experimental period     |
| RCest                                      | % bw/d | estimated daily food consumption rate of an individual fish (see equation 13)              |
| RC   | % bw/d | substitute of RCest for mathematical modeling of growth potential                          |
| RCn-max                                    | % bw/d | calculated maximum RCest at a given W in the natural diet feeding condition (see eq. 22)   |
| RCc-max                                    | % bw/d | calculated maximum RCest at a given W in the commercial diet feeding (see eq. 23)          |
| RCn-man                                    | % bw/d | calculated RCest for maintenance at a given W in the natural diet feeding (see eq. 34)     |
| RCc-man                                    | % bw/d | calculated RCest for maintenance at a given W in the commercial diet feeding (see eq. 34)  |
| Cm   | g/day  | average amount of food consumed daily by a fish in a group (see equation 9)                |
| Cest                                       | g/day  | estimated amount of food consumed daily by an individual fish (see equation 12)            |
| C  | g/day  | substitute of Cest in mathematical modeling for growth potential                           |

Table 2 Continued

| symbol | unit  | description  |
|--------|-------|--|
| Cn-max | g/day | calculated maximum Cest at a given W in the natural diet feeding condition (eq. 25)  |
| Cc-max | g/day | calculated maximum Cest at a given W in the commercial diet feeding condition (equ. 26)  |
| Ct     | g/day | amount of food given to a group of fish during an experimental period in days  |
| Fm     | none  | average food conversion rate (gross growth efficiency) of fish in a group  |
| Fest   | none  | estimated food conversion rate of an individual  |
| Fc     | none  | food conversion efficiency expressed as a ratio between the amount of food consumed versus absolute growth rate ( $F_c = C : WG$ ) |

#### 4. Energy related factors

|                        |            |   |
|------------------------|------------|---|
| I                      | calories   | amount of energy intaken by a fish  |
| R                      | calories   | energy used for total metabolism  |
| Rs                     | calories   | energy used for standard metabolism   |
| Rsda                   | calories   | energy used for food intake and processes   |
| Ra                     | calories   | energy used for activity  |
| U                      | calories   | energy lost in excretion  |
| F                      | calories   | energy lost in defecation   |
| P                      | calories   | energy gain or loss in body tissues   |
| OCstd                  | ml-Ox/min  | calculated total oxygen consumption of an individual for standard metabolism (see eq. 37) |
| ORstd                  | ml-Ox/g/m* | calculated oxygen consumption rate per unit body weight for standard metabolism           |
| Ec(c-max)<br>Ec(n-max) | calories   | energy equivalent for weight-specific maximum amount of food consumed (see eq. 26)        |

\* ml Ox/g/m : milli-liter of oxygen per body weight per minute

Table 2 Continued

| symbol                   | unit     | description  |
|--------------------------|----------|--|
| Erc(c-max)<br>Erc(n-max) | cal/g/d* | energy equivalent for weight-specific maximum food consumption rate (see Table 15)     |
| Ec(c-man)<br>Ec(n-man)   | cal/day  | energy equivalent for weight-specific maintenance food consumption (see Table 15)      |
| Ewg(c-max)<br>Ewg(n-max) | cal/day  | energy equivalent for weight-specific maximum absolute growth rate (see Table 15)      |
| Eg(c-max)<br>Eg(n-max)   | cal/g/d  | energy equivalent for weight-specific maximum instantaneous growth rate (see Table 15) |
| Ewg(stv)                 | cal/day  | energy equivalent for weight-specific weight loss in absolute rate (see Table 15)      |
| Eg(stv)                  | cal/g/d  | energy equivalent for weight-specific weight loss in instantaneous rate (see Table 15) |

5. Condition indices

|     |      |   |
|-----|------|---|
| K   | none | absolute weight-length index of a fish (eq. 6)                                      |
| RK  | none | relative weight-length index of a fish compared with natural population (see eq. 7) |
| dK  | none | average daily change of condition index of a fish during an experimental period     |
| dRK | none | average daily change of relative condition index during an experimental period      |

6. Others

|       |      |  |
|-------|------|--|
| t     | days | experimental periods   |
| n     | none | number of fish and observations  |
| p(T)  | none | probability of student's T-test  |
| p(F)  | none | probability of covariance (F-test)   |
| p(D)  | none | probability of Hoeffding's measure in correlation analysis (null hypothesis: $p=0$ ) |
| r     | none | correlation coefficient  |
| $r^2$ | none | coefficient of determination   |
| se    | none | standard error   |

---

\* cal/g/d: cal/g-body weight/day

## CHAPTER III

## REVIEW OF LITERATURE

## Biology of Black Sea Bass

The black sea bass, Centropristis striata L. (Subfamily Serraninae, Family Serranidae) is a common bottom dwelling fish found along the Atlantic coast of North America from Massachusetts to Florida. The primary habitats of black sea bass in nature are hard bottom and wrecks in coastal water, where they range in depths from 10 to 120 m (Kendall, 1977). In a population study by Cupka et al. (1977) and Mercer (1978) two separate populations of black sea bass were reported. The northern population which occurs from high latitudes to Virginia is characterized by seasonal migration into deep waters in cold seasons while the southern population remains yeararound in coastal water of North Carolina and lower latitudes.

The black sea bass is an opportunistic, carnivorous, visual feeder. The dietary items found in nature are, in order of importance, crustaceans, fish, molluscs, and echinoderms (Cupka et al., 1977; Chee, 1977; Kendall, 1977). Adults prefer crabs and fish while young black sea bass eat shrimps, isopods, and amphipods. Also, there is a variation in food consumption seasonally associated with spawning cycles, in which less feeding occurs during the spawning seasons.

Growth of black sea bass in nature varies depending on population, sex, and age (Mercer, 1978). The northern population grows faster than the southern population at all ages except age 1. Males are usually

larger than females at all ages greater than two, and grow faster in both populations. However, isometric growth was observed in length-weight relationships of both sexes and populations. Calculated mean annual growth rates by Mercer (1978) for both northern and southern populations were 33 - 78 mm and 24 - 54 mm SL respectively for age one to seven year-old fish in combined sexes. The calculated standard length of the northern and southern populations were 88 and 87 mm SL at age one and 365 and 294 mm SL at age seven respectively. Recorded maximum longevity is 20 years (Lavenda, 1949). Kendall (1977) reported without details that black sea bass reared in captivity grew from a mean of 265 g and 170 mm SL to 880 g and 284 mm SL over nine month period.

The black sea bass are protogynous hermaphrodites (Lavenda, 1949; Cupka et al., 1977; Mercer, 1978). Sex reversal occurs between breeding seasons when the fish reach the range of 100 - 379 mm SL and 1 - 7 years in ages. Sexual maturity of females generally occurs at age 2 and at a length of approximately 170 mm SL while males mature at age 1 and older. Spawning is considered to occur continuously in the spawning seasons and to be triggered by temperature (Cupka et al., 1977; Kendall, 1977; Mercer, 1978). Females of 1 - 5 years old produce 30,000 - 122,000 small planktonic eggs offshore in depths of 18 - 45 m during the spring and summer (Musik and Mercer, 1977; Tucker, 1983). Spawning seasons slightly vary depending on latitudes and fertilization occurs externally (Kendall, 1972).

Larvae of the northern population of the black sea bass occur inshore and offshore (4 - 82 km) in the range from New Jersey to North Carolina where the ranges of depths, temperatures, and salinity are 15 -

51 m, 14.3 - 28.0 °C, and 30.3 - 34.6 o/oo respectively (Kendall, 1972; Musik and Mercer, 1977; Briggs, 1978). Eggs (0.9 - 1.0 mm in diameter) have moderately narrow perivitelline space and yolk, possessing a single small oil globule and a plain membrane (Kendall, 1972; Tucker, 1983).

Juveniles of the black sea bass occur in saline areas of estuaries along the coast from Florida to Massachusetts (Cupka et al., 1977). The Chesapeake Bay is regarded the primary nursery ground for the northern population. Larvae were found abundantly in high salinity water of the Bay (more than 18 o/oo) in summer and fall but gradually move into deep water as they grow larger (Kendall, 1977; Musik and Mercer, 1977).

Several species of Centropristis are found on the Atlantic coast. C. melana, the southern black sea bass, has been disputed as a subspecies of C. striata due to its morphological overlapping (Miller, 1959; Bortone, 1977). However, many authors at present consider C. melana and C. striata are separated taxonomically at the species level due to their morphological and meristic differences (Bailey et al., 1970; Cupka et al., 1977; Musik and Mercer, 1977; Mercer, 1978).

## Principle and Methodology in Bioenergetic Studies

### Theoretical Principles of Methodology

The laws of conservation of energy must be adhered to by fish as other living systems. Matter and energy can be converted but never destroyed. A fish gains matter and energy in food (including endogenous energy source such as yolk), and loses the absorbed energy and matter as result of catabolism, which provides energy for maintenance and activity (Ivlev, 1939). When the gain is greater than the loss, energy is converted and deposited to the body tissues mostly in the form of protein, resulting in growth. If exogenous sources of energy (dietary energy) are insufficient to cover catabolism for maintenance and activity, growth of some organs or body components may occur at the expense of initial (endogenous) sources previously stored in growth (Brody, 1945; Fry, 1947, 1964; Kleiber, 1961). The metabolic and growth alternatives available to fish according to the law of thermodynamics and conservation of matter were well demonstrated in the studies of Winberg (1961a), Taylor (1962), Beamish and Dickie (1967), Davis (1967), Warren and Davis (1967), Edwards et al. (1971, 1972), Solomon and Brafield (1972), Niimi and Beamish (1974), Kitchell et al. (1974), Elliott (1976a, 1976b), Brett (1976a), Brett and Groves (1979), Sullivan and Smith (1982), and Kerr (1982).

The thermodynamics in energy balance of fish was well expressed by Krueger et al. (1968) in the following equation;

$$E_t = E_o + E_f - (H_s + H_{sda} + H_a + E_{ex}) \quad (14)$$

'E' indicates that available chemical energy is not oxidized while 'H' represents degradation of the chemical energy into heat. This expression reveals the basic patterns of energy transformation during a period in physiological process units. It indicates that any fish at a specified time ( $t_0$ ) has an energy content, 'E<sub>0</sub>', equivalent to its heat of combustion. Subsequently over a period of time 't' the energy content of the food taken is 'E<sub>f</sub>' and at time 't' the remaining energy content of the fish is 'E<sub>t</sub>'. Energy losses developed due to standard metabolism, metabolic requirements of exercise, and food-related specific dynamic action for feeding are represented by 'H<sub>s</sub>', 'H<sub>a</sub>', and 'H<sub>sda</sub>' respectively while energy lost by excretion and defecation were expressed as 'E<sub>ex</sub>'.

When 'E<sub>t</sub>-E<sub>0</sub>' is positive, it indicates an increase in protein, carbohydrates, or fat in body. If 'E<sub>t</sub>-E<sub>0</sub>' is negative, food deprivations or conditions of starvation prevail. When reproductive outputs and secretion are considered, they are categorized in 'E<sub>t</sub>' as additional energy output displaced to another form rather than energy lost in the system.

The right hand side of the expression consists of major allocation components in fish energetics. The catabolic metabolism (or total metabolism), in which chemical energy is converted to work and heat, consists of three basic components; standard metabolism (basal metabolism or minimal metabolism), specific increments of heat production with food intake (SDA), and the metabolism for muscular activity and for feeding. Fishes are poikilotherms and the heat is arbitrarily produced due to the incomplete transformation of energy from one phase to another. All



catabolic metabolisms in energy expenditure processes are directly related to heat production though the levels of the production depend on the metabolic substrates and end-products. The difficulties in energetic study of fish have arisen due to the incomplete energy transfer in anabolic and catabolic processes by energy loss through heat production. However, most authors agreed that the equation 14 was adequate expression for energetic study in defining the energy allocation in relation to physiological processes though various modifications are found frequently in many studies due to the purposes and circumstances of experimentation.

#### General and Specific Approaches in Methodology

Numerous approaches have been used to investigate the total or partial energy allocation during energy transformation to establish the energetics of fish at physiological or ecological levels. Complicated catabolic processes take place during energy expenditure and have caused major difficulties and varieties in energetic studies. Various methods have been developed to measure energy expenditure during the catabolic processes. Typical methods used in previous studies for estimating the total catabolic metabolisms are: (1) the quantitative measurement of heat produced by fish in metabolism, (2) the measurement of the oxygen consumed and the estimation based on calorific equivalent, (3) estimation from the changes of organic body substances, and (4) estimation from the heat of combustion. The principles of all four methods are based on the degradation of chemical energy into heat in catabolic processes.

Each method has advantages and drawbacks depending on the experimentation and the type of information provided such as time

required, the accuracy and the adequacy of the data for specific purposes, and the experimental designs that may be allowable or that may have to be excluded. However, most previous studies indicate that no single method could properly determine the entire energy expenditure patterns of a fish in each process of catabolic metabolism. Variations in biochemical and physiological states of fish between intra- and inter-specific levels hinder application of the information obtained from one experiment to another.

Among the three components of catabolic metabolism (standard metabolism, SDA, and activity) in equation 14, the basal rate of heat production (standard metabolism) is usually described as the minimum recordable metabolism compatible with normal existence (Brody, 1945; Fry, 1947; Huges, 1964). It is represented by the state of metabolism of a fish, in which only basal physiological processes for living is allowed without any external movement. Most fishes usually show spontaneous activities in any circumstances and, practically, it is extremely difficult to approximate zero activity in fish. In several studies, basal rate of metabolism for fish were predicted from data of oxygen consumption by extrapolation to zero activity along metabolic activity curves, which were obtained from oxygen consumption rates at various swimming speeds (Fry, 1957; Job, 1955; Blazka and Cepela, 1960; Smith, 1965; Edwards, 1968, 1969, 1976b; Kutty, 1968a, 1968b; Elliott, 1969, 1976b; Beamish, 1970; Jones, 1971; Brett, 1976a, 1976b). Drugs were sometimes used to attain minimum activity, but their effects on metabolism have not been sufficiently investigated (Krueger et al., 1968; Brett and Groves, 1979). Due to the difficulties of measuring standard metabolism in fish caused by

spontaneous movement, compromised values were frequently derived by replacing standard metabolism with post-digestive starvation-maintenance costs neglecting small components from exercise and excretion (Saunders, 1953; Beamish, 1964a, 1964b, 1964c; Beamish and Mookherjee, 1964; Smith, 1965; Rao, 1968; Edwards et al., 1970; Wallace, 1973; Smith, 1976; Kinne, 1977; Tarr, 1978). Metabolism of fish in anaerobic condition was also investigated due to the importance of oxygen debt for energy consumption efficiency (Blazka, 1958; Kutty, 1969a; Weihs, 1974).

Specific dynamic action (SDA) was clearly defined by Kleiber (1961) as 'the heat increment derived from the biochemical transformation of ingested foods into a metabolizable, excretable form'. A major contribution of SDA comes from deamination of protein but other organic matter such as lipid and carbohydrate metabolism are also involved in this type of energy expenditure. For fish, the first experimental determination of SDA was reported by Warren and Davis (1967). The difficulties in measuring the pure SDA in feeding metabolism are caused by the metabolic excitation accompanying feeding. To properly identify SDA segment in the metabolism of a fish, it is absolutely necessary to separate the energy expenditure of excitability and increased activity (occurring in conjunction with food intake) from SDA by rigorous experimental techniques as shown by Beamish (1974). Due to the difficulties, many investigators (Paloheimo and Dickie, 1966a; Pierce and Wissing, 1974; Brett, 1976b; Elliott, 1975d, 1976a; Tandler and Beamish, 1979, 1980, 1981) measured the whole energy expenditure in feeding without separating SDA component to examine total feeding costs in the energetic of fish. This was represented by a term of 'apparent SDA' to describe the

total energy expenditure related to meals and feeding (Beamish, 1974).

Fish activities are more or less related to feeding and locomotion (attacking, escaping, migrating, jumping, etc.). The scope of activity was initially interpreted by Fry (1957) to describe the energy expenditure for maintenance and the maximum activity in aerobic conditions. The energy expenditure for locomotive activity was continuously interested due to its high energy consumption rate and direct effect on available energy loss for growth (Basu, 1959; Saunder, 1963; Brett, 1963, 1964, 1965, 1983; Brett and Sutherland, 1965; Rao, 1968; Kutty, 1969b; Beamish, 1970; Brett and Glass, 1973; Ware, 1978; Brett and Blackburn, 1978). The maximum activity was defined and measured by continuous sustained swimming speed of fish which requires maximum oxygen consumption (Brett, 1965, 1971). Burst swimming motion observed frequently in nonpelagic fishes results in difficulties in defining energy expenditure for maximum activity due to the oxygen debt by anaerobic respiration and irregular pulse motion of the fishes (Kutty, 1969a; Weihs, 1973, 1974). The order of magnitude of active metabolic rate is 10 - 20 times maintenance level while maximum bursts can reach 10 times active metabolic rate (Brett, 1972).

Paloheimo and Dickie (1965, 1966a, 1966b) initially reported that feeding was a major factor evoking the animal activities and the maximum metabolic rate was accompanied by maximum food intake. Thus, the efficiency decreases in the conversion of food to body energy with increase in meal size as suggested by 'K-line phenomenon'. Kerr (1971a, 1971b, 1971c, 1982) reanalyzed some previous studies to confirm that the 'K-line phenomenon' commonly occurred in fish. Some authors attempted to figure the activity-related energy consumption from natural populations by

determining feeding and growth rates (Gerking, 1962; Kohler, 1964; Ricker, 1971; Smith, 1973; Stillwell and Kohler, 1982; Stewart, et al., 1983; Majkowski and Hearn, 1984). However, with few exceptions, most work concerned with energy expenditure provides unclear results in separating true locomotion activity from feeding activity and in defining energy expenditure due to variation of movement and various muscular activities.

Feces is a major energy loss. Various terms have been used to describe the substantially absorbed portion of food by fish (digestability, absorption, assimilation, availability, etc.). Fecal production of fish greatly varies depending on species, life stages, seasons, and quantity and quality of foods (Hunt, 1960; Pandian, 1967a, 1967b, 1970; Brett et al., 1970b; Kelso, 1972; Daan, 1973; Bryan, 1975; Elliott, 1976b; Windell et al., 1978a; Buddington, 1979; Brett and Groves, 1979). Various mechanical, chemical, and physiological techniques were used to collect feces in laboratory experiments. Siphoning off the gross particulate matter and supplementing this with fine-pore filtration are common techniques for collecting feces of fish (Menzel, 1960; Pandian, 1967b; Beamish, 1972; Solomon and Brafield, 1972; Elliott, 1975b; Windell et al., 1978a, 1978b; Choubert et al., 1981). The addition of an inert reference material to the diet (chromic oxide, radioactive isotopes, etc.) was also used frequently to examine the digestion rates (Daan, 1973; Cho et al., 1974; Bryan, 1975; Fange and Groves, 1979; Lied et al., 1981). When the feces could not be separated, the wet combustion method was used for calorific evaluation of total waste products based on the oxycalorific equivalent and chemical compositions of waste products (Solomon and Brafield, 1972; Brett, 1979).

In addition to the feces, excreta (metabolites) are other unoxidized compounds lost in waste products, which mostly consist of nitrogenous compounds. The production of nitrogenous excreta was frequently used to interpret the condition of fish energetics by relating feeding and catabolic substrates (exogenous or endogenous energy sources) (Gerking 1955a, 1955b, 1971; Wood, 1958; Nose, 1967; Fromm and Gillet, 1968; Birkett, 1969; Forster and Goldstein, 1969; Holme and Donaldson, 1969; Savitz, 1971, 1977; Kutty, 1972; Brett and Zala, 1975; Smith and Thorpe, 1976; Elliott, 1976a; Rychly and Mariana, 1977; Paulson, 1980; Jobling, 1981; Steffens, 1981). The nitrogenous excreta originates from incomplete protein catabolism and intake of excess or unbalanced nitrogenous substances (Brett and Groves, 1979). Since urea and uric acid production is generally negligible in excretory products of fish (less than 10%), most studies have focused on ammonia production rates in energy loss by excretion (Elliott and Davison, 1975).

Growth has the lowest immediate priority in energy allocation of individual fish but in the long run growth and reproduction dictate the species survival (Bertalanffy, 1951, 1957; Brett, 1970a, Fry, 1971; Kutty and Mohamed, 1975; Brett and Groves, 1979; Boulekbache, 1981). Generally, growth of fish is measured by morphological references such as length and weight (wet weight and dry weight). Change of body composition related to food and energy intake was frequently used for evaluating growth of fish (Brett et al., 1969). In terms of wet weight the energy gained is often overestimated by inclusion of water contents. Lipid and water concentrations inversely substitute in constituents of body chemical composition depending on the input level of exogenous energy source

(Gerking, 1955b; Savitz, 1971; Andrew and Stickney, 1972; Duncan and Klekowski, 1975; Dowgiallo, 1975;; Elliott, 1976b; Murray et al., 1977; Marais and Kissil, 1979; Reinitz, 1983). Caloric retention measured by direct combustion in calorimeters is also used frequently to eliminate the bias due to change of organic components of body substances related to growth (Job, 1960; Kleiber, 1961). Gerking (1952) first described nitrogen retention as a growth index since no continuous tissue elaboration can proceed without protein.

It is well recognized that environmental factors affect the growth of fish not only in energy expenditure through metabolic activities but also by regulating the individual as an ecological unit (Kohler, 1964; Kutty, 1981). To define the environments for growth of fish, most previous studies in fish energetics concentrated on the catabolic aspects of metabolism in relation to the influence of abiotic and biotic factors. To understand the energetics of fish in nature or in relation to environments, manipulation of various environmental factors in laboratories was commonly used in previous energetic studies of fish.

Among various environmental factors, several factors are primarily referred to in most energetic studies of fish due to their strong effects on growth (Beamish et al., 1975b; Brett, 1979). Elliott (1976b) and Brett(1979) pointed out that any attempt at growth modeling for fish must included at least the three factors: ration, size, and temperature as the most important independent variables. Tremendous outputs from numerous experiments in growth-related environments of fish have been accumulated. The importance of the two major environmental factors, food and temperature in growth and energetics of fish was well reflected in the

amount of literatures. The major concerns of food in energetics of fish were (1) nutritional or energetic qualities of foods (Menzel, 1960; Adron et al., 1969; Phillips and Duma, 1969; Brett, 1970c; Halver, 1971, 1972; Cowey et al., 1972; Cochran and Rice, 1972; Cho et al., 1974, 1976; Bryan, 1975; Schalles and Wissing, 1976; Smith, 1971, 1976; Smith, et al. 1978; Buddington, 1979; Cowey and Sargent, 1979; Reinitz and Hitzel, 1979; Kaushik, 1980; Tarr and Hill, 1982), and (2) quantities of foods affecting growth (Pentelov, 1939; Winberg, 1956; Hunt, 1960; Gerking, 1962; Davis, 1963, 1966; Paloheimo and Dickie, 1965, 1966a, 1966b; Pandian, 1967a, 1967b, 1970; LeBrasseur, 1969; Brett, 1970b, 1976b; Kelso, 1972; Andrew and Stickney, 1972; Beamish, 1972; Daan, 1973; Wallace, 1973; Elliott, 1975a, 1975b, 1975c, 1979; Huisman, 1976; Jones, 1978; Jones and Hipslop, 1978; Cochran, 1979; Marais and Kissil, 1979; Brusle, 1981; Stillwell and Kohler, 1982; Majkowski and Hearn, 1984).

Temperature affects on overall pattern of energetics of fish by regulating each physiological processes through enzyme activities. Energy intake in food consumption and pattern of energy allocation for each physiological process in energetics of fish are inevitably influenced by temperature (Well, 1935; Brown, 1946, 1951, 1957; Fry and Hart, 1948; Graham, 1949; Baldwin, 1957; Winberg, 1959; Johnson and Charlton, 1960; Kinne, 1960; Swift, 1964; Marr, 1966; Savitz, 1969; Brett, 1971, 1974). However, environmental factors have been found to function at species-specific and individual physiological levels rather than generalized patterns. Transfer of fish energetic information from one species to another or from laboratories to nature is still limited due to variation resulting from fluctuation of ecological and physiological parameters.



### Approaches in Mathematical Modeling

Mathematical modeling is frequently utilized to improve knowledge through systematic combination based on accumulated information and/or proper hypothesis testing.

When fish have not been exposed to practical culture, the potentials of the fish in culture are frequently estimated from laboratory experiments, mainly concerned with the growth potentials in modified environments. For black sea bass, which are tolerant of a wide variety of habitat conditions, a model of the processes that regulate energetics may be used as a sensitive tool in inferring ecological relationships.

In general, to simulate a bioenergetic model, a process integrating diverse existing knowledge into a unified framework is necessary. This type of modeling has three phases. The first step is to mathematically state what is known about the energetic controlling processes. This requires a critical evaluation of the results of both laboratory and field studies. Second, the relation of these processes to independent variables must be evaluated. These relations comprise the model hypotheses. If the hypothesis is rigorous, validity of results will depend on validity of the analysis of sub-processes. Finally, the model is used as an analytical tool. A sensitivity analysis can indicate which part of the current understanding of energetics requires further experimentation. Given a working simulation model, various ecological conditions may be evaluated with respect to their implications for fish energetics.

A few types of energetic models were simulated in the previous energetic studies of fish based on laboratory experiments and hypothesis.

Various equations have been derived to explain the relationships between growth and environmental factors or growth itself of fish. Most variations were found in growth equations (i.e., Schmalhausen curve, Hayes and Armstrong curve, Logistic growth curve, Gompertz curve, Putter curves, Johnson curve, and Richard function). Among those curves, Schmalhausen's exponential growth curve was widely used for laboratory studies of fish (Ricker, 1979). Since most of the laboratory studies of growth were conducted during a short period compared to the whole life span of fish, the exponential growth rate is regarded to be adequate to describe the growth of young fish.

Among several bioenergetic models established in previous studies (Paloheimo and Dickie, 1965, 1966a, 1966b; Kerr, 1971a, 1971b, 1971c, 1982; Kitchell et al., 1974, 1977; Elliott, 1976b; Brett 1976a, 1979; Kitchell and Stewart, 1977; Ware, 1978; Kitchell and Break, 1980; Kitchell, 1983; Stewart et al., 1983), Kitchell's and Elliott's models appear to be adequate in terms of (1) facilitating understanding of growth related to multiple factors, (2) application to practical work for culture study, and (3) the fitness between estimated values and the experimental outputs. Ricker (1979) and Brett (1979) criticized the energetic models developed by Elliott because of (1) poor curve fitting, which is only applicable to short life span, and (2) unreliability of mathematical modeling to practical work where unknown factors are frequently involved resulting in irregular relationships between variables. They suggested the Brett's tabular presentation (1971, 1976a, 1979), of which the relationships of the factors involved in bioenergetics of fish were presented in graphic modelings without mathematical expressions, was

adequate to describe the relation between growth and environmental factors. But in practical points, those tabular presentations have several disadvantages: (1) limitation in expandability in various culture conditions, (2) no allowance for direct application to practical work without perfect data collection, (3) the requirement of a great amount of data for modeling, and (4) limitation in expressing the variations produced in experiments and statistical processes.

As Kitchell (1977) pointed out, the purpose of modeling is not only for the evaluation of the past and present studies but also for understanding what parts of the information are required for future studies. Considering the lack of information on the black sea bass in nature and laboratories, it may not be unreasonable to select mathematical expression-type modeling to simplify the basic relationships between the important physiological and the environmental variables underlying basic pattern of the energy budget shown by Elliott (1976b):

$$I = F + U + R + P$$

and

$$R = R_s + R_d + R_a$$

where I is the total energy content of the food consumed by the fish, F is the energy value of the feces, U is the energy value of the excretory products, P is the total change in energy value of body materials (gain or loss in energy content), and R is the total energy of metabolism which is subdivided into three components:  $R_s$ , the energy equivalent to that released in the course of metabolism in unfed and resting fish (standard metabolism),  $R_a$ , the energy required for swimming and other activity,  $R_d$ ,

the energy required for digestion, movement and deposition of food materials.

The equation is accessed by three variables through the experimentation in this study: (1) weight of the fish, (2) calculated and estimated food consumption rate or quantity of food consumed, and (3) food type. Each unit of the equation will be expressed as a function of the three variables in combined or separated forms.

Since the data relating to the feces and excretory products were not sufficient for estimating assimilation efficiency, the physiologically available energy was estimated from food conversion efficiency and weight loss in starvation tests. Standard metabolism is expressed as a function of weight of the fish. Energy consumed in active metabolism and specific dynamic action was not directly measured but maximum energy expenditure related to food consumption was estimated from the difference of energy expenditure and energy intake from gross assimilation efficiency, and maximum and maintenance food consumption rates.

## CHAPTER IV

## RESULTS

## Patterns of Growth

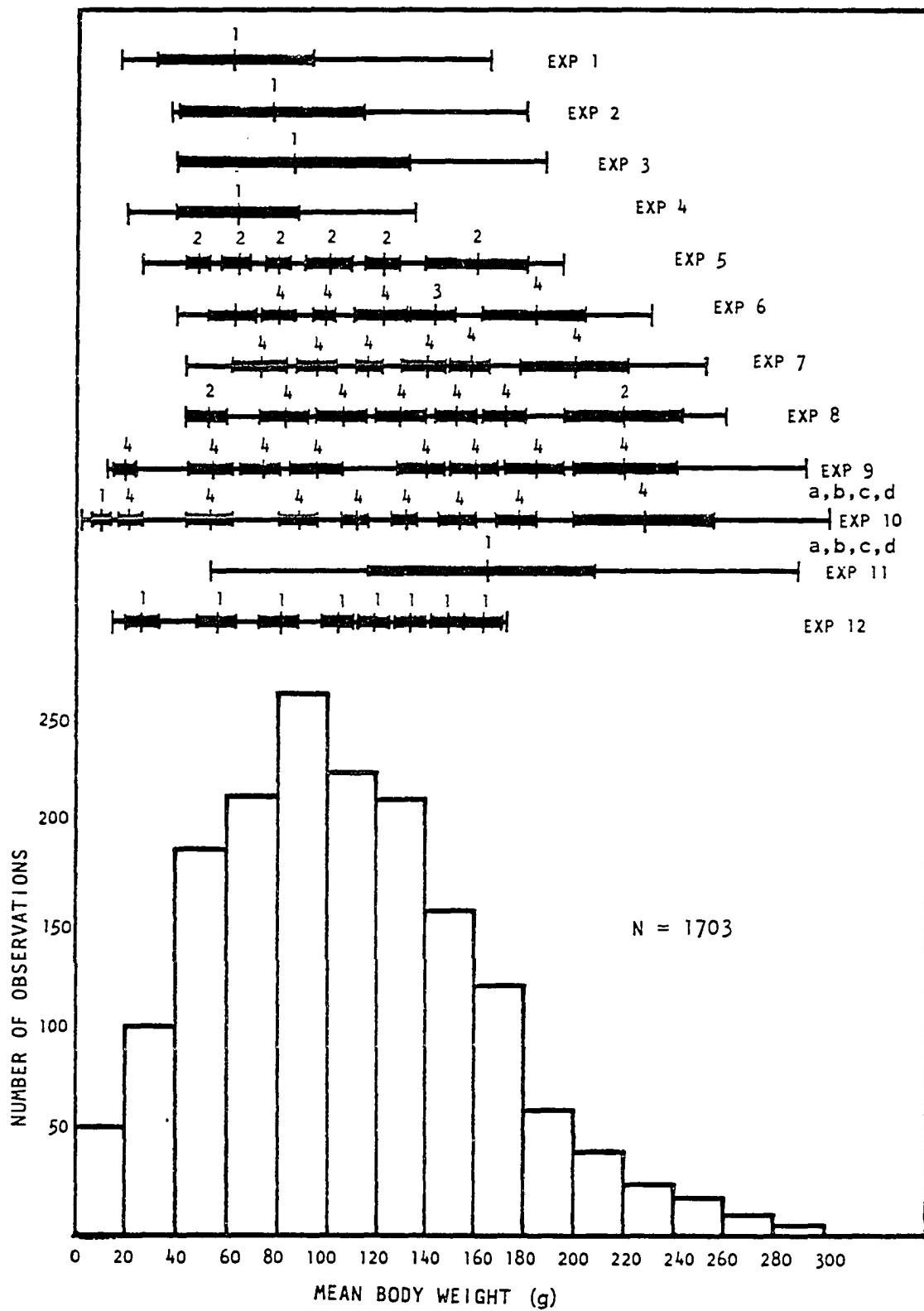
A total of 1703 observations were obtained from 346 individuals in the experiments for the growth study. During the experiments large variation of growth rates was observed not only between individuals in an experiment but also between experiments. The differences of food type and feeding level as well as the weight of the fish in each experiment varied the growth rate of fish.

The range of a mean body weight of all tested fish was from 4.3 g to 295.2 g with the average of 107.8 g (n=1703). Approximately 95 % of the total observations was conducted with fish having mean body weights in a range from 10 g to 210 g. Only 81 observations were obtained from individuals weighing more than 210 g. The weight of fish used in all experiments combined (n=1703) showed a normal distribution as well as those in each experiment. The range of weights of the fish in each experiment varied as shown in Figure 1. The averages of mean body weight of fish in each experiment ranged from 63.6 - 154.0 g. Except for the four preliminary experiments (experiment 1, 2, 3, and 4) and one starvation experiment (experiment 11), the average mean body weight of fish in each experiment was similar in a range of 99.0 - 133.9 g. The average weight of test fish in each experiment increased slightly as they were repeatedly exposed in the series of the experiments.

The mean body weights, growth rates, and food consumption rates of

Figure 1.

Distribution of mean body weights ( $W$ , grams) of fish in each experiment (horizontal bar) and in all experiments combined (histogram). Numbers on horizontal line indicate number of replicate groups in each size class. Thin line indicates range of weight of test fish. Solid bar indicates standard deviation of weight of each size class. Vertical line in the middle of the solid bar indicates average weight of fish in each size class.



fish in each experiment are summarized in Table 3 and 4. The averages of mean body weight, growth rates, food consumption rate of each group in all experiments are listed in Appendix C. The weights of fish, growth rates, and food consumption rates of groups of fish in each feeding condition are summarized in Table 5. The results obtained from all individuals in each feeding condition are summarized in Table 6. Correlation analysis was performed at two levels (individual and group levels) in each experiment and in each feeding condition and the results are summarized in Tables 7 through 10.

In statistical analysis the data obtained from experiment 10 were excluded due to experimental errors caused by deteriorated water quality of the culture system. However, the results obtained for growth and food consumption rates of fish in experiment 10 were listed in tables for reference.

#### Weight-Specific Growth Pattern

During the experiments, the fish (n=1703) were exposed to three types of discrete feeding conditions: (1) starved (n=212), (2) natural diet feeding (n=330), and (3) commercial diet feeding (n=1161). The patterns and the magnitudes of growth varied depending on feeding conditions as well as weights of fish. Under the same feeding condition, the growth of fish was primarily affected by the weight of fish.

##### 1) Weight-specific growth in starvation experiments

In three starvation experiments (Experiments 9a, 10a, and 11) the fish showed the similar patterns in both magnitude and trend of weight loss in relation to body weight of fish (see Table 3 and 9). A total 212



Table 3. Summary of the averages and ranges of mean body weight and growth rates of fish in each experiment.

| No. of Exp.   | No. of fish | mean body weight (W, g) |            | absolute growth rate (WG, g/day) | inst. growth rate (G, % bd. wt./day) |
|---|-------------|-------------------------|------------|----------------------------------|--------------------------------------|
|   |             | average                 | range      | average (range)                  | average (range)                      |
| <u>I. Starvation Experiments</u>                            |             |                         |            |                                  |                                      |
|   |             | *                       |            |                                  |                                      |
|   | 9a 66       | 105.7 (7.1)             | 12.3/260.1 | -0.40 (-1.00/-0.09)              | -0.44 (-0.90/-0.21)                  |
|   | 10a 70      | 108.7 (8.2)             | 11.2/295.2 | -0.41 (-1.10/-0.10)              | -0.46 (-1.00/-0.10)                  |
|   | 11 76       | 154.0 (6.3)             | 49.8/282.1 | -0.64 (-1.22/-0.20)              | -0.44 (-0.75/-0.14)                  |
| <u>II. Natural Diet Experiments (satiated feeding)</u>      |             |                         |            |                                  |                                      |
| <u>A. No size-sorting and single daily feeding</u>          |             |                         |            |                                  |                                      |
|   | 1 75        | 63.9 (3.6)              | 18.7/165.8 | 0.24 (-0.14/0.81)                | 0.32 (-0.57/1.07)                    |
|   | 2 74        | 77.6 (4.8)              | 21.0/180.4 | 0.29 (-0.32/0.93)                | 0.37 (-0.48/1.08)                    |
|   | 3 74        | 85.3 (4.6)              | 23.4/187.0 | 0.26 (-0.40/1.28)                | 0.45 (-0.38/1.90)**                  |
| <u>B. Size-sorting and double daily feeding</u>             |             |                         |            |                                  |                                      |
|   | 9b 53       | 134.6 (7.9)             | 34.8/278.5 | 0.79 ( 0.07/1.63)**              | 0.60 ( 0.13/1.40)                    |
|   | 10b 54      | 143.0 (8.2)             | 40.3/267.7 | 0.25 (-0.61/1.19)                | 0.16 (-0.54/0.83)                    |
| <u>III. Commercial Diet Experiments ***</u>                 |             |                         |            |                                  |                                      |
| <u>A. Satiated-single daily feeding</u>                     |             |                         |            |                                  |                                      |
|   | 5 180       | 89.7 (2.6)              | 34.8/159.9 | 1.05 ( 0.10/2.21)                | 1.25 ( 0.14/2.24)                    |
|   | 6 177       | 109.3 (2.9)             | 41.7/231.3 | 0.85 (-0.10/1.77)                | 0.84 (-0.07/1.90)                    |
|   | 7 187       | 120.2 (3.2)             | 43.9/253.6 | 0.81 (-0.58/2.22)                | 0.72 (-0.38/2.54)                    |
|   | 8 186       | 133.0 (3.6)             | 44.0/271.6 | 0.77 (-0.28/2.23)                | 0.58 (-0.57/1.19)                    |
| <u>B. Satiated-double daily feeding</u>                     |             |                         |            |                                  |                                      |
|   | 9c 70       | 133.9 (3.5)             | 11.9/291.6 | 1.32 (-0.09/2.89)                | 1.16 (-0.11/3.39)                    |
|   | 10c 80      | 112.2 (4.0)             | 4.3/254.9  | 0.15 (-0.52/1.50)                | 0.51 (-0.47/3.09)                    |
| <u>C. Reduced-single daily feeding</u>                      |             |                         |            |                                  |                                      |
|   | 9d 65       | 124.0 (3.1)             | 12.3/293.6 | 0.84 (-0.21/2.14)                | 0.76 (-0.23/2.49)                    |
|   | 10d 59      | 120.5 (3.2)             | 13.7/248.6 | 0.00 (-1.10/1.38)                | 0.09 (-0.71/2.19)                    |
| <u>D. Reduced-half daily feeding</u>                        |             |                         |            |                                  |                                      |
|   | 12 54       | 99.0 (2.7)              | 15.8/181.8 | 0.36 (-0.69/1.18)                | 0.42 (-0.74/1.81)                    |
| <u>E. Reduced-single daily feeding with no size-sorting</u> |             |                         |            |                                  |                                      |
|   | 4 103       | 63.6 (2.3)              | 20.6/133.1 | 0.53 (-0.45/1.95)                | 0.86 (-0.65/2.45)**                  |

\*Numbers in the parenthesis are standard errors.

\*\* Standard errors are 0.06. Others are less than 0.05.

\*\*\* Size-sorting of fish was applied to all except for experiment 4.

Table 4. Summary of the averages of group food consumption rates (RCm), amounts of food consumed by groups (Cm), estimated individual food consumption rates (RCest), and amounts of food by individuals (Cest) in each experiment.

| exp. no.   | no. of fish & (group) | RCm<br>avg. (range) | Cm<br>avg. (range) | RCest<br>avg. (range) | Cest<br>avg. | Fm/Fest<br>avg./avg. |
|--|-----------------------|---------------------|--------------------|-----------------------|--------------|----------------------|
| <u>I. Natural Diet Experiments (satiated feeding only)</u>           |                       |                     |                    |                       |              |                      |
| <u>A. Single daily feeding (no size-sorted)</u>                      |                       |                     |                    |                       |              |                      |
| 1  | 75 (1)                | 5.1 ( - )           | 3.2 ( - )          | 5.0 (0.6-10.4)        | 3.2          | 0.06/0.06            |
| 2  | 74 (1)                | 4.2 ( - )           | 3.3 ( - )          | 4.3 (0.0-8.3)         | 3.3          | 0.08/0.08            |
| 3  | 74 (1)                | 3.9 ( - )           | 3.3 ( - )          | 4.0 (0.5-12.5)        | 3.3          | 0.07/0.07            |
| <u>B. Double daily feeding (size-sorted)</u>                         |                       |                     |                    |                       |              |                      |
| 9b   | 53 (7)                | 2.5 (1.5-3.1)       | 3.6 (0.8-5.2)      | 2.5 (1.2-4.2)         | 3.4          | 0.23/0.23            |
| 10b  | 54 (7)                | 1.9 (0.9-2.8)       | 2.7 (0.8-4.4)      | 1.9 (0.0-4.0)         | 2.8          | 0.07/0.08            |
| <u>II. Commercial Diet Experiments (size-sorting) *</u>              |                       |                     |                    |                       |              |                      |
| <u>A. Satiated-single daily feeding</u>                              |                       |                     |                    |                       |              |                      |
| 5  | 180 (12)              | 1.5 (1.4-1.8)       | 1.5 (0.7-2.4)      | 1.5 (0.6-2.7)         | 1.4          | 0.80/0.80            |
| 6  | 177 (22)              | 1.2 (0.8-1.9)       | 1.2 (0.8-2.0)      | 1.1 (0.3-2.4)         | 1.2          | 0.72/0.71            |
| 7  | 187 (25)              | 0.9 (0.5-1.4)       | 1.1 (0.4-1.7)      | 1.0 (0.0-2.3)         | 1.1          | 0.72/0.69            |
| 8  | 186 (24)              | 0.9 (0.6-1.2)       | 1.2 (0.3-2.2)      | 0.9 (0.0-1.5)         | 1.2          | 0.60/0.59            |
| <u>B. Satiated-double daily feeding</u>                              |                       |                     |                    |                       |              |                      |
| 9c   | 70 (9)                | 1.5 (1.0-1.9)       | 1.6 (0.3-2.6)      | 1.5 (0.0-3.4)         | 1.6          | 0.83/0.80            |
| 10c  | 80 (10)               | 1.1 (0.6-2.0)       | 0.8 (0.2-1.7)      | 1.1 (0.0-3.6)         | 0.8          | 0.36/0.39            |
| <u>C. Reduced-single daily feeding</u>                               |                       |                     |                    |                       |              |                      |
| 9d   | 65 (8)                | 0.8 (0.6-1.4)       | 0.9 (0.3-1.4)      | 0.8 (0.0-2.5)         | 0.9          | 0.92/0.87            |
| 10d  | 59 (8)                | 0.6 (0.4-1.1)       | 0.6 (0.2-1.1)      | 0.6 (0.0-2.3)         | 0.6          | 0.18/0.22            |
| <u>D. Reduced-half daily feeding</u>                                 |                       |                     |                    |                       |              |                      |
| 12   | 56 (8)                | 0.8 (0.5-1.4)       | 0.7 (0.3-1.0)      | 0.8 (0.0-2.0)         | 0.7          | 0.52/0.45            |
| <u>E. Reduced-single daily feeding (no size-sorted)</u>              |                       |                     |                    |                       |              |                      |
| 4  | 103 (1)               | 1.0 ( - )           | 0.6 ( - )          | 1.0 (0.0-2.3)         | 0.6          | 0.84/0.84            |
| * Size-sorting of fish was applied to all except for experiment 4.   |                       |                     |                    |                       |              |                      |
| Symbols indicate :   |                       |                     |                    |                       |              |                      |
| RCm (average food consumption rate of a fish in a group, % bw/d)     |                       |                     |                    |                       |              |                      |
| Cm (average amount of food consumed daily by a fish in a group, g/d) |                       |                     |                    |                       |              |                      |
| Fm (average food conversion rate of a fish in a group)               |                       |                     |                    |                       |              |                      |
| RCest (estimated food consumption rate of a fish, % bw/d)            |                       |                     |                    |                       |              |                      |
| Cest (estimated amount of food consumed by a fish, g/day)            |                       |                     |                    |                       |              |                      |
| Fest (estimated food conversion rate, WG/Cest)                       |                       |                     |                    |                       |              |                      |

Table 5. Summary of the averages of group mean body weights (Wm), group growth rates (WGm and Gm), group food consumption rates (RCm), and group food conversion rates (Fm) in each feeding condition.

| No. of groups   | avg. mean body wt. (Wm, g) | avg. absol. growth rate (WGm, g/day) | avg. instant. growth rate (Gm, % bwpd)* | avg. food consum. rate (RCm, % bwpd) | food conversion rate (Fm) |
|---|----------------------------|--------------------------------------|---|--------------------------------------|---------------------------|
| <u>I. Starvation Experiments (exp. 9a, 10a, and 11)</u>               |                            |                                      |   |                                      |                           |
| 3 (212)   | 122.8<br>(105.7/154.1)     | -0.48<br>(-0.64/-0.40)               | -0.45<br>(-0.46/-0.44)**                | -                                    | -                         |
| <u>II. Natural Diet Experiments (Satiated feeding only)</u>           |                            |                                      |   |                                      |                           |
| <u>A. No size-sorting and single daily feeding (exp. 1, 2, and 3)</u> |                            |                                      |   |                                      |                           |
| 3 (223)   | 75.7<br>(63.9/85.3)        | 0.27<br>(0.24/0.29)                  | 0.38<br>(0.32/0.45)                     | 4.7<br>(4.4/4.9)                     | 0.07<br>(0.06/0.08)       |
| <u>B. Size-sorting and double daily feeding (exp. 9b)</u>             |                            |                                      |   |                                      |                           |
| 7 (53)  | 144.9<br>(54.6/256.0)      | 0.81<br>(0.19/1.06)                  | 0.58<br>(0.34/0.82)                     | 2.5<br>(1.5/3.1)                     | 0.23<br>(0.17/0.28)       |
| <u>III. Commercial Diet Experiments (Size-sorting***)</u>             |                            |                                      |   |                                      |                           |
| <u>A. Satiated-single daily feeding (exp. 5, 6, 7, and 8)</u>         |                            |                                      |   |                                      |                           |
| 83 (730)  | 120.0<br>(45.7/225.4)      | 0.84<br>(0.0/1.44)                   | 0.76<br>(0.0/1.73)                      | 1.1<br>(0.5/1.9)                     | 0.69<br>(0.69/1.27)       |
| <u>B. Satiated-double daily feeding (exp. 9c)</u>                     |                            |                                      |   |                                      |                           |
| 9 (70)  | 121.0<br>(18.1/242.8)      | 1.22<br>(0.34/1.75)                  | 1.46<br>(0.71/2.09)                     | 1.5<br>(1.0/1.9)                     | 0.83<br>(0.65/1.83)       |
| <u>C. Reduced-single daily feeding (exp. 9d)</u>                      |                            |                                      |   |                                      |                           |
| 8 (65)  | 124.2<br>(19.4/233.0)      | 0.82<br>(0.23/1.27)                  | 0.76<br>(0.48/1.22)                     | 0.8<br>(0.6/1.4)                     | 0.90<br>(0.85/1.06)       |
| <u>D. Reduced-half daily feeding (exp. 12)</u>                        |                            |                                      |   |                                      |                           |
| 8 (54)  | 103.9<br>(23.9/173.9)      | 0.36<br>(0.16/0.56)                  | 0.41<br>(0.17/0.87)                     | 0.8<br>(0.5/1.4)                     | 0.50<br>(0.32/0.72)       |
| <u>E. Reduced-single daily feeding with no size-sorting (exp. 4)</u>  |                            |                                      |   |                                      |                           |
| 1 (103)   | 63.6                       | 0.53                                 | 0.86                                    | 1.0                                  | 0.84                      |

\* bwpd: body weight per day

\*\* Numbers in parenthesis are ranges (minimum/ maximum).

\*\*\* Size-sorting was applied in all experiments except exp. 4.

All fish in each experiment are regarded as one group in experiments 1, 2, and 3 due to no size-sorting.

Table 6. Summary of the averages of mean body weight (W), growth rates (WG and G), estimated food consumption rate (RCest) and estimated food conversion rate (Fest) of individuals in each feeding condition.

| No. of fish  | avg. mean body wt. (W, g) | avg. absol. growth rate (WG, g/day) | avg. instant. growth rate (G, % bwpd)* | avg. est. food consum. rate (RCest, % bwpd) | avg. est. food con. rate (Fest) |
|--|---------------------------|-------------------------------------|--|---|---------------------------------|
| <u>I. Starvation Experiments (Exp. 9a, 10a, and 11)</u>              |                           |                                     |  |   |                                 |
| 212 (3)**  | 124.0<br>(11.2/295.2)     | -0.49<br>(-1.22/-0.09)              | -0.45<br>(-0.98/-0.14)***              | -   | -                               |
| <u>II. Natural Diet Experiments (Satiated feeding only)</u>          |                           |                                     |  |   |                                 |
| A. <u>Single daily feeding with no size-sorting</u> (exp. 1, 2, 3)   |                           |                                     |  |   |                                 |
| 223 (3)  | 75.6<br>(18.7/187.0)      | 0.27<br>(-0.4/1.28)                 | 0.38<br>(-0.57/1.9)                    | 4.7<br>(0/12.5)                             | 0.07<br>(0.00/0.15)             |
| B. <u>Double daily feeding with size-sorting</u> (exp. 9b)           |                           |                                     |  |   |                                 |
| 53 (7)   | 134.6<br>(34.8/278.5)     | 0.79<br>(0.07/1.63)                 | 0.60<br>(0.13/1.40)                    | 2.5<br>(1.2/4.2)                            | 0.23<br>(0.10/0.34)             |
| <u>III. Commercial Diet Experiments (Size-sorted**)</u>              |                           |                                     |  |   |                                 |
| A. <u>Satiated-single feeding</u> (exp. 5, 6, 7, and 8)              |                           |                                     |  |   |                                 |
| 730 (83)   | 113.3<br>(34.8/271.6)     | 0.87<br>(-0.58/2.23)                | 0.84<br>(-0.57/2.54)                   | 1.1<br>(0.0/2.7)                            | 0.70<br>(0.00/1.32)             |
| B. <u>Satiated-double daily feeding</u> (exp. 9c)                    |                           |                                     |  |   |                                 |
| 70 (9)   | 115.4<br>(12.3/284.1)     | 1.20<br>(-0.19/2.89)                | 1.28<br>(-0.74/3.89)                   | 1.5<br>(0.0/3.4)                            | 0.80<br>(0.00/1.45)             |
| C. <u>Reduced-single daily feeding</u> (exp. 9d)                     |                           |                                     |  |   |                                 |
| 65 (8)   | 117.8<br>(14.4/293.6)     | 0.81<br>(-0.21/1.77)                | 0.77<br>(-0.45/2.87)                   | 0.8<br>(0.0/2.5)                            | 0.87<br>(0.00/1.35)             |
| D. <u>Reduced-half daily feeding</u> (exp. 12)                       |                           |                                     |  |   |                                 |
| 54 (8)   | 99.0<br>(15.8/181.8)      | 0.36<br>(-0.69/1.18)                | 0.42<br>(-0.74/1.81)                   | 0.8<br>(0.0/2.0)                            | 0.45<br>(0.00/1.08)             |
| E. <u>Reduced-single daily feeding with no size-sorting</u> (exp. 4) |                           |                                     |  |   |                                 |
| 103 (1)  | 63.6<br>(20.6/133.1)      | 0.53<br>(-0.45/1.95)                | 0.86<br>(-0.65/2.45)                   | 1.0<br>(0.0/2.3)                            | 0.84<br>(0.00/0.94)             |
| * bwpd: body weight per day  |                           |                                     |  |   |                                 |
| ** Numbers in parenthesis are the number of groups.                  |                           |                                     |  |   |                                 |
| *** Numbers in parenthesis are ranges (minimum/ maximum).            |                           |                                     |  |   |                                 |

Table 7. Summary of correlation analysis between groups of fish in each experiment (correlation between group mean body weight (Wm), group growth rates (WGm and Gm), food consumption rate (RCm), amount of food consumed (Cm), and food conversion rate (Fm)).

| Exp. No.  |      | Wm vs. |        |        |        | Cm vs. |        | RCm vs. |        |
|---|------|--------|--------|--------|--------|--------|--------|---------|--------|
| No. of  | grp. | WGm    | Gm     | Fm     | RCm    | Cm     | WGm    | Gm      | WGm    |
| <u>I. Natural Diet Experiments (Satiated feeding)</u> |      |        |        |        |        |        |        |         |        |
| 9b (7)  |      | 0.63*  | -0.31* | -0.76  | 0.04*  | 0.91   | 0.89   | 0.07*   | 0.76   |
| 10b (7)   |      | 0.73*  | 0.28*  | 0.34*  | 0.19*  | 0.88   | 0.93   | 0.65*   | 0.69*  |
| <u>II. Commercial Diet Experiments</u>                |      |        |        |        |        |        |        |         |        |
| <u>A. Satiated-single daily feeding</u>               |      |        |        |        |        |        |        |         |        |
| 5 (12)  |      | 0.94   | -0.88  | -0.80  | 0.09*  | 0.99   | 0.94   | -0.89   | 0.10*  |
| 6 (22)  |      | 0.41   | -0.80  | -0.57  | -0.68  | 0.81   | 0.70   | -0.40*  | 0.04*  |
| 7 (25)  |      | 0.16*  | -0.65  | -0.70  | -0.56  | 0.72   | 0.74   | -0.05*  | 0.63   |
| 8 (24)  |      | 0.76   | 0.07*  | 0.26*  | -0.11* | 0.89   | 0.94   | 0.41    | 0.48   |
| <u>B. Satiated-double daily feeding</u>               |      |        |        |        |        |        |        |         |        |
| 9c (9)  |      | 0.86   | -0.86  | -0.68  | -0.67  | 0.91   | 0.98   | -0.75   | -0.27* |
| 10c (10)  |      | -0.37* | -0.74  | -0.77  | -0.84  | 0.94   | -0.16* | -0.73   | 0.52*  |
| <u>C. Reduced-single daily feeding</u>                |      |        |        |        |        |        |        |         |        |
| 9d (8)  |      | 0.91   | -0.84  | 0.20*  | -0.76  | 0.92   | 0.99   | -0.69*  | -0.63* |
| 10d (8)   |      | -0.59* | -0.69* | -0.69* | -0.85  | 0.95   | -0.59* | -0.68*  | 0.65*  |
| <u>D. Reduced-half daily feeding</u>                  |      |        |        |        |        |        |        |         |        |
| 12 (8)  |      | 0.46*  | -0.78  | -0.58* | -0.82  | 0.89   | 0.75   | -0.57*  | -0.11* |

\* statistically insignificant :  $p(D) > 0.05$

Experiments 1, 2, 3, and 4 were excluded because of no size class.

Symbols indicate:

Wm : average of mean body weight of a fish in a group

WGm : average absolute growth rate of a fish in a group

Gm : average instantaneous growth rate of a fish in a group

Cm : average amount of food consumed by a fish in a group

RCm : average food consumption rate of a fish in a group

Fm : average food conversion rate of a fish in a group

Table 8. Summary of correlation analysis between groups of fish in each feeding condition (correlation between group mean body weight (Wm), group growth rates (WGm and Gm), food consumption rate (RCm), amount of food consumed (Cm), and food conversion rate (Fm)).

| Number<br>of<br>groups  | Wm vs. |        |        |       |      | Cm vs. |        | RCm vs. |      |
|---|--------|--------|--------|-------|------|--------|--------|---------|------|
|   | WGm    | Gm     | Fm     | RCm   | Cm   | WGm    | Gm     | WGm     | Gm   |
| <u>I. Natural Diet Experiments</u>                            |        |        |        |       |      |        |        |         |      |
| A. <u>Satiated-double daily feeding</u> (exp. 9b)             |        |        |        |       |      |        |        |         |      |
| 7   | 0.63*  | -0.31* | -0.76  | 0.04* | 0.91 | 0.89   | 0.07*  | 0.76    | 0.92 |
| <u>II. Commercial Diet Experiments</u>                        |        |        |        |       |      |        |        |         |      |
| A. <u>Satiated-single daily feeding</u> (exp. 5, 6, 7, and 8) |        |        |        |       |      |        |        |         |      |
| 83  | 0.35   | -0.57  | -0.44  | -0.49 | 0.69 | 0.83   | 0.02*  | 0.50    | 0.87 |
| B. <u>Satiated-double daily feeding</u> (exp. 9c)             |        |        |        |       |      |        |        |         |      |
| 9   | 0.86   | -0.86  | -0.68  | -0.67 | 0.91 | 0.98   | -0.75  | -0.27*  | 0.74 |
| C. <u>Reduced-single daily feeding</u> (exp. 9d)              |        |        |        |       |      |        |        |         |      |
| 8   | 0.91   | -0.84  | 0.20*  | -0.76 | 0.92 | 0.99   | -0.69* | -0.63*  | 0.98 |
| D. <u>Reduced-half daily feeding</u> (exp. 12)                |        |        |        |       |      |        |        |         |      |
| 8   | 0.46*  | -0.78  | -0.58* | -0.82 | 0.89 | 0.75   | -0.57* | -0.11*  | 0.94 |

\* statistically insignificant:  $p(D) > 0.05$

Symbols indicate:

Wm : average mean body weight of a fish in a group

WGm : average absolute growth rate of a fish in a group

Gm : average instantaneous growth rate of a fish in a group

Cm : average amount of food consumed by a fish in a group

RCm : average food consumption rate of a fish in a group

Fm : average food conversion rate of a fish in a group

Experiments 1, 2, 3, and 4 were excluded because of no size-sorting.

Table 9. Summary of correlation analysis between individuals in each experiment (correlation between mean body weight (W), growth rates (WG and G), estimated food consumption rate (RCest), estimated amount of food consumed (Cest), and estimated food food conversion rate (Fest).

| number<br>of<br>exp.                                     | W vs.  |        |        |        |       | RCest vs. |      | Cest vs. |        |
|--|--------|--------|--------|--------|-------|-----------|------|----------|--------|
|  | WG     | G      | Fc     | RCest  | Cest  | WG        | G    | WG       | G      |
| <u>I. Starvation Experiments</u>                         |        |        |        |        |       |           |      |          |        |
| 9a (66) **   | -0.84  | 0.75   | -      | -      | -     | -         | -    | -        | -      |
| 10a (70)   | -0.87  | 0.69   | -      | -      | -     | -         | -    | -        | -      |
| 11 (76)  | -0.58  | 0.58   | -      | -      | -     | -         | -    | -        | -      |
| <u>II. Natural Diet Experiments (Satiated feeding)</u>   |        |        |        |        |       |           |      |          |        |
| <u>A. Single daily feeding (no size-sorted)</u>          |        |        |        |        |       |           |      |          |        |
| 1 (75)   | 0.78   | 0.47   | 0.59   | 0.26   | 0.88  | 0.72      | 0.97 | 0.95     | 0.78   |
| 2 (74)   | 0.53   | -0.01* | 0.23*  | -0.29  | 0.77  | 0.56      | 0.96 | 0.95     | 0.56   |
| 3 (74)   | -0.33  | -0.60  | -0.55  | -0.68  | 0.09* | 0.82      | 0.99 | 0.91     | 0.64   |
| <u>B. Double daily feeding (size-sorted)</u>             |        |        |        |        |       |           |      |          |        |
| 9b (53)  | 0.52   | -0.07* | -0.40  | 0.15*  | 0.81  | 0.88      | 0.95 | 0.91     | 0.46   |
| 10b (54)   | 0.40   | 0.10*  | 0.08*  | 0.09*  | 0.69  | 0.86      | 0.92 | 0.92     | 0.67   |
| <u>III. Commercial Diet Experiments (size-sorted***)</u> |        |        |        |        |       |           |      |          |        |
| <u>A. Satiated-single daily feeding</u>                  |        |        |        |        |       |           |      |          |        |
| 5 (180)  | 0.65   | -0.42  | -0.65  | 0.11*  | 0.89  | 0.74      | 0.68 | 0.88     | -0.07* |
| 6 (177)  | 0.36   | -0.45  | -0.30  | -0.40  | 0.68  | 0.52      | 0.91 | 0.85     | 0.25   |
| 7 (187)  | 0.25   | -0.27  | -0.33  | -0.17  | 0.58  | 0.86      | 0.96 | 0.91     | 0.54   |
| 8 (186)  | 0.57   | 0.05*  | 0.11*  | -0.11* | 0.75  | 0.75      | 0.96 | 0.95     | 0.64   |
| <u>B. Satiated-double daily feeding</u>                  |        |        |        |        |       |           |      |          |        |
| 9c (70)  | 0.72   | -0.50  | -0.43  | -0.38  | 0.83  | 0.19*     | 0.91 | 0.97     | -0.20* |
| 10c (59)   | -0.12* | -0.65  | -0.72  | -0.51  | 0.52  | 0.75      | 0.84 | 0.74     | -0.06* |
| <u>C. Reduced-single daily feeding</u>                   |        |        |        |        |       |           |      |          |        |
| 9d (65)  | 0.67   | -0.29* | 0.23*  | -0.43  | 0.78  | 0.19*     | 0.96 | 0.97     | 0.19*  |
| 10d (59)   | -0.23* | -0.52  | -0.62  | -0.40  | 0.29  | 0.85      | 0.85 | 0.80     | 0.33   |
| <u>D. Reduced-half daily feeding</u>                     |        |        |        |        |       |           |      |          |        |
| 12 (56)  | 0.24*  | -0.25* | -0.11* | -0.31  | 0.55  | 0.69      | 0.98 | 0.92     | 0.48   |
| <u>E. Reduced-single daily feeding (no size-sorting)</u> |        |        |        |        |       |           |      |          |        |
| 4 (103)  | 0.25   | -0.14  | 0.03*  | -0.24  | 0.45  | 0.78      | 0.99 | 0.98     | 0.74   |

\* statistically insignificant:  $p(D) > 0.05$

\*\* Numbers in parenthesis are number of fish in each experiment

\*\*\* Size-sorting of fish was applied to all except for experiment 4.

Table 10. Summary of correlation analysis between individuals in each feeding condition (correlation between mean body weight (W), growth rates (WG and G), estimated food consumption rate (RCest), estimated amount of food consumed (Cest), and estimated food food conversion rate (Fest).

| number<br>of<br>fish   | W vs. |        |        |       |      | RCest vs. |      | Cest vs. |        |
|--|-------|--------|--------|-------|------|-----------|------|----------|--------|
|  | WG    | G      | Fc     | RCest | Cest | WG        | G    | WG       | G      |
| <u>I. Starvation Experiments</u>                                       |       |        |        |       |      |           |      |          |        |
| 212  | -0.79 | 0.64   | -      | -     | -    | -         | -    | -        | -      |
| <u>II. Natural Diet Experiments (Satiated feeding)</u>                 |       |        |        |       |      |           |      |          |        |
| <u>A. Single daily feeding without size-sorting (exp. 1, 2, and 3)</u> |       |        |        |       |      |           |      |          |        |
| 223  | 0.24  | -0.14  | 0.02*  | -0.35 | 0.56 | 0.71      | 0.96 | 0.93     | 0.62   |
| <u>B. Double daily feeding with size-sorting (exp. 9b)</u>             |       |        |        |       |      |           |      |          |        |
| 53   | 0.52  | -0.07* | -0.40  | 0.15* | 0.81 | 0.88      | 0.95 | 0.91     | 0.46   |
| <u>III. Commercial Diet Experiments (size-sorted**)</u>                |       |        |        |       |      |           |      |          |        |
| <u>A. Satiated-single daily feeding (exp. 5, 6, 7, and 8)</u>          |       |        |        |       |      |           |      |          |        |
| 730  | 0.32  | -0.40  | -0.31  | -0.31 | 0.61 | 0.70      | 0.91 | 0.89     | 0.34   |
| <u>B. Satiated-double daily feeding (exp. 9c)</u>                      |       |        |        |       |      |           |      |          |        |
| 70   | 0.72  | -0.50  | -0.43  | -0.38 | 0.83 | 0.19*     | 0.91 | 0.97     | -0.20* |
| <u>C. Reduced-single daily feeding (exp. 9d)</u>                       |       |        |        |       |      |           |      |          |        |
| 65   | 0.67  | -0.29* | 0.23*  | -0.43 | 0.78 | 0.19*     | 0.96 | 0.97     | 0.19*  |
| <u>D. Reduced-half daily feeding (exp. 12)</u>                         |       |        |        |       |      |           |      |          |        |
| 56   | 0.24* | -0.25* | -0.11* | -0.31 | 0.55 | 0.69      | 0.98 | 0.92     | 0.48   |
| <u>E. Reduced-single daily feeding with no size-sorting (exp. 4)</u>   |       |        |        |       |      |           |      |          |        |
| 103  | 0.25  | -0.14  | 0.03*  | -0.24 | 0.45 | 0.78      | 0.99 | 0.98     | 0.74   |

\* statistically insignificant:  $p(0) > 0.05$

\*\* Size-sorting of fish was applied to all except for experiment 4.

Symbols indicate;

W : mean body weight of a fish

WG : absolute growth rate of a fish

G : instantaneous growth rate of a fish

RCest : estimated food consumption rate of a fish (see eq. 11)

Cest : estimated amount of food consumed of a fish (see eq. 10)

Fest : estimated food conversion rate of a fish



starved fish weighing 11.2 - 295.2 g typically showed negative absolute growth rates (WG, positive weight loss) in a range from -1.22 to -0.1 g/day. The range of the average absolute and instantaneous growth rates (WGm and Gm) and the average mean body weight of fish of each experiment were -0.64 - -0.40 g/day, -0.46 - -0.44 % of body weight/day. and 105.7 - 154.0 g respectively. Among various feeding conditions, starved fish showed the minimum variation in growth rates between individuals having similar weights (see Figure 2).

The absolute growth rate (g/day) of individuals decreased as the weight of the fish increased in each starvation experiment ( $r(WG-W) = -0.87$  -  $-0.58$ ,  $p(D) < 0.01$ ) while the instantaneous growth rate (% of body weight/day) increased as the weight of the fish increased ( $r(G-W) = 0.58$  -  $0.75$ ,  $p(D) < 0.01$ ) (see Table 9). The correlation coefficients, -0.79 and 0.64 was respectively obtained for weight-specific absolute and instantaneous growth (WG-W and G-W) from 212 individuals (see Table 10 and Figure 2).

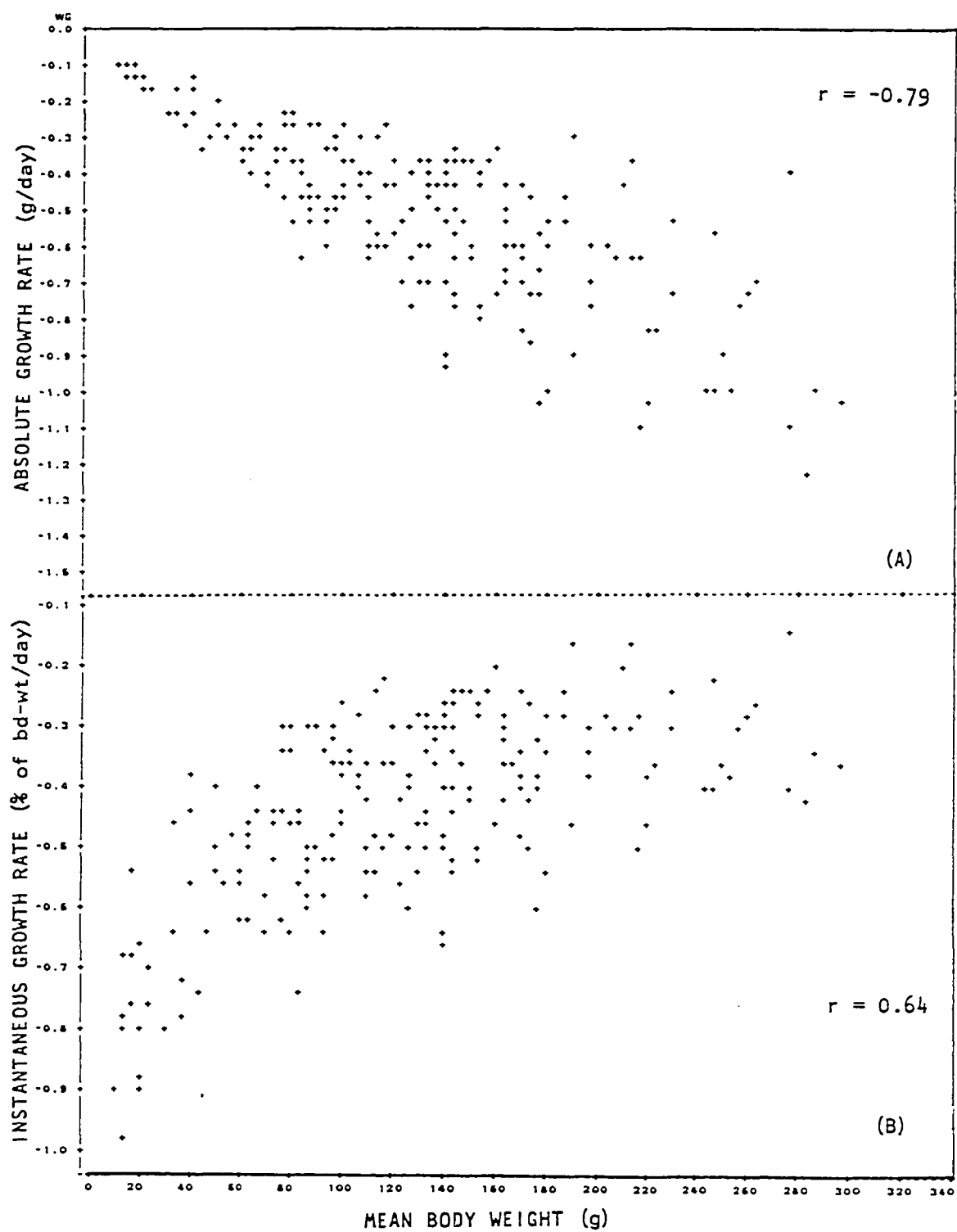
## 2) Weight-specific growth in natural diet experiments

The fish fed the natural diet at satiation feeding level ( $n=330$ ) had a large variation in the absolute and the instantaneous growth rates (WG = -0.61 - 1.63 g/day and G = -0.57 - 1.90 % of body weight/day) (see Figure 3). The weight range of the fish ( $W=18.7$  - 278.5 g) was similar to that of the starved individuals ( $W=11.2$  - 295.2 g).

In the three experiments (experiment 1, 2, and 3) where no size-sorting was performed, poor average absolute and instantaneous growth rates (WGm = 0.24 - 0.29 g/day and Gm = 0.32 - 0.45 % of body weight/day) were found in each experiment despite the high feeding levels (RCm = 3.9 -

Figure 2.

Growth rates versus mean body weights of all fish in three starvation experiments (n=212): (A) absolute growth rate versus mean body weight (WG vs. W) and (B) instantaneous growth rate versus mean body weight (G vs. W) ('r' = correlation coefficient).



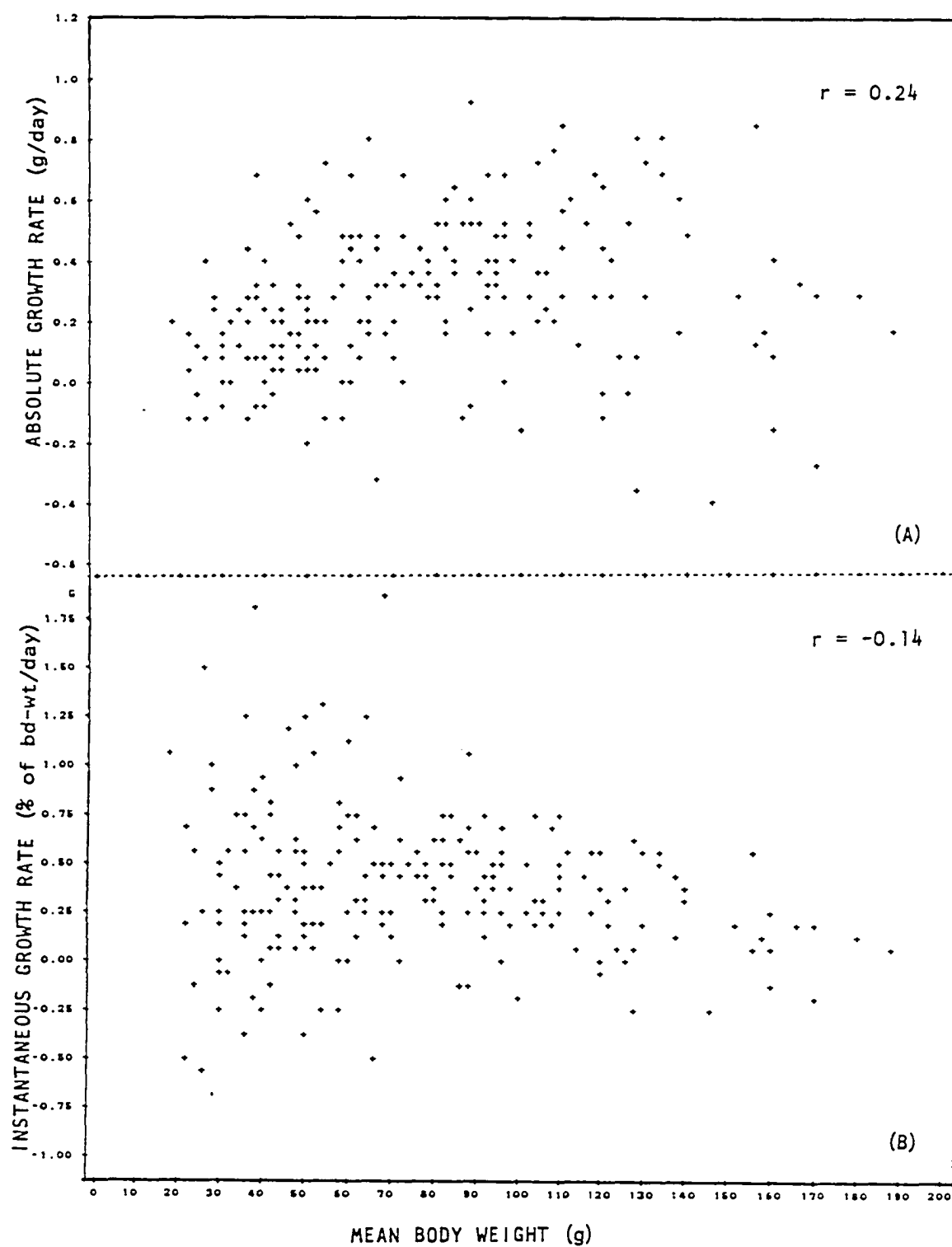
5.1 % of body weight/day). As shown in Table 9, the absolute growth rate of the fish in Experiments 1 and 2 showed positive correlation with mean body weight ( $r(WG-W)=0.78$  and  $0.52$ ,  $p(D)<0.01$ ), which indicated that the weight-specific absolute growth pattern was normal: WG increased as W increased. However, poor and abnormal weight-specific instantaneous growth patterns were found in the two experiments ( $r(G-W)=0.47$ ,  $p(D)<0.01$  and  $-0.01$ ,  $p(D)>0.1$ ). The small fish did not grow faster than the large fish in terms of percent of body weight resulting in the poor or insignificant G-W correlation. An abnormal and reverse pattern of correlation was found between growth and weight of fish in experiment 3 ( $r(WG-W)=-0.33$  and  $r(G-W)=-0.60$ ) where many large fish grew less than the small fish in terms of absolute growth rate (WG, g/day). The correlation coefficients obtained from all individuals in this feeding condition ( $n=223$ ) were poor but significant for WG-W relation ( $r=0.24$ ,  $p(D)<0.05$ ) and G-W relation ( $r=-0.14$ ,  $p(D)<0.05$ ) as shown in Figure 3.

In experiment 9b where size-sorting was performed, the average growth rates of fish (WG=0.79 g/day and G=0.60 % of body weight per day,  $n=53$ ) were significantly higher than those found in the rest of the natural diet experiments ( $p(T)<0.05$ ) (see Table 3). The pattern of weight-specific absolute growth was typical in experiment 9b ( $r(WG-W)=0.52$ ,  $p(D)<0.01$ ) but insignificant relation was found in the weight-specific instantaneous growth rate ( $r(G-W)=-0.07$ ,  $p(D)>0.05$ ,  $n=53$ ).

The correlation coefficients obtained between group mean body weights and average growth rates of groups were insignificant ( $r(WGm-Wm)=0.63$ ,  $r(Gm-Wm)=-0.31$ ,  $n=7$ ,  $p(D)>0.05$ ). This was caused by low growth rates of the fish in the smallest size class (0.34 % of body weight/day)

Figure 3.

Growth rates versus mean body weights of fish in experiment 1, 2, and 3 (n=223, no size-sorted and satiated natural diet feeding): (A) absolute growth rate versus mean body weight, and (B) instantaneous growth rate versus mean body weight ('r'= correlation coefficient).



(see Figure 6). When this group was not counted, the rest of the size groups of the fish showed the high correlations in weight-specific growth pattern ( $r(WGm-Wm)=0.89$ ,  $r(Gm-Wm)=0.96$ ,  $n=6$ ,  $p(D)<0.05$ ).

In experiment 10b of which the condition was similar to experiment 9b, low absolute growth rates (average 0.25 g/day) were recorded from the most individuals despite size sorting and twice satiated daily feeding. Poor feeding response was observed in all size groups resulting in the lowest food consumption rate ( $RCm=1.90\%$  of body weight/day) among the experiments applying the natural diet (see Table 4). The groups of the fish consuming less than 2 % of body weight per day revealed extremely low instantaneous growth rate ( $Gm=0.0 - 0.19\%$  of body weight/day) regardless of the weight. Poor and insignificant correlations between growth rates and weights were found for individuals ( $r(WG-W)=0.40$ ,  $p(D)<0.05$  and  $r(G-W)=0.1$ ,  $p(D)>0.05$ ) and for groups ( $r(WGm-Wm)=0.73$ ,  $p(D)>0.05$ ,  $r(Gm-Wm)=0.28$ ,  $p(D)>0.05$ ,  $n=7$ ) with large variation of growth rates of individuals in the same weight range.

### 3) Weight-specific growth in the commercial diet experiments

A total of 1161 fish weighing 4.3 - 293.6 g were used in the commercial feeding experiments. They showed larger variation in their growth rates ( $WG=-0.69 - 2.89$  g/day, and  $G=-0.74 - 3.39\%$  of body weight) than those found in natural diet or starvation experiments.

Among 10 commercial diet feeding experiments, satiated feeding was performed in six experiments (experiments 5, 6, 7, 8, 9c and 10c) and reduced feeding was applied for the rest of the experiments (experiments 4, 12, 9d, and 10d). The average mean body weight of fish in each experiment was similar in a range of 99.0 - 133.0 g except for experiment

4 (average  $W=63.6\text{g}$ ) where no size-sorting was performed. The average body weight of all individuals in each feeding condition was also similar in a range of  $103.9 - 124.2\text{ g}$  except for experiment 4 (see Table 5).

In the four experiments where the fish were fed at satiated level with single feeding frequency (experiments 5, 6, 7, and 8), the average absolute and instantaneous growth rates in each experiment varied ( $WG=0.77 - 1.05\text{ g/day}$  and  $G=0.58 - 1.25\%$  of body weight/day) but they were mostly much higher than those observed in the natural diet-satiated feeding experiments. The highest average absolute and instantaneous growth rates were recorded in experiment 5 despite the smallest average mean body weight ( $WG=1.05\text{ g/day}$ ,  $G=1.25\%$  of body weight/day,  $W=89.7\text{ g}$ ,  $n=180$ ) among the four experiments. The fish in experiment 8 where average food consumption rate was  $0.9\%$  of body weight/day showed the lowest growth rates among the four experiments ( $WG=0.77\text{ g/day}$ ,  $G=0.58\%$  of body weight/day).

The variation of growth rates between individuals having similar weights was large in each experiment and weakened the correlation between individual growth rates and mean body weights (see Table 9). Fish having weight loss ( $n=8$ ) were also found in three of the four experiments. The highest correlation in  $GW-G$  relation ( $r=0.65$ ) and  $G-W$  relation ( $r=-0.42$ ) were found from 180 individuals in experiment 5. The other three experiments showed poor but significant correlation in  $WG-W$  relation ( $r=0.25 - 0.57$ ,  $p(D)<0.05$ ) and  $G-W$  relation ( $r=-0.45 - -0.27$ ,  $p(D)<0.05$ ) except for the weight-specific instantaneous growth in experiment 8 ( $r(G-W)=0.05$ ,  $p(D)>0.05$ ).

The correlations between individual growth rates and mean body

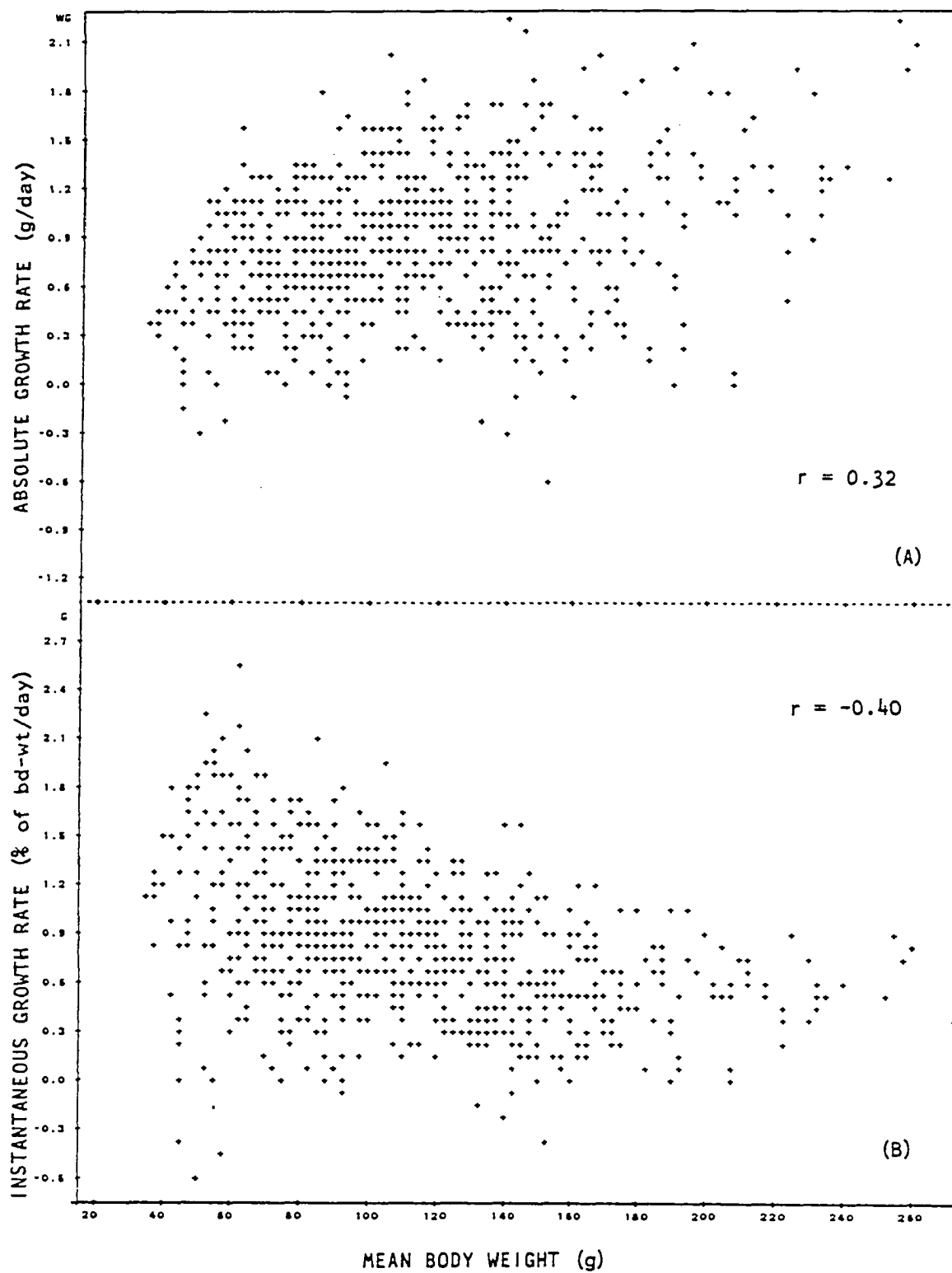


weights obtained in this feeding condition was weak but significant ( $r(WG-W)=0.32$ ,  $r(G-W)=-0.40$ ,  $p(D)<0.05$ ,  $n=730$ ) (see Figure 4 and Table 10). The slow and some negative growth of the fish in small size groups of experiment 7 and 8 resulted in weak G-W correlation while low growth rates of large fish in experiment 6 and 8 resulted in poor WG-W correlation. The variation of food consumption rates between experiments (average  $RCm=0.5 - 1.9$  % of body weight/day, and average  $Cm=1.0 - 1.5$  g/day) and between groups ( $RCm=0.5 - 1.9$  % of body weight/day,  $Cm=0.3 - 2.7$  g/day) in each experiment also influenced the weight-specific growth pattern in this feeding condition.

In each experiment weight-specific growth pattern was more clearly reflected in correlation between average group growth rates and average group mean body weights than those obtained between individual growth rates and mean body weights. Highly positive and significant correlations were found between the average instantaneous growth rates of groups and the average body weights of groups in three of the four experiments ( $r(Gm-Wm)=-0.65 - -0.88$ ). Highly significant and positive correlations were also found between average absolute growth rates ( $WGm$ ) and average group mean body weights ( $Wm$ ) in experiment 5 ( $r=0.94$ ) and experiment 8 ( $r=0.76$ ) (see Table 7). For all groups of fish in the feeding condition ( $n=83$ ) the correlation coefficients found in  $WGm-Wm$  and  $Gm-Wm$  relations were as low as 0.35 and -0.57 respectively ( $n=83$ ) and were similar to those found at individual comparison ( $n=800$ ). Different food consumption rates between experiments significantly resulted in the variation of magnitude of growth rate in the same feeding condition ( $p(T)<0.05$ , see Table 7) and also reduced the weight-specific growth correlation.

Figure 4.

Growth rates versus mean body weights of fish in experiment 5, 6, 7, and 8 (n=730, size-sorted and satiated-single daily commercial diet feeding): (A) absolute growth rate versus mean body weight, and (B) instantaneous growth rate versus mean body weight ('r'= correlation coefficient).



The fish in two experiments (experiment 9c and 10c) were fed twice daily at satiation feeding levels. The average growth rates in experiment 9c ( $WG=1.25$  g/day,  $G=1.16$  % of body weight/day,  $n=70$ ) were similar to those obtained from the experiments applied satiated-single daily feeding frequency. The weight-specific growth pattern was well reflected in the correlation coefficients obtained between groups ( $r(WG-Wm)=0.86$ ,  $r(Gm-Wm)=-0.86$ ) and between individuals ( $r(WG-W)=0.72$ ,  $r(G-W)=-0.50$ ,  $n=70$ ).

The fish tested in the four reduced feeding experiments (experiments 4, 9d, 10d and 12) showed the irregular patterns in magnitude of growth and weight-specific growth relation. Individual growth rates extremely varied in each experiment and the differences of average growth rate between experiments were also large (average  $WG=0.0 - 0.84$  g/day, average  $G=0.09 - 0.86$  % of body weight/day). In experiment 9d and 4 the average absolute and instantaneous growth rates ( $WG=0.84$  g/day,  $G=0.76$  % of body weight/day) were as high as those observed in satiation feeding experiments while the lowest average absolute and instantaneous growth rates were recorded in experiment 12 ( $WG=0.36$  g/day,  $G=0.42$  % of body weight,  $n=54$ ) despite the same average food consumption rates of fish in the two experiments ( $RCm=0.8$  % of body weight/day). In experiment 4 where fish were fed daily 1.0 % of body weight without size-sorting, the average instantaneous growth rate ( $G=0.86$  % of body weight/day) was higher than some of those found in satiated feeding experiments. However, the average mean body weight of the fish in the experiment was much smaller (average  $W=63.6$  g) than those observed in the satiated feeding experiments (average  $W=89.7 - 133.9$  g).

The patterns of weight-specific growth of fish in the reduced

commercial diet feeding experiments were different between experiments but, generally, poor correlations were found in WG-W and G-W relationships. In experiment 9d where reduced single daily feeding was applied, the correlation found between absolute growth rate and weight was weak but significant ( $r(WG-W)=0.67$ ,  $p(D)<0.05$ ) while insignificant G-W relation ( $r=-0.29$ ,  $p(D)>0.05$ ) was found. In contrast, highly significant weight-specific growth patterns ( $r(WGm-Wm)=0.91$ ,  $r(Gm-Wm)=-0.84$ ,  $n=8$ ) were found in correlations between growth rates and weight for groups of fish in the same experiment. This indicated that the variation of growth between individuals in a group was large and reduced the weight-growth correlation between individuals. No significant weight-growth correlation was found between groups in experiments 10d and 12.

#### Food-Specific Growth Pattern

Through feeding experiments, one of two types of diets (commercial and natural diets) was used in each experiment and group feeding was applied to groups of fish instead of individual feeding. In five natural diet feeding experiments where fish were fed at satiated level with single or double daily feeding frequency, the average food consumption rate (RCm) ranged from 1.9 to 5.1 % of body weight/day in each experiment. In commercial diet feeding experiments where satiated and reduced feeding level were performed, the average food consumption rates were much lower than those recorded in the natural diet feeding experiments (0.6 - 1.5 % of body weight/day).

The variation of average food consumption rates (Cm and RCm) between groups in each experiment where fish were sorted into groups by size

(experiment 9b) was also larger in natural diet feeding experiments ( $C_m=0.8 - 5.2$  g/day,  $RC_m=1.5 - 3.1$  % of body weight/day) (see Table 4). The average amounts of food consumed by groups of fish ( $C_m$ ) in the natural diet feeding experiments showed the same tendency as food consumption rate ( $RC_m$ ) in a range of  $0.8 - 5.2$  g/day.

The results obtained from 8 feeding experiments where group sorting was applied (experiments 5, 6, 7, 8, 9b, 9c, 9d, and 12) indicated that the growth of fish was strongly affected by food consumption regardless of food types (see Table 7, Figures 5 and 6). The correlation in  $G_m$ - $C_m$  (the average amounts of food consumed by groups of fish vs. the average absolute growth rates of groups) of each experiment showed the highly significant and positive correlation in all experiments ( $r=0.70 - 0.99$ ,  $p(D)<0.01$ ). Average food consumption rates of groups ( $RC_m$ ) also showed the highly significant and positive correlation to average instantaneous growth rates of groups ( $G_m$ ) in each experiment ( $r(RC_m-G_m)=0.74 - 0.98$ ,  $p(D)<0.01$ ) except for experiment 5.

Highly significant and positive correlations also occurred between food consumption rate and growth rates in each feeding condition as shown in Table 8. The highest values of correlations coefficients in  $RC_m$ - $WG_m$  and  $C_m$ - $WG_m$  relations were found in experiment 9d where reduced commercial diet feeding was performed to eight groups of fish ( $r(C_m-WG_m)=0.99$ ,  $r(RC_m-G_m)=0.98$ ,  $p(D)<0.01$ ). The groups of fish in other feeding conditions also showed highly significant and positive correlations in  $WG_m$ - $C_m$  ( $r=0.75 - 0.98$ ) and  $RC_m$ - $G_m$  relationships ( $r=0.74 - 0.94$ ).

On the other hand, insignificant correlations were found from  $C_m$ - $G_m$  relationships in the seven experiments and from  $RC_m$ - $WG_m$  relationships in

Figure 5.

Average group growth rates versus food consumption rates of groups of fish in experiment 9b (n=7): (A) average group absolute growth rate versus amount of food consumed by group (WGm vs. Cm), and (B) average group instantaneous growth rate versus group food consumption rate (Gm vs. RCm) ('r'=correlation coefficient).

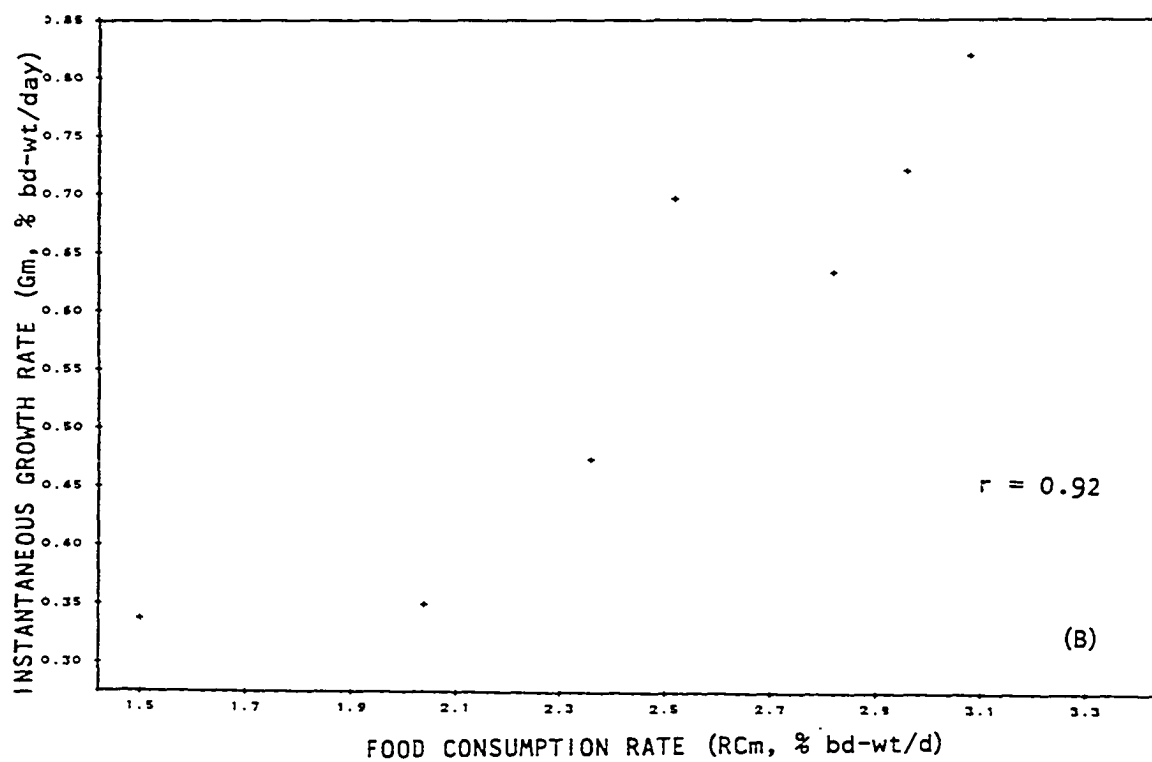
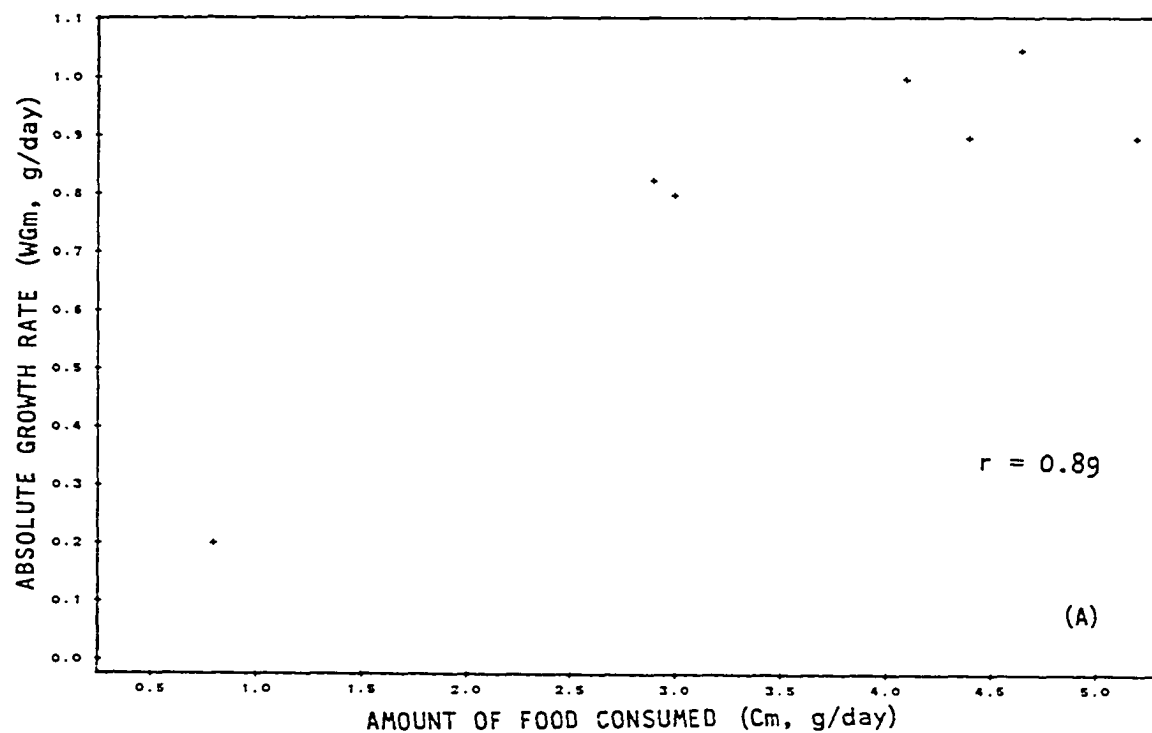
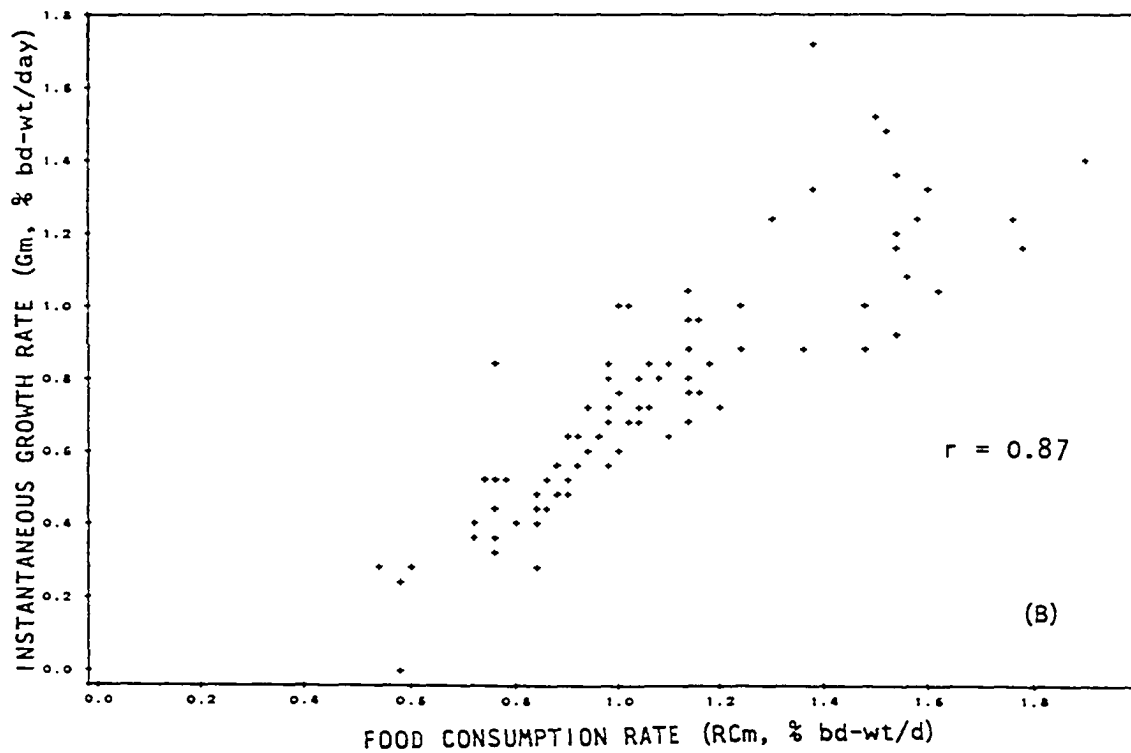
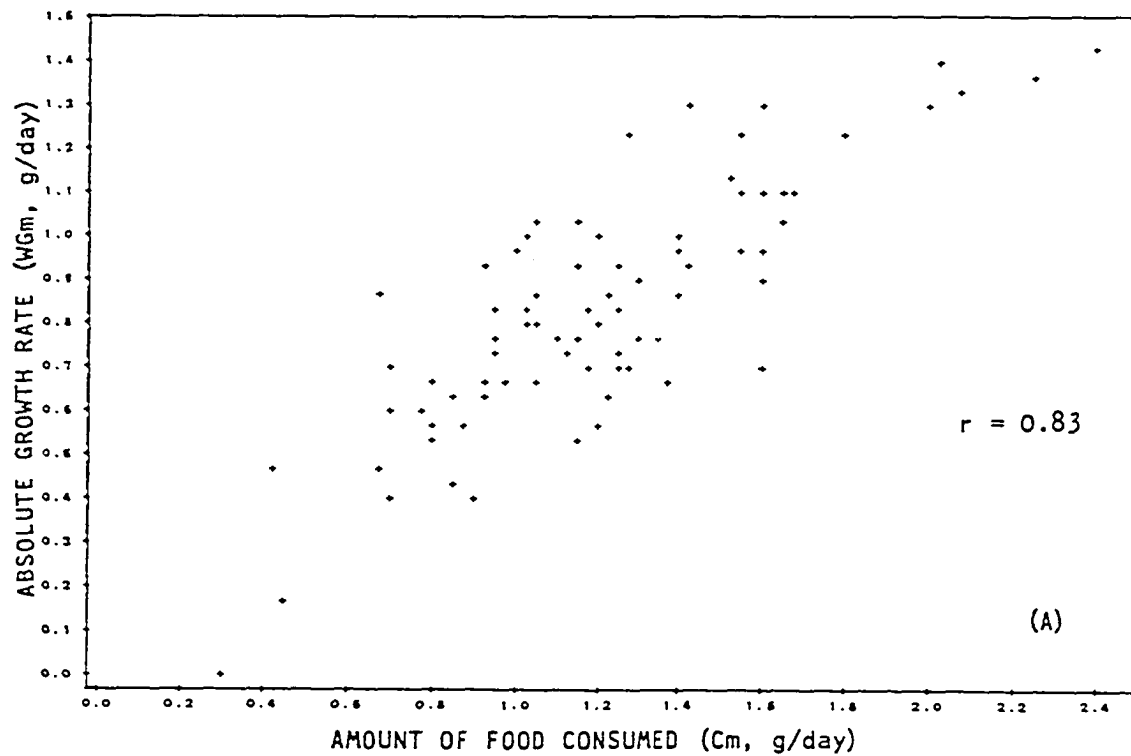




Figure 6.

Average group growth rates versus group food consumption rates in experiments 5, 6, 7, and 8 ( $n=83$ ): (A) average group absolute growth rate versus amount of food consumed by the group ( $WG_m$  vs.  $C_m$ ), and (B) average group instantaneous growth rate versus group food consumption rate ( $G_m$  vs.  $RC_m$ ) ( $r$ =correlation coefficient).



the eight of 11 feeding experiments (including experiments 10b, 10c, and 10d: see Table 7). Significant and negative correlations were found between average amounts of food consumed ( $C_m$ ) and average instantaneous growth rates of groups ( $G_m$ ) in the three commercial diet-satiated feeding experiments (experiments 5, 9c, and 10c). Significant and positive correlations were found between  $RC_m$  and  $WG_m$  in the three of 11 experiments (experiments 9b, 7, and 8) where feeding conditions were not the same.

When food-specific growth pattern was considered for all groups of fish in each feeding condition, only one significant  $C_m$ - $G_m$  correlation was found in the satiated-double frequency commercial diet feeding condition (experiment 9c,  $r=-0.75$ ,  $n=9$ ,  $p(D)<0.05$ ). A positive correlation in  $WG_m$ - $RC_m$  was found from satiated natural diet feeding (experiment 9b,  $r=0.76$ ,  $n=7$ ,  $p(D)<0.05$ ) and satiated commercial diet-single feeding experiments (experiments 5, 6, 7, and 8,  $r=0.50$ ,  $n=83$ ,  $p(D)<0.05$ ) (see Table 8).

Overall feeding experiments indicated that the magnitude of growth was affected by food type and feeding level, resulting in the growth differentiation of fish between feeding conditions but the pattern of food consumption-specific growth was similar between experiments or between feeding conditions: (1) average absolute growth rate of a group of fish ( $WG_m$ ) increased as the average amount of food consumed by the group ( $C_m$ ) increased, (2) average group food consumption rate ( $RC_m$ ) positively affected to average instantaneous growth rate of the group ( $G_m$ ), and (3) no uniform pattern was found between experiments or feeding conditions in  $RC_m$ - $WG_m$  and  $C_m$ - $G_m$  relationships.

#### Effects of Diets on Pattern and Magnitude of Growth

### 1) Growth pattern in relation to diet type

Through all experiments some typical patterns were found in the relationships between the growth rates, feeding condition and weight of the fish regardless of diet type. As food was provided to fish, the magnitude of growth generally increased but the variation of growth between individuals or groups having the same weights also increased resulting in complex growth pattern affected by both weight and food.

Regardless of diet type, positive correlation coefficients were commonly found between absolute growth rates and weights ( $WG-W$  or  $WGm-Wm$ ) of the fed fish in most experiments while negative correlation coefficients were found in the correlations in the starvation experiments. This indicated that positive absolute growth rate (g/day) increased as the weight of fish increased and the absolute rate of weight loss (g/day) of starved fish increased as the weight of fish increased. An inverse relationships were found between instantaneous growth rates (% of body weight/day) and mean body weights ( $G-W$  or  $Gm-Wm$ ). The weight gain in percent of body weight per day decreased as the weight of fish increased, and the weight loss of fish in percent of body weight per day also decreased as the weight of fish increased.

Food consumption rates ( $RCm$ ) were also significantly and positively related to instantaneous growth rates ( $Gm$ ) in both diet types indicating that increased food consumption rate resulted in the increment of instantaneous growth rate. Highly significant and positive correlations obtained between the average amounts of food consumed by groups of fish ( $Cm$ ) and the average absolute growth rates of the groups of fish ( $WGm$ ) showed that absolute growth rate increased as the amount of food consumed

by fish increased (see Tables 7 and 8).

The patterns of the relationships between the growth rates, the weight of the fish, and the food consumption rates found in all experiments indicated that all experiments showed similar general tendencies in the relationships between growth and applied conditions regardless of food type but a few exceptions also existed depending on experiments.

## 2) Magnitude of growth and food consumption in relation to diet type

Magnitude of growth and food consumption of fish showed large difference between two diet types. The averages of food consumption rates (RCm) and the amounts of food consumed (Cm) of the groups of fish in satiated natural diet feeding (RCm=3.1 % of body weight/day, Cm=3.5 g/day, n=10) were significantly different from the groups of fish fed the commercial diet at satiated level (RCm=1.1 % of body weight/day, Cm=1.2 g/day, n=92) ( $p(T) < 0.05$ ). Comparing the average food consumption rates (RCm), the groups of fish fed the natural diet consumed more food than those fed the commercial diet by a factor of 2.8 in satiated feeding. The average amount of food consumed by groups (Cm) was also higher in the natural diet feeding by a factor of 2.9 than those in the commercial diet.

When the growth rates of individuals fed at satiation level were compared in two diets, the average individual absolute and instantaneous growth rates of fish fed the natural diet (n=276) were 0.37 g/day and 0.42 % of body weight/day respectively while the corresponding values for the commercial diet (n=800) were 0.90 g/day and 0.88 % of body weight/day (see Figure 5 and 6). The fish fed the commercial diet at satiated level showed significantly larger growth rates than the fish fed the natural

diet by a factor of 2.1 for instantaneous growth rate and 2.4 for absolute growth rate ( $p(T) < 0.05$ ).

In experiments 9b and 9c similar rearing conditions were applied in both experiments except for the type of diet: (1) the size groups were duplicated, (2) satiated-double feeding levels were applied, and (3) the average growth rates of fish were the highest among the observed growth rates in each diet feeding experiments.

Despite the similarity in applied conditions except for the diets, large difference was found in magnitude of growth rates as well as food consumption rate between the two experiments (see Appendix C, Figure 7 and 8). In the commercial diet-satiated feeding (experiment 9c) 1.32 g/day of the average absolute growth rate was obtained from 70 fish ( $RC_m = 1.5\%$  of body weight/day) while the average absolute growth rate, 0.79 g/day was found from 53 individuals fed the natural diet at satiation level ( $RC_m = 2.5\%$  of body weight/day) (see Table 3). The difference of the average individual growth rates of fish between two diet experiments (experiments 9b and 9c) was significant ( $p(T) < 0.01$ ). Comparing the results obtained from the two experiments, the fish fed the commercial diet obtained more weight gains than the fish fed the natural diet by a factor of 1.9 for the instantaneous growth rate and 1.5 for the absolute growth rate.

Food consumption of fish also differed significantly between the two experiments where satiated-double feeding frequency was applied ( $C_m = 3.6$  g/day,  $RC_m = 2.5\%$  of body weight/day for the natural diet and 1.6 g/day,  $RC_m = 1.5\%$  of body weight/day for the commercial diet respectively) ( $p(T) < 0.01$ ). Fish involved in the natural diet feeding consumed more food than those fed commercial diet at satiation feeding by a factor of 1.7 for

Figure 7.

Group food consumption rates versus group mean body weights of groups of fish in experiments 9a, 9b, 9c, and 9d (n=28): (A) average amount of food consumed by group versus group mean body weight ( $C_m$  vs.  $W_m$ ), and (B) average group food consumption rate versus group mean body weight ( $RC_m$  vs.  $W_m$ ). Symbols: o (no feeding, experiment 9a), 1 (reduced commercial diet feeding, experiment 9d), 2 (satiated commercial diet feeding, experiment 9c), and 4 (satiated natural diet feeding, experiment 9b).

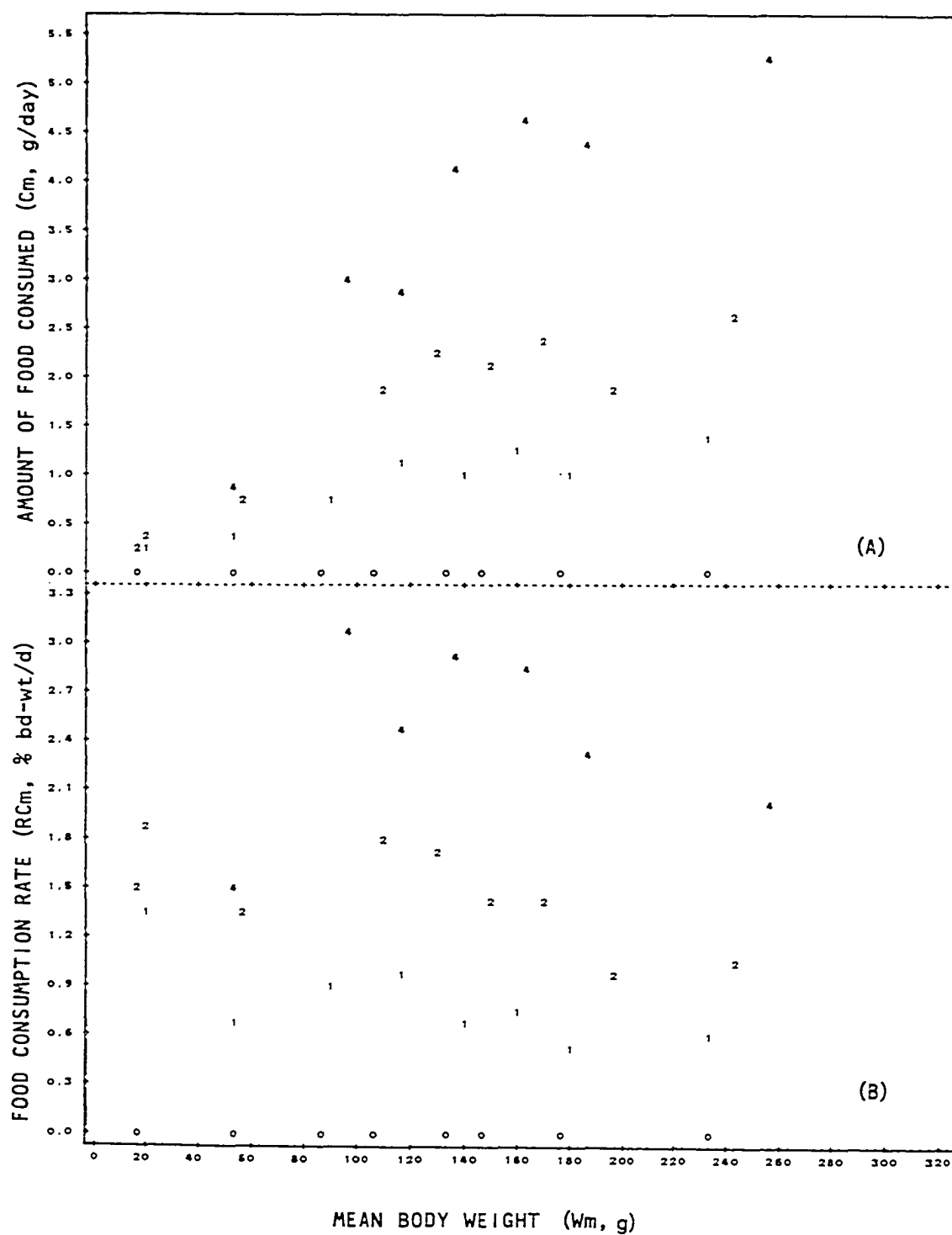
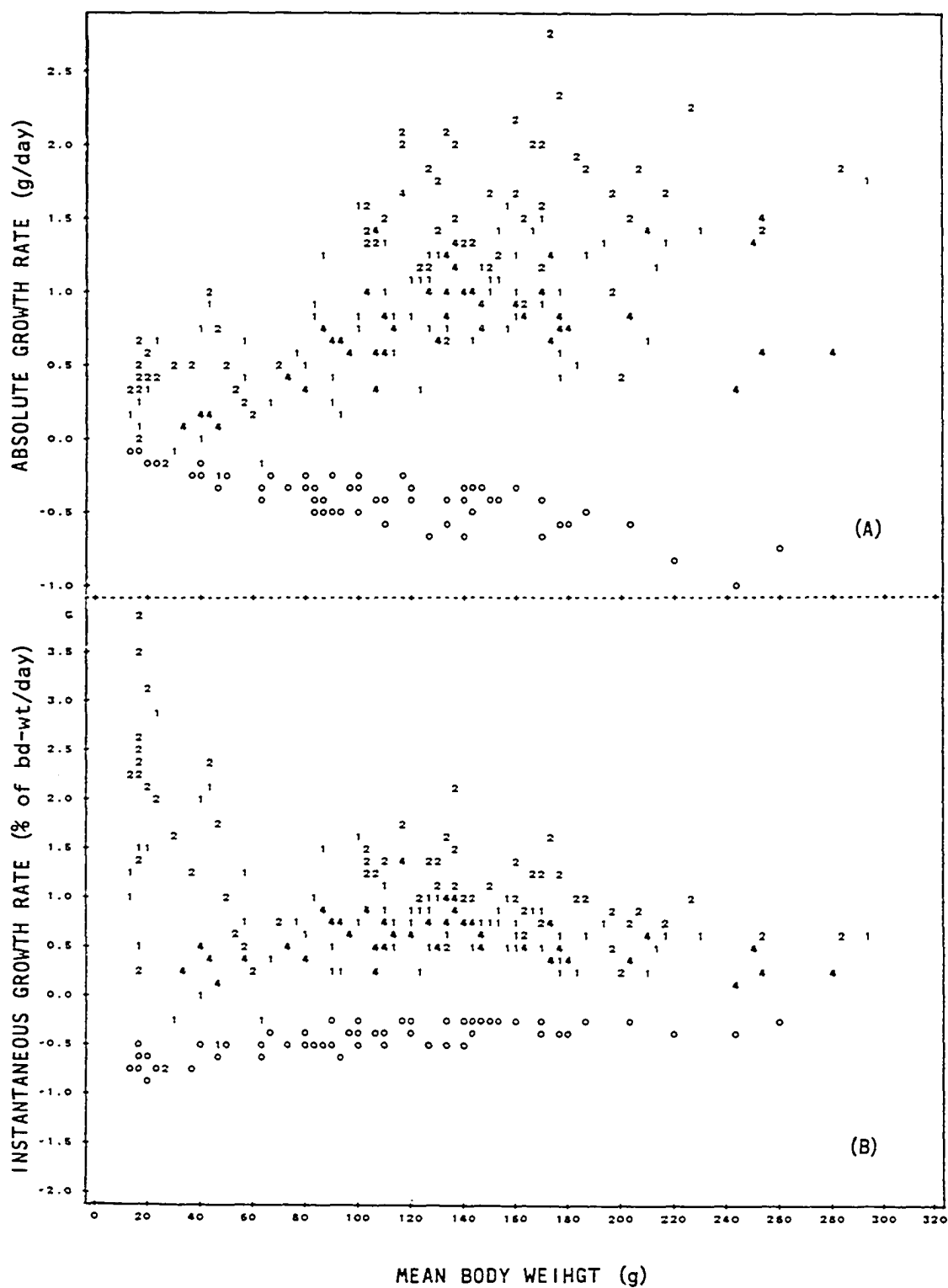




Figure 8.

Growth rates versus mean body weights of individual fish in experiments 9a, 9b, 9c, and 9d: (A) absolute growth rate versus mean body weight ( $WG$  vs.  $W$ ) and (B) instantaneous growth rate versus mean body weight ( $G$  vs.  $W$ ). Symbols:  $\circ$  (no feeding, experiment 9a), 1 (reduced commercial diet feeding, experiment 9d), 2 (satiated commercial diet feeding, experiment 9c), and 4 (satiated natural diet feeding, experiment 9b).



food consumption rate ( $RC_m$ ) and 2.3 for the amount of food consumed ( $C_m$ ). The average food conversion rate of the fish fed the natural diet in experiment 9b ( $F_m=0.23$ ) was much lower than that of the fish fed the commercial diet in experiment 9c ( $F_m=0.83$ ).

Since the culture conditions and the weights of fish were similar between satiated commercial and natural diet feeding experiments or between experiments 9b and 9c, the differences in food consumption rates and growth rates of fish between two experiments were regarded as the effects of diets themselves. The results of the comparison between two diet types at satiated feeding level indicated that the natural diet was significantly inferior to the commercial diet in terms of amounts of food requirement for the resultant growth: the fish fed the natural diet resulted in poor growth rate even in satiation feeding, but consumed more food than the fish fed the commercial diet. When the diets were evaluated at wet-weight base without considering energy contents, the natural diet was regarded to be inferior to the commercial diet in culturing the fish due to (1) low growth rate, (2) low food conversion efficiency (gross growth efficiency), and (3) more food required for growth. If two diets are applied to each size replicate group of fish at the same feeding level, the commercial diet will give much higher growth rate of the fish by a factor of 3 - 7 according to the food conversion rate ( $0.37/3.5$  vs.  $0.90/1.2$  in all satiated feeding experiments and  $0.79/3.6$  vs.  $1.32/1.6$  in experiments 9b and 9c). The averages of growth rates and food consumption of fish in all satiated feeding experiments and experiment 9 are summarized in Table 11.

The results obtained from the former sections showed the

Table 11. Summary of the average growth rates and food consumption of the fish in all satiated feeding experiments and in experiment 9b and 9c.

| specification                                 | natural diet | commercial diet | ratio (C/N) | comparison | p(T)<br>(Ho: C=N) |
|---|--------------|-----------------|-------------|------------|-------------------|
| <u>I. All Satiated Feeding Experiments*</u>   |              |                 |             |            |                   |
| number of fish                                | 276          | 800             | -           | -          | -                 |
| no. of groups                                 | 10           | 92              | -           | -          | -                 |
| average mean body weight (g)                  | 86.9         | 115.1           | 1.3         | N > C      | >0.05             |
| absolute growth rate (WG, g/day)              | 0.37         | 0.90            | 2.4         | N < C      | <0.05             |
| instant. growth rate (G, % bw/d)              | 0.42         | 0.88            | 2.1         | N < C      | <0.01             |
| average food consumption rate (RCm, % bw/day) | 3.1          | 1.1             | 0.36        | N > C      | <0.01             |
| average amount food consumed (Cm, g/day)      | 3.5          | 1.2             | 0.38        | N > C      | <0.01             |
| <hr/>   |              |                 |             |            |                   |
| <u>II. Experiment 9b and 9c</u>               |              |                 |             |            |                   |
| number of fish                                | 53           | 70              | -           | -          | -                 |
| no. of groups                                 | 7            | 8               | -           | -          | -                 |
| average mean body weight (g)                  | 134.6        | 133.9           | 1.0         | N = C      | >0.50             |
| absolute growth rate (WG, g/day)              | 0.79         | 1.32            | 1.7         | N < C      | <0.05             |
| instant. growth rate (G, % bw/d)              | 0.60         | 1.16            | 1.9         | N < C      | <0.01             |
| food comsum. rate (RCm, % bw/day)             | 2.5          | 1.5             | 0.59        | N > C      | <0.01             |
| amount of food consum. (Cm, g/d)              | 3.6          | 1.6             | 0.43        | N > C      | <0.01             |

\* Experiment 1, 2, 3, 5, 6, 7, 8, 9b, and 9c.

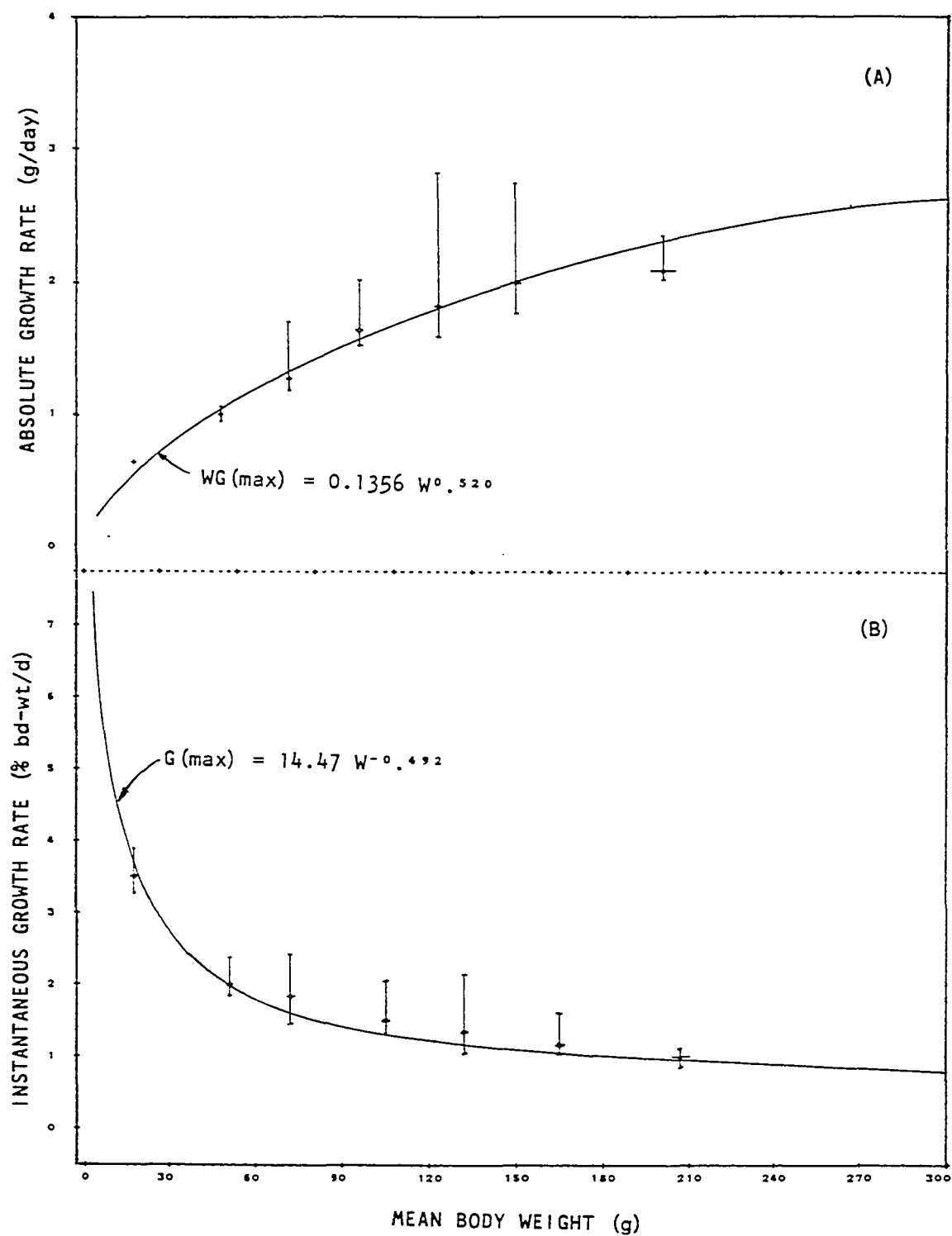
possibility to establish the relationships between applied factors and growth of the fish through mathematical expression. The group food consumption rates ( $RC_m$  and  $C_m$ ) is substituted with estimated individual food consumption ( $RC_{est}$  and  $C_{est}$ ) for the following section. The estimated food consumption of individuals ( $RC_{est}$  and  $C_{est}$ ) was regarded to be correctly derived considering the results that: (1) the average estimated food consumption rate for individuals ( $RC_{est}$  and  $C_{est}$ ) showed similar magnitude to average group food consumption rate in each experiment ( $RC_m$  and  $C_m$ ) (see Table 4), (2) highly significant correlation found between growth and food consumption in group comparison indicated the growth is dominantly and proportionally influenced by food consumption even in different weight groups, and (3) correlation coefficients between the factors obtained using  $C_{est}$  and  $RC_{est}$  were similar to those found using  $RC_m$  and  $C_m$  (see Table 7, 8, 9, and 10).

#### Maximum Weight-Specific Growth

The growth rates observed from 1076 individuals involved in satiation feeding (experiments 1, 2, 3, 5, 6, 7, 8, 9b, and 9c) showed large variation over the observed weight range. The numbers of selected upper 10 % values in 7 weight intervals from a total 1076 observations were 109 for the maximum absolute growth rate and 111 for the maximum instantaneous growth rate. As shown in figure 9, the observed maximum absolute growth rate rapidly increased in small weight but the magnitude of change gradually was reduced to asymptotic pattern as the mean body weight of fish increased. The equation derived for the maximum absolute growth rate using group arrangement and regression analysis was:

Figure 9.

Maximum weight-specific growth rates of fish fed at satiated feeding level: (A) maximum absolute growth rate versus mean body weight ( $WG_{max}$  vs.  $W$ ) and (B) maximum instantaneous growth rate versus mean body weight ( $G_{max}$  vs.  $W$ ). Data-points indicate representative growth rates in weight intervals and the corresponding mean body weights in group arrangement. Thick and thin vertical bars indicate standard error and range of selected growth rates in each weight interval respectively. Horizontal line indicates mean value of the selected growth rate with standard error of selected mean body weights in each weight interval. Number of weight groups is seven. The number of selected observations is 111 for maximum absolute growth rate and 109 for maximum instantaneous growth rate.



$$WG(max) = 0.1356 W^{0.520} \quad (r^2=0.98, n=7) \quad (15)$$

where WG (max) is the maximum absolute growth rate in g/day and W is mean body weight in grams. The calculated WG(max) from all individuals (n=1076) under satiated feeding levels in both commercial and natural diets indicated the maximum possible growth rates of the fish increased exponentially as mean body weight of fish increased. The equation showed good fitting with the observations over the weight range of fish in the experiments with the values of determination coefficient, 0.98.

The reverse pattern was found in the maximum weight-specific instantaneous growth rate as shown in Figure 9. As the mean body weight increased, the maximum instantaneous growth rates decreased. The equations derived using group arrangement and regression analysis was:

$$G(max) = 14.47 W^{-0.492} \quad (r^2=0.98, n=7) \quad (16)$$

where G(max) is the maximum instantaneous growth rate in % of mean body weight/day and W is mean body weight of fish. The equation showed close fitting to the observations with the high values of 'r<sup>2</sup>', 0.98. The equation indicated that the possible maximum instantaneous weight gain expressed as percent of body weight of fish decreased exponentially as the fish weight increased. The equation showed that the maximum instantaneous growth rate changed rapidly following the weight change as the weight of fish decreased.

When the weight-specific maximum absolute and instantaneous growth rates were expressed for each food type, significant difference was found between the growth rates of fish fed the different diets as shown in



Figure 10 ( $p(F) < 0.01$ ). The equations of weight-specific maximum absolute and instantaneous growth rates obtained from fish fed the natural and commercial diets ( $n=276$  and  $800$  respectively) using the group arrangement were:

$$WG(n-max) = 0.04 W^{0.70} \quad (r^2=0.98, n=4) \quad (17)$$

$$G(n-max) = 3.32 W^{-0.25} \quad (r^2=0.97, n=4) \quad (18)$$

$$WG(c-max) = 0.145 W^{0.51} \quad (r^2=0.98, n=7) \quad (19)$$

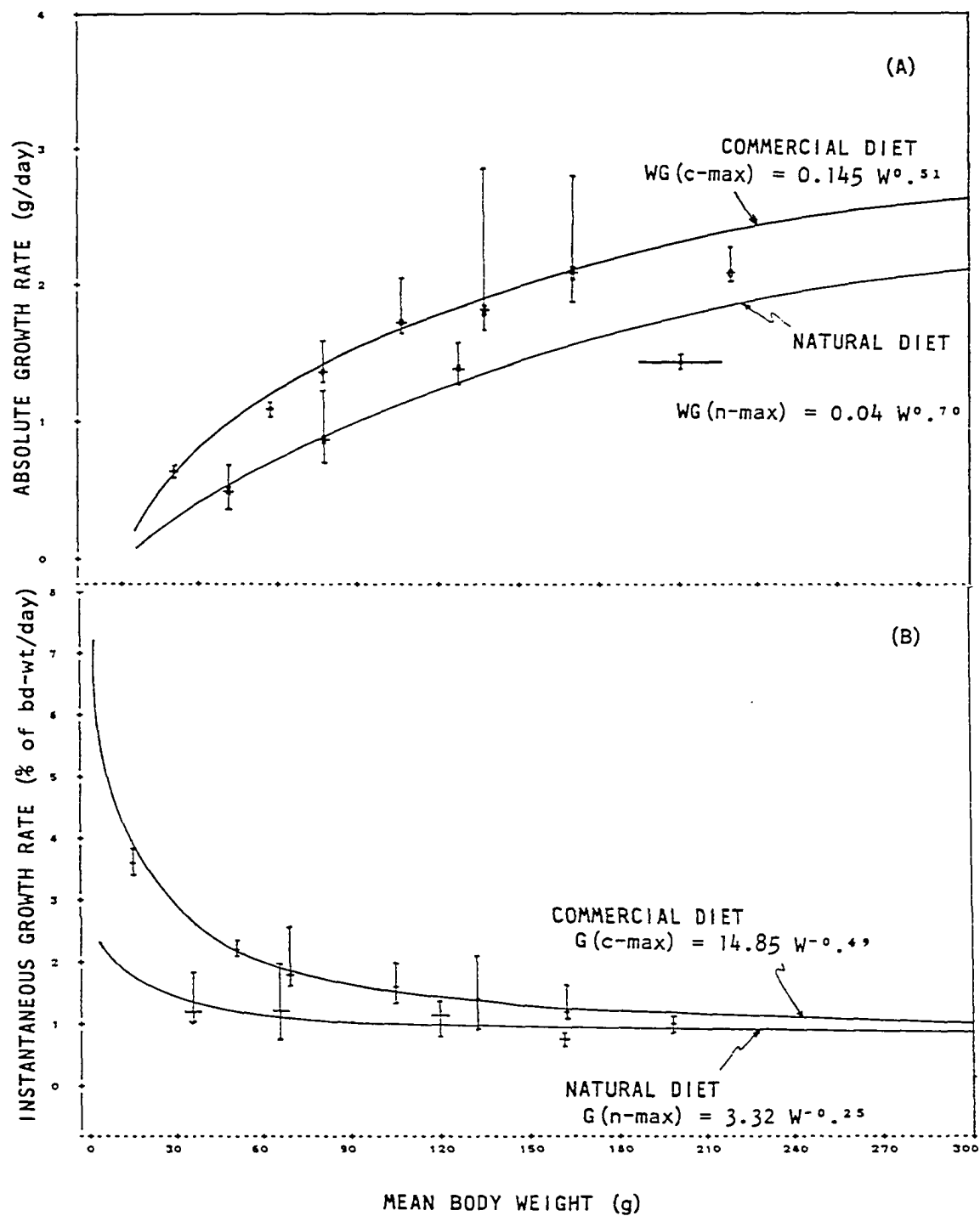
$$G(c-max) = 14.85 W^{-0.49} \quad (r^2=0.98, n=7) \quad (20)$$

where  $WG(n-max)$  and  $G(n-max)$  were the calculated maximum absolute and instantaneous growth rates expressed in g/day and % of body weight/day respectively for fish fed the natural diet at a given weight ( $W$ ) in grams and  $WG(c-max)$  and  $G(c-max)$  were the counterparts for the fish fed the commercial diet. The equations indicated that maximum weight-specific absolute growth rate decreased exponentially as weight increased while a reverse pattern was found in maximum weight-specific instantaneous growth rate.

Through the range of mean body weight of the tested fish (4.3 - 295.2 g), fish fed the commercial diet revealed higher values of calculated maximum absolute and instantaneous growth rates than those fed the natural diet. The calculated maximum absolute and instantaneous growth rates of fish of 4.3 g in mean body weight were 0.11 g/day and 2.14 % of body weight /day in natural diet feeding, and 0.31 g/day and 7.27 % of body weight/day in commercial diet feeding. The absolute and instantaneous growth rates of a fish weighing 295.2 g are 2.14 g/day and 0.80 % of body weight per day in natural diet feeding and 2.64 g/day and

Figure 10.

Maximum weight-specific growth rates of fish for two diet types: (A) maximum absolute growth rate versus mean body weight ( $WGc\text{-max}$  vs.  $W$  and  $WGn\text{-max}$  vs.  $W$ ) and (B) maximum instantaneous growth rate versus mean body weight ( $Gc\text{-max}$  vs.  $W$  and  $Gn\text{-max}$  vs.  $W$ ). Data-points indicate representative growth rates in weight intervals and the corresponding mean body weights in group arrangement. Thick and thin vertical bars indicate standard error and range of selected growth rates in each weight interval respectively. Horizontal line indicates mean value of the selected growth rate with standard error of selected mean body weights in each weight group. The number of weight groups is seven for fish fed commercial diet and four for fish fed natural diet.



0.91 % of body weight per day in commercial diet feeding respectively. Through the weight range, calculated maximum growth rates in satiated feeding indicated that fish fed the commercial diet grew faster than those fed the natural diet by a factor of 1.1 - 3.7 for the instantaneous growth rate and 1.3 - 2.7 for the absolute growth rate respectively. The commercial diet significantly produced higher growth rates than the natural diet at satiated feeding level ( $p(F) < 0.01$ ).

#### Weight-Specific Weight Loss in Starvation

A total of 212 fish involved in the starvation experiments showed the tendency that the weight loss expressed in g/day increased as the weight of fish increased while the instantaneous rate of weight loss expressed in percent of body weight per day decreased as the weight of fish increased. The equations obtained for weight-specific absolute and instantaneous weight loss using group arrangement were:

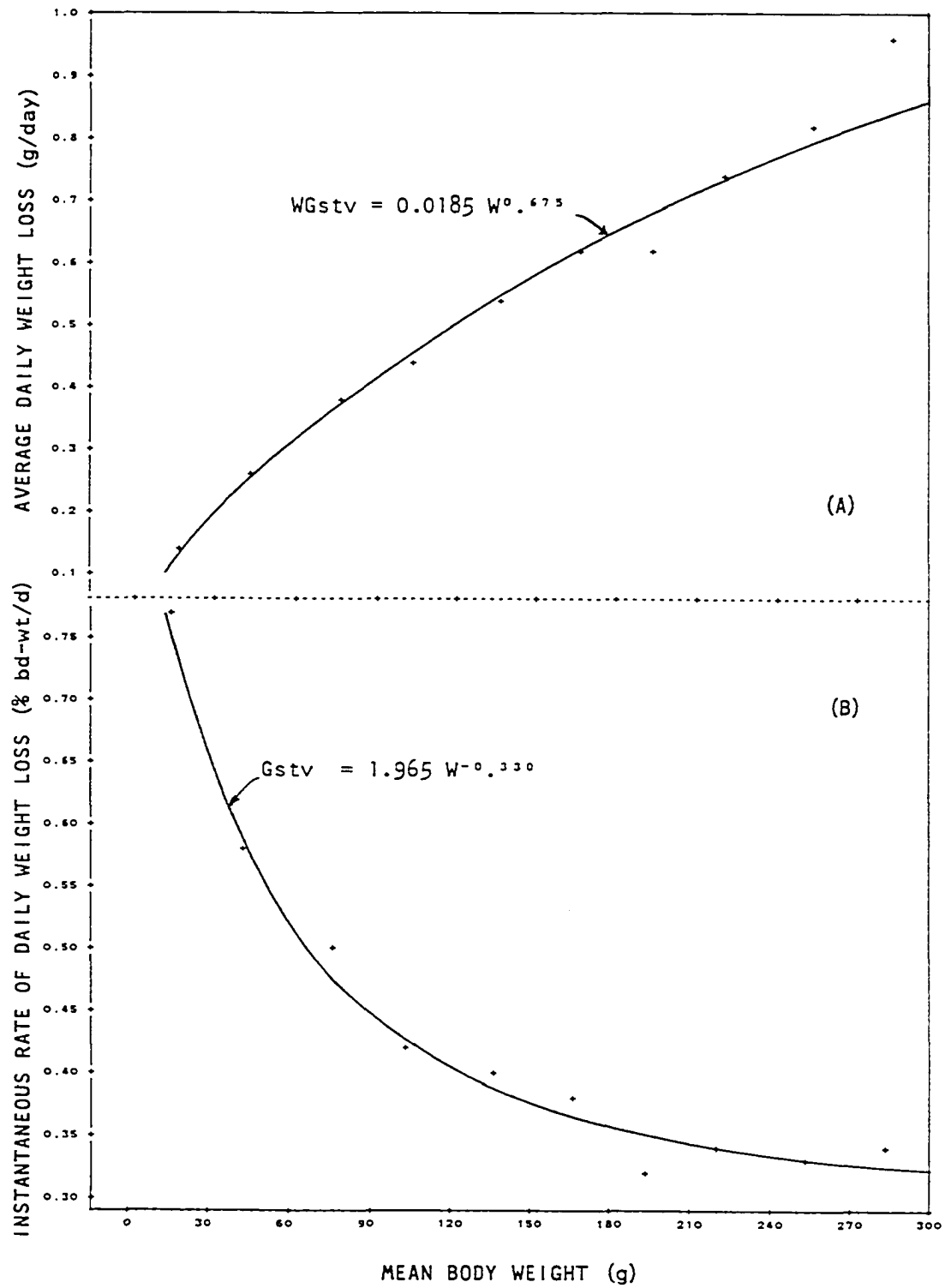
$$WG_{stv} = 0.0185 W^{0.675} \quad (r^2=0.99, n=10) \quad (21)$$

$$G_{stv} = 1.965 W^{-0.330} \quad (r^2=0.99, n=10) \quad (22)$$

where  $WG_{stv}$  and  $G_{stv}$  are the calculated absolute and instantaneous rates of weight loss expressed in g/day and % of body weight/day respectively at the corresponding mean body weight ( $W$ ) (see Figure 11). The equations indicated that the absolute rate of weight loss increased as weight of fish increased but a reverse pattern was found in the instantaneous rate of weight loss. As shown in Figure 2, as the absolute rate of weight loss increased, the variation of weight loss between individuals having the same weights also increased. The high values of determination

Figure 11.

Weight-specific weight loss of starved fish: (A) average daily weight loss versus mean body weight ( $WG_{stv}$  vs.  $W$ ) and (B) instantaneous rate of daily weight loss versus mean body weight ( $G_{stv}$  vs.  $W$ ). Data-points indicate mean values of weight loss in weight intervals and the corresponding mean body weights in group arrangement. The number of weight groups is 10.



coefficients of the equations reflected the good fitting of the equations to the observations.

#### Maximum Weight-Specific Food Consumption Rate

When estimated amounts of food consumed by individuals ( $C_{est}$ ) were related to the weight, the maximum values of amounts of food consumed by individuals ( $C_{est}$ , g/day) tended to increase as body weight of fish increased (see Figure 12). The averages of the selected upper 10 % values ( $n=83$  in the commercial diet feeding and  $n=22$  in the natural diet feeding) in each weight interval showed that the amount of food consumed by individuals ( $C_{est}$ ) increased as weight of fish increased in both diet types but were also significantly different between two diet types ( $p(F)<0.01$ ). The equations of the weight-specific maximum amount of food consumed ( $C_{est}$ , g/day) in each diet type were:

$$C(n-max) = 1.08 W^{0.41} \quad (r^2=0.83, n=4) \quad (23)$$

and

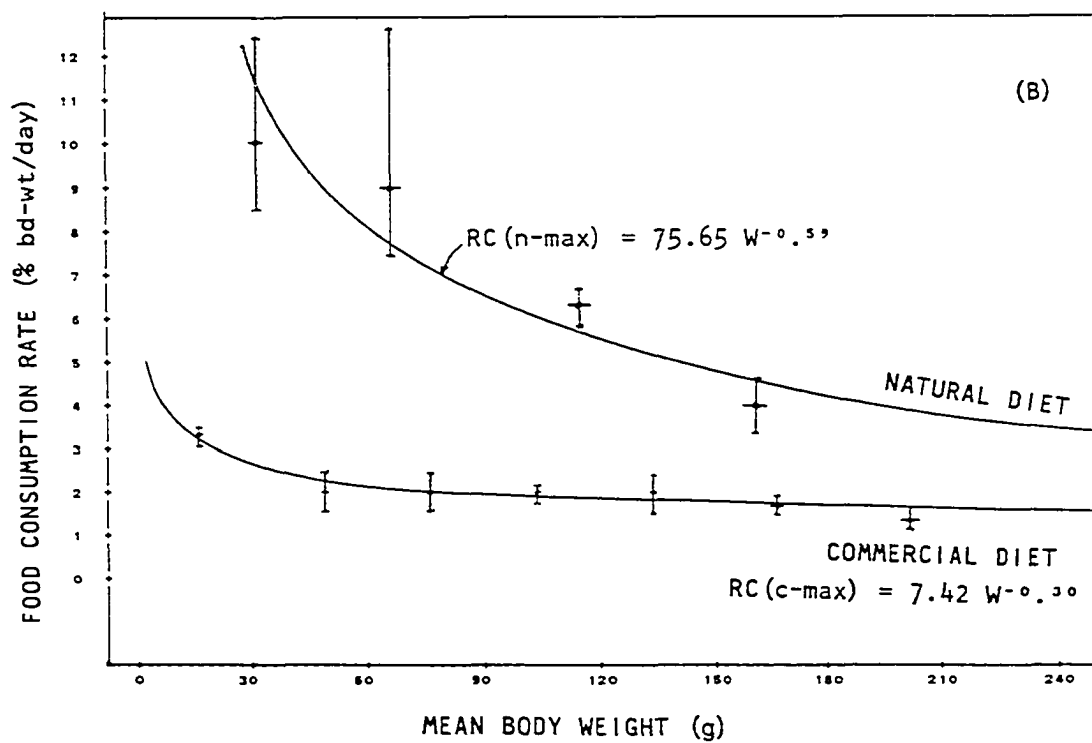
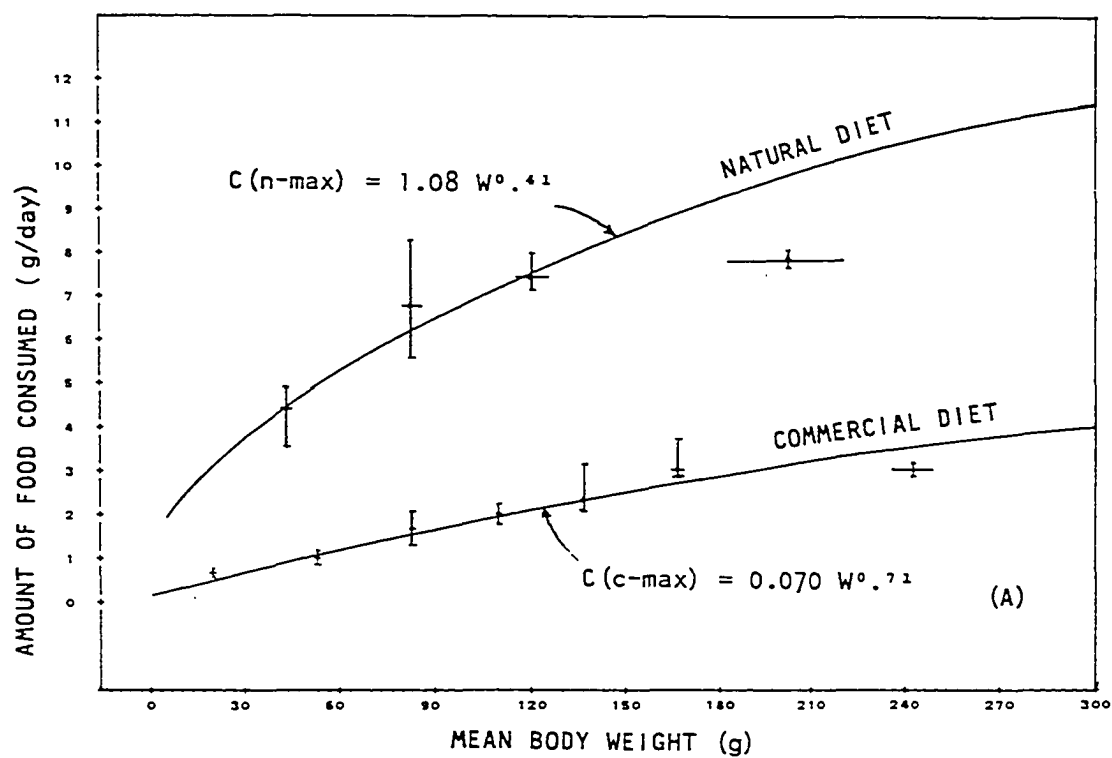
$$C(c-max) = 0.070 W^{0.71} \quad (r^2=0.98, n=7) \quad (24)$$

Where  $C(n-max)$  and  $C(c-max)$  are the calculated maximum amount of food consumed daily (g/day) at the corresponding mean body weight ( $W$ ) in the natural and the commercial diet feeding respectively. The exponent, 0.71 in  $C(c-max)$  was much larger than that found in  $C(n-max)$ . The equations indicated that the maximum amounts of food consumed by individuals exponentially increased as the fish weight increased. The difference of maximum food consumption between two diets at the same weight decreased as weight of fish increased, which indicated that the food consumption of

Figure 12.

Weight-specific maximum food consumption for two diet types: (A) maximum amount of food consumed by individual versus mean body weight ( $C_n\text{-max}$  vs.  $W$  and  $C_c\text{-max}$  vs.  $W$ ) and (B) maximum food consumption rate versus mean body weight ( $RC_n\text{-max}$  vs.  $W$  and  $RC_c\text{-max}$  vs.  $W$ ). Data-points indicate representative values of food consumption in weight intervals and the corresponding mean body weights in group arrangement. Thick and thin vertical bars indicate standard error and range of selected growth rates in each weight interval respectively. Horizontal line indicates mean value of selected growth rate with standard error of selected mean body weights in each weight interval. The number of weight intervals is seven for the commercial diet and four for the natural diet.





fish fed the commercial diet increased more rapidly than that of fish fed the natural diet as weight increased. However, determination coefficient ( $r^2$ ), 0.83 in C(n-max) indicated relatively poor fitting of the equation to the real observations compared to the high ' $r^2$ ' value in C(c-max) of 0.98. The calculated maximum amount of food consumed by fish having 4.3 g and 295.2 g were 0.20 g/day and 3.97 g/day in commercial diet feeding and 1.96 g/day and 11.13 g/day in natural diet feeding. For the calculated amounts of food consumed by individuals (Cest), fish fed the natural diet showed higher values than those fed the commercial diet by a factor of 2.5 - 7.7 over the weight range.

When individual food consumption rates (RCest, % of body weight/day) were related to weight of fish, the weight-specific maximum food consumption pattern was opposite to that found between weight and the amount of food consumed by individuals (Cest). The selected values of food consumption rate in each weight interval tended to decrease as weight of fish increased. Though the tendency was the same in two diet types, the magnitude of food consumption rate were significantly different between two diets over the observed weight range ( $p(T) < 0.01$ ). The equations for the weight-specific maximum food consumption rate (RCmax) derived using group arrangement and regression analysis for each food type were:

$$RC(n-max) = 75.65 W^{-0.59} \quad (r^2=0.88, n=4) \quad (25)$$

and

$$RC(c-max) = 7.42 W^{-0.30} \quad (r^2=0.94, n=7) \quad (26)$$

where RC(n-max) and RC(c-max) are the weight-specific maximum food

consumption rate (% of body weight/day) of fish fed the natural diet and the commercial diet respectively and  $W$  is mean body weight of fish. The equations indicated that the food consumption rate ( $R_{Cest}$ ) decreased exponentially in both diet feeding as weight of fish increased.

The calculated maximum food consumption rate of fish having 4.3 g and 295.2 g were 4.79 % of body weight/day and 1.35 % of body weight/day in the commercial diet and 32.0 % of body weight/day and 2.64 % of body weight/day in the natural diet respectively. Fish fed the natural diet showed higher values than those fed the commercial diet for the calculated individual food consumption rate ( $R_{Cest}$ ) by a factor of 2.9 - 5.6 over the weight range.

#### Growth in Relation to Food and Weight

During the experiments a complicated pattern of growth of fish was found in relation to food and weight. The results of analysis indicated that growth of fish was related to food consumption rate and body weight regardless of diet type but the magnitudes of growth rate and food consumption rate were significantly different between fish fed different diets. To properly estimate growth rate in relation to food type, food consumption rate, and body weight the fish, multivariable analysis was performed using simple regression analyses and group arrangement. The equations established for the relationships between growth and influencing factors using simple regression analysis and group arrangement are summarized in Table 12

##### 1) Growth-Weight relationship for fixed food consumption rates

Table 12. Summary of group arrangement and regression analysis between growth rates (WG and G), food consumption (RCest and Cest), and body weight of fish (W) in the commercial diet feeding.

12a. Absol. growth rate (WG) vs. Est. food consumption rate (RCest)  
(subgroup : mean body weight)

| abs. growth rate (WG) vs food consumption rate (RCest)* |  |                                      |                    |   |                       |   |                        |
|---|--|--------------------------------------|--------------------|---|-----------------------|---|------------------------|
| interval<br>num.  | weight<br>interval<br>(min/max)<br>(g) | number<br>of sub<br>group<br>(RCest) | num.<br>of<br>fish | const. of<br>proport-<br>ionality<br>(A1) | expo-<br>nent<br>(B1) | coeff.<br>determ-<br>ination<br>(r <sup>2</sup> ) | p (T)<br>(Ho:<br>B1=0) |
| 1   | 4/30                                   | 6                                    | 46                 | 0.1792                                    | 0.1455                | 0.95  | p<0.001                |
| 2   | 30/60                                  | 7                                    | 134                | 0.3646                                    | 0.3129                | 0.96  | p<0.001                |
| 3   | 60/90                                  | 6                                    | 221                | 0.4574                                    | 0.4867                | 0.99  | p<0.001                |
| 4   | 90/120                                 | 7                                    | 213                | 0.5864                                    | 0.4557                | 0.96  | p<0.001                |
| 5   | 120/150                                | 7                                    | 179                | 0.6362                                    | 0.5365                | 0.99  | p<0.001                |
| 6   | 150/180                                | 7                                    | 129                | 0.7205                                    | 0.6526                | 0.99  | p<0.001                |
| 7   | 180/210                                | 4                                    | 61                 | 0.7795                                    | 0.7874                | 0.91  | p<0.001                |
| 8   | 210/300                                | 4                                    | 39                 | 0.8748                                    | 0.9189                | 0.85  | p<0.01                 |

\* Equation:  $\ln(WG) = (A1) + (B1) \ln(RC) - 1$

12b. Instantaneous growth rate (G) vs. food consumption rate (RCest)  
(subgroup : mean body weight)

| inst. growth rate (G) vs food consumption rate (RCest)* |  |                                      |                    |   |                       |   |                        |
|---|--|--------------------------------------|--------------------|---|-----------------------|---|------------------------|
| interval<br>num.  | weight<br>interval<br>(min/max)<br>(g) | number<br>of sub<br>group<br>(RCest) | num.<br>of<br>fish | const. of<br>proport-<br>ionality<br>(A2) | expo-<br>nent<br>(B2) | coeff.<br>determ-<br>ination<br>(r <sup>2</sup> ) | p (T)<br>(Ho:<br>B2=0) |
| 1   | 4/30                                   | 6                                    | 46                 | 0.6857                                    | 0.6766                | 0.91  | p<0.001                |
| 2   | 30/60                                  | 7                                    | 134                | 0.6095                                    | 0.5608                | 0.98  | p<0.001                |
| 3   | 60/90                                  | 6                                    | 221                | 0.5682                                    | 0.6003                | 0.99  | p<0.001                |
| 4   | 90/120                                 | 7                                    | 213                | 0.5728                                    | 0.4321                | 0.97  | p<0.001                |
| 5   | 120/150                                | 7                                    | 179                | 0.5227                                    | 0.4215                | 0.98  | p<0.001                |
| 6   | 150/180                                | 7                                    | 129                | 0.5183                                    | 0.4328                | 0.98  | p<0.001                |
| 7   | 180/210                                | 4                                    | 61                 | 0.4818                                    | 0.5094                | 0.99  | p<0.001                |
| 8   | 210/300                                | 4                                    | 39                 | 0.4767                                    | 0.4196                | 0.99  | p<0.001                |

\* Equation:  $\ln(G) = (A2) + (B2) \ln(RC) - 1$

Table 12. continued

12c. Absolute growth rate (WG) vs. amount of consumed food (Cest)  
(subgroup : mean body weight )

| abs. growth rate (WG) x amount of consumed food (Cest)* |                               |                             |              |                                |               |  |                 |
|---|-------------------------------|-----------------------------|--------------|--------------------------------|---------------|--|-----------------|
| interval num.   | weight interval (min/max) (g) | number of sub group (RCest) | num. of fish | const. of proportionality (A3) | exponent (B3) | coeff. determination (r <sup>2</sup> ) | p(T) (Ho: B3=0) |
| 1   | 4/30                          | 6                           | 46           | 0.4147                         | 0.1413        | 0.93                                   | p<0.001         |
| 2   | 30/60                         | 7                           | 134          | 0.5818                         | 0.3033        | 0.96                                   | p<0.001         |
| 3   | 60/90                         | 6                           | 221          | 0.5969                         | 0.5089        | 0.99                                   | p<0.001         |
| 4   | 90/120                        | 7                           | 213          | 0.5655                         | 0.4517        | 0.97                                   | p<0.001         |
| 5   | 120/150                       | 7                           | 179          | 0.4799                         | 0.5033        | 0.99                                   | p<0.001         |
| 6   | 150/180                       | 7                           | 129          | 0.3990                         | 0.6545        | 0.99                                   | p<0.001         |
| 7   | 180/210                       | 4                           | 61           | 0.2667                         | 0.7771        | 0.99                                   | p<0.001         |
| 8   | 210/300                       | 4                           | 39           | 0.1171                         | 0.8960        | 0.97                                   | p<0.001         |

\* Equation:  $\ln(WG) = (A3) + (B3) \ln(RC) - 1$

12d. Instantaneous growth rate (G) vs. amount of food consumed (Cest)  
(subgroup : mean body weight)

| inst. growth rate (G) vs daily consumed food (Cest)* |                               |                             |              |                                |               |  |                 |
|--|-------------------------------|-----------------------------|--------------|--------------------------------|---------------|--|-----------------|
| interval num.  | weight interval (min/max) (g) | number of sub group (RCest) | num. of fish | const. of proportionality (A4) | exponent (B4) | coeff. determination (r <sup>2</sup> ) | p(T) (Ho: B4=0) |
| 1  | 4/30                          | 6                           | 46           | 1.9096                         | 0.7551        | 0.98                                   | p<0.01          |
| 2  | 30/60                         | 7                           | 134          | 0.9979                         | 0.5427        | 0.98                                   | p<0.001         |
| 3  | 60/90                         | 6                           | 221          | 0.7402                         | 0.6271        | 0.99                                   | p<0.001         |
| 4  | 90/120                        | 7                           | 213          | 0.5539                         | 0.4282        | 0.97                                   | p<0.005         |
| 5  | 120/150                       | 7                           | 179          | 0.3999                         | 0.4184        | 0.98                                   | p<0.001         |
| 6  | 150/180                       | 7                           | 129          | 0.3052                         | 0.4339        | 0.98                                   | p<0.01          |
| 7  | 180/210                       | 4                           | 61           | 0.1501                         | 0.5026        | 0.99                                   | p<0.05          |
| 8  | 210/300                       | 4                           | 39           | 0.1309                         | 0.4087        | 0.85                                   | p<0.05          |

\* Equation:  $\ln(G) = (A4) + (B4) \ln(RC) - 1$

Table 12. continued

12e. Absolute growth rate (WG) vs. mean body weight (W)  
(subgroup : food consumption rate (RCest))

| abs. growth rate (WG) x mean body weight (W) |                                     |                         |              |                                |               |  |                 |
|--|-------------------------------------|-------------------------|--------------|--------------------------------|---------------|--|-----------------|
| interval num.                                | food consumption interval (min/max) | number of sub group (W) | num. of fish | const. of proportionality (A5) | exponent (B5) | coeff. determination (r <sup>2</sup> ) | p(T) (Ho: B5=0) |
| 1  | 0.0/0.3                             | 6                       | 29           | 0.7888                         | -0.2587       | 0.85                                   | p<0.01          |
| 2  | 0.3/0.6                             | 6                       | 99           | -0.3150                        | 0.0928        | 0.58*                                  | p>0.01          |
| 3  | 0.6/0.9                             | 8                       | 221          | -0.8550                        | 0.2806        | 0.93                                   | p<0.001         |
| 4  | 0.9/1.2                             | 8                       | 269          | -0.8618                        | 0.3156        | 0.95                                   | p<0.001         |
| 5  | 1.2/1.5                             | 8                       | 217          | -0.6816                        | 0.3038        | 0.99                                   | p<0.001         |
| 6  | 1.5/1.8                             | 6                       | 119          | -0.6894                        | 0.3302        | 0.99                                   | p<0.001         |
| 7  | 1.8/2.4                             | 6                       | 75           | -0.7539                        | 0.3646        | 0.98                                   | p<0.001         |

\* statistically insignificant : p(T)>0.01

\*\* Equation:  $\ln(WG) = (A5) + (B5) \ln(W) - 1.0$

12f. Instantaneous growth rate (G) vs. mean body weight (W)  
(subgroup : food consumption rate (RCest))

| inst. growth rate (G) vs mean body weight (W)** |                                     |                         |              |                                |               |  |                 |
|---|-------------------------------------|-------------------------|--------------|--------------------------------|---------------|--|-----------------|
| interval num.                                   | food consumption interval (min/max) | number of sub group (W) | num. of fish | const. of proportionality (A6) | exponent (B6) | coeff. determination (r <sup>2</sup> ) | p(T) (Ho: B6=0) |
| 1   | 0.0/0.3                             | 6                       | 29           | -2.1150                        | 0.3449        | 0.82                                   | p<0.01          |
| 2   | 0.3/0.6                             | 6                       | 99           | 0.0461                         | 0.0116        | 0.03*                                  | p>0.01          |
| 3   | 0.6/0.9                             | 8                       | 221          | 0.3031                         | 0.0171        | 0.25*                                  | p>0.01          |
| 4   | 0.9/1.2                             | 8                       | 269          | 0.7608                         | -0.04653      | 0.65                                   | p<0.01          |
| 5   | 1.2/1.5                             | 8                       | 217          | 1.3054                         | -0.1339       | 0.90                                   | p<0.001         |
| 6   | 1.5/1.8                             | 6                       | 119          | 1.4491                         | -0.1364       | 0.95                                   | p<0.001         |
| 7   | 1.8/2.4                             | 6                       | 75           | 1.5869                         | -0.1467       | 0.96                                   | p<0.001         |

\* statistically insignificant: p(T)>0.01

\*\* Equation:  $\ln(G) = (A6) + (B6) \ln(W) - 1.0$

The growth rates of individuals having the same weights should differ if fish were subjected to different food consumption rates as found in correlation analysis. When the observations obtained from the commercial diet experiments (n=1024) were grouped by estimated individual food consumption rate (RCest) using group arrangement method, the effects of food consumption rate on the absolute growth rate of fish having the same weight of fish were distinctly revealed as shown in Figure 13. Each single line expressed as 'RC' number indicated a interval of food consumption rate (a fixed food consumption rate) in percent of body weight per day.

For a fixed food consumption rate, absolute growth rate increased as weight of fish increased. At the same weight, absolute growth rate increased as 'RC' number increased, which indicated that absolute growth rate increased as food consumption rate increased. Simultaneously, the distance between two lines, which represented the difference of growth rate between two fixed food consumption rates, decreased as 'RC' number increased at the same weight. The overall pattern indicated that growth rate rapidly increased as food consumption rate increased at low food consumption rate but the increment of absolute growth rate was reduced as food consumption rate approached maximum. The high values of ' $r^2$ ' in each equation indicated good fitting of the equations to the observations.

In instantaneous growth rate (% of body weight/day), the tendency was exactly opposite to that found in absolute growth rate (see Figure 14). The growth differentiation at different food consumption rate expressed as 'RC' number decreased as weight of fish increased. In small fish the difference of growth rate at different food consumption rate was

Figure 13.

Absolute growth rate versus mean body weight within fixed food consumption rates (WG vs.  $W / RC$ ) for fish fed the commercial diet. RCnumber and the number in parenthesis indicate group number of food consumption rate and range of food consumption rate (% of body weight/day) of corresponding group respectively. Solid line indicates that value of exponent of equation is significantly different from zero ( $p(T) < 0.01$ ) and dotted line indicates not significantly different from zero (see Table 12e for details).



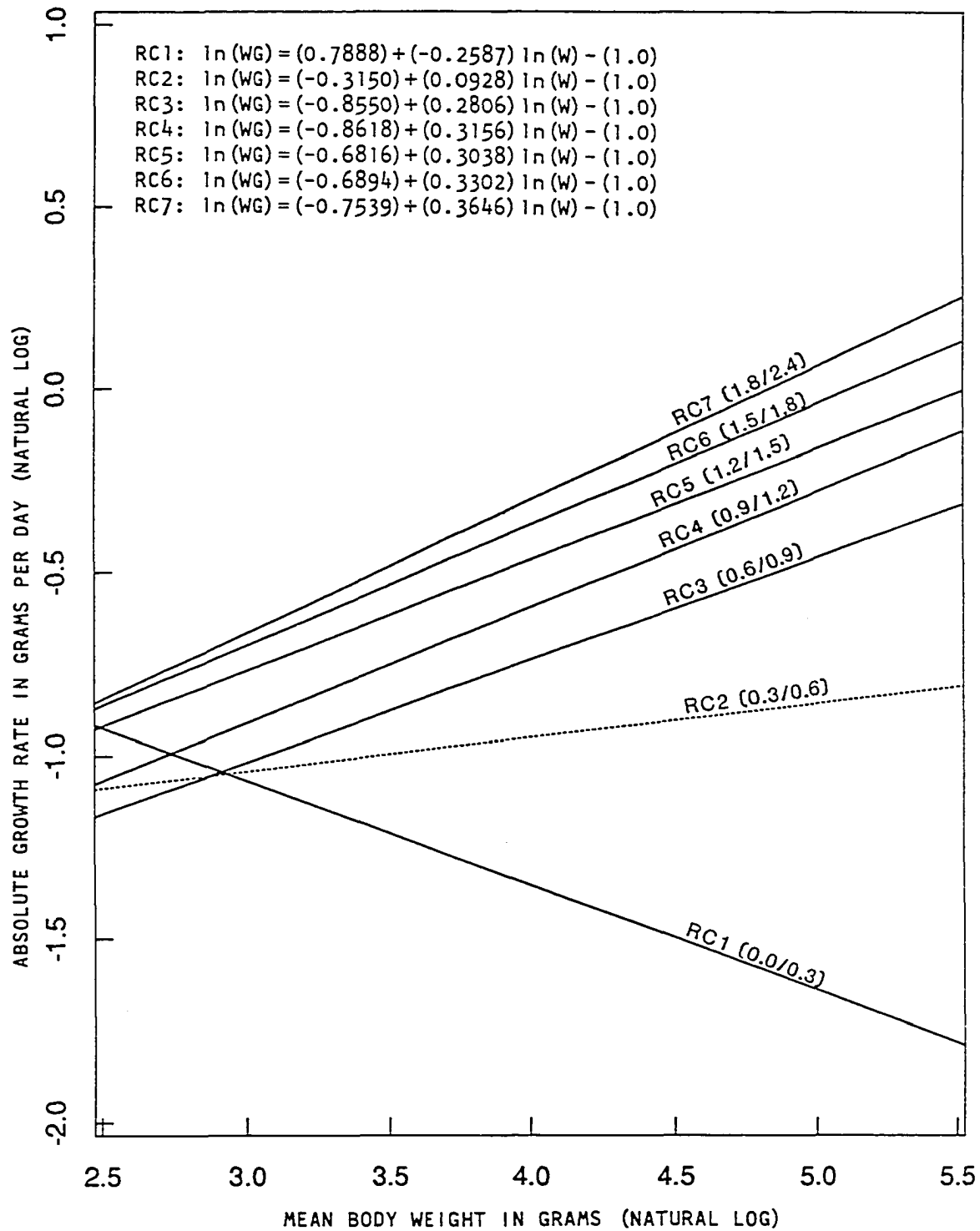
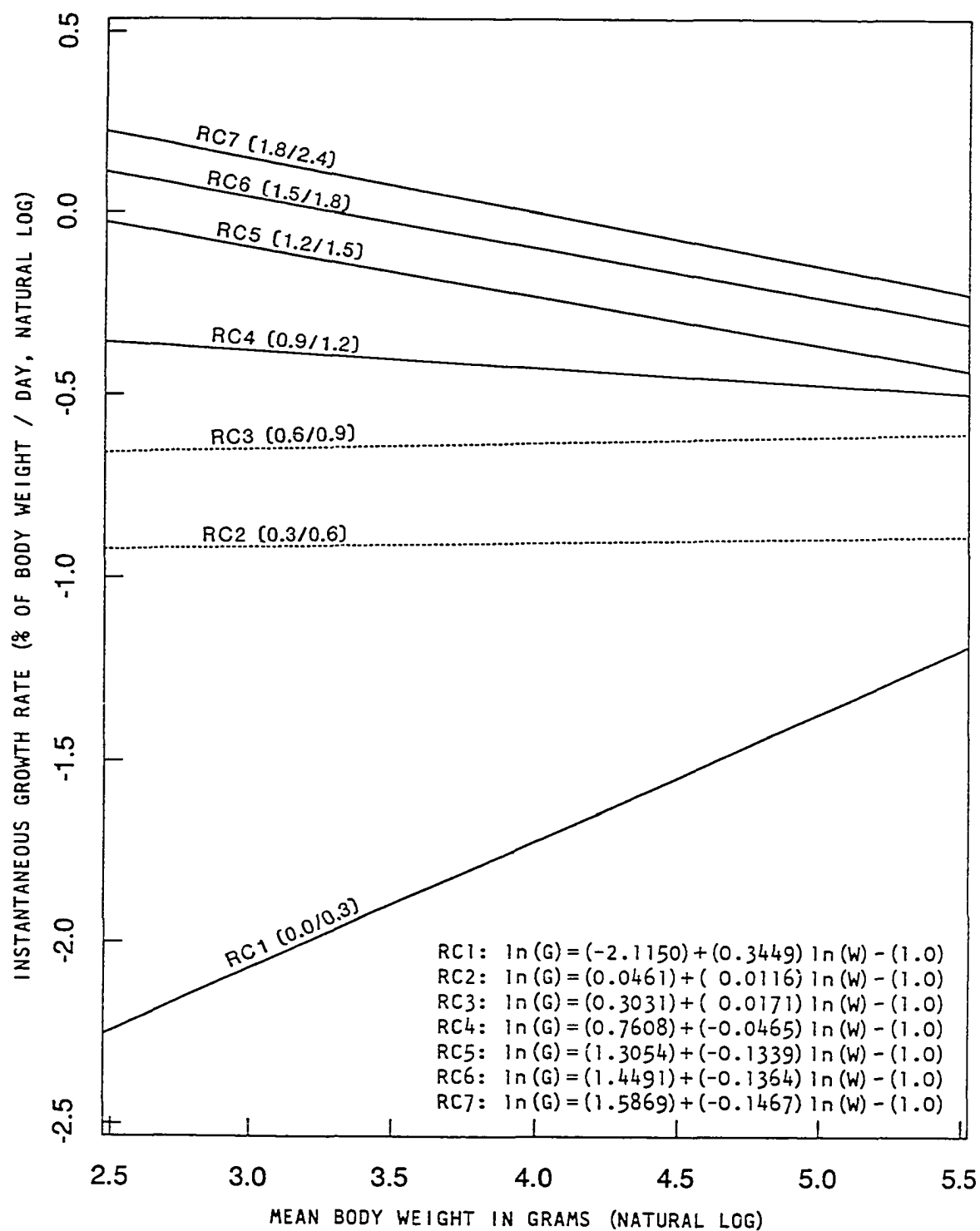


Figure 14.

Instantaneous growth rate versus mean body weight within fixed food consumption rates (G vs. W / RC) for fish fed commercial diet. RCnumber and number in parenthesis indicate group number of food consumption rate and range of food consumption rate (% of body weight/day) of corresponding group respectively. Solid line indicates that value of exponent of equation is significantly different from zero ( $p(T) < 0.01$ ) and dotted line indicates not significantly different from zero (see Table 12f for details).



large but the difference decreased as weight of fish increased. the equations obtained from each fixed food consumption rate (0.3 % interval) fitted well to the observations with the values of determination coefficients ( $r^2$ ) higher than 0.85 (mostly higher than 0.95) except for two insignificant slopes of regression lines found from food consumption levels of 0.3 - 0.6 % of body weight/day and 0.6 - 0.9 % body weight/day (RC2,  $r^2 = 0.03$ ,  $p(T) > 0.01$  and RC3,  $r^2 = 0.25$ ,  $p(T) > 0.01$ ) (see Table 12f). Similar results were obtained in the absolute growth rate except for the poor fitting at the lower food consumption rate (less than 1.2 % of body weight per day) (see Table 12e).

Certain uniform trends were found between the exponents and between the constants of proportionality of the equations for the seven grouped food consumption rates. The constants of proportionality increased as the food consumption rates increased while the exponents decreased as the food consumption rates increased. The tendencies found in both exponents and the constants of proportionality showed relationships with food consumption rate and revealed good fitting to a power function of the food consumption rate. Using these equations a generalized equation was developed to describe the instantaneous growth of the fish as a primary function of the weight and the secondary function of the food consumption rate:

$$\ln G(c) = \ln(A1) + (B1) \ln(W) - C1 \quad (27)$$

$$A1 = 2.280 (RC)^{1.2446} \quad (r^2=0.98, n=7)$$

$$B1 = 0.934 (RC)^{-0.1558} - C2 \quad (r^2=0.92, n=7)$$

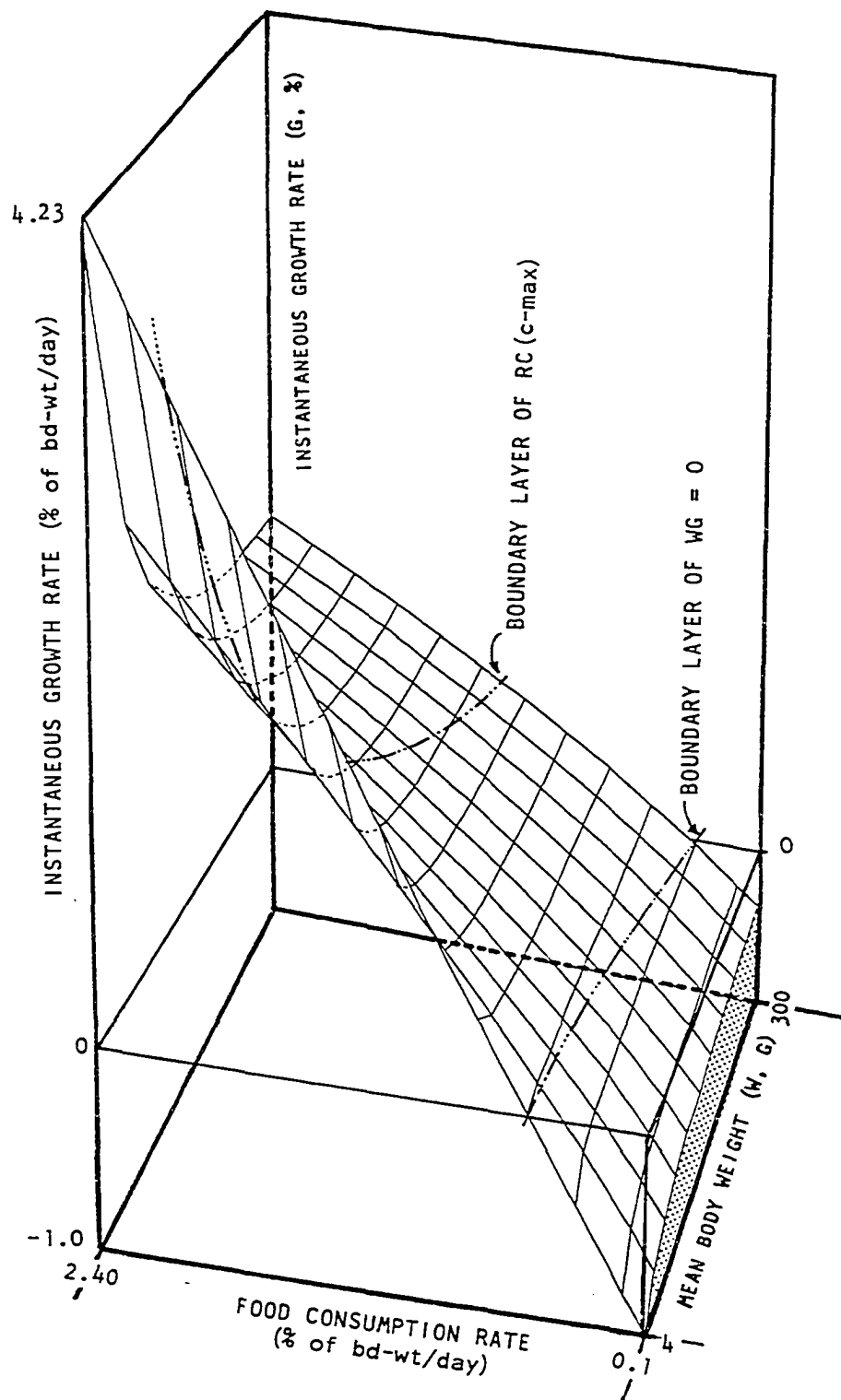
$$C1 = 1, \text{ and } C2 = 1$$

where  $G(c)$  is the instantaneous growth rate (% of body weight/day) of a fish which weighs 'W' in grams and consumes food at 'RC' level (% of body weight/day). The constants of proportionality (A1) and the exponents (B1) were expressed as a power function of the food consumption rate (RC) while C1 and C2 were correction constants. The resultants of the equation were shown in Figure 15. The instantaneous growth rate integrated to zero as the weight of fish increased while the growth rates always increased as food consumption rates increased. The pattern shown in the figure coincided with the observations not only in tendencies but also in magnitude of the growth rate of the fish. However, the maximum food consumption rate was a function of weight as shown in equation 26 and the limit of potential growth rate of a fish at a given weight was also subjected to the maximum limit of weight-specific food consumption rate of the individual. The estimated growth rate in the maximum food consumption rate (equation 27) showed good fitting (less than 10 %) to the calculated maximum instantaneous growth rate (see equation 20) in the weight range from 60 g to 240 g. However, the largest difference (31 %) between the two values occurred at the smallest size of the test fish (4.3 g).

The fish fed the natural diet (n=276) showed poor relation between the growth rates and food consumption rate at the same body weight. Though the relationship between instantaneous growth rate and mean body weight could be expressed as exponential equation for fish consumed more than 6 % of the body weight/day and for fish fed less than 2 % of the body weight/day, no consistent trend was found between growth and weight at intermediate feeding levels with low values of determination coefficients ( $r^2 < 0.36$ ).

Figure 15.

Overall relationship between instantaneous growth rate ( $G$ , % of body weight/day), food consumption rate ( $RC_{est}$ , % of body weight/day) and weight ( $W$ , g) of fish fed commercial diet in three-dimensional array (see equation 27 for details).



# 1) Growth related to food consumption rate for fixed weights

When the absolute growth rate of fish fed the commercial diet was related to continuous food consumption rate ( $RC_{est}$ ), a pattern similar to that found in the previous section was observed. The variation of the absolute growth rates between each weight interval (a fixed weight group) at the same food consumption rate increased as the food consumption rates increased. In group arrangement, a consistent tendency was found as shown in Figure 16. The difference of the absolute growth rates between weight groups increased as the food consumption rate increased. At the same food consumption rate the difference of the absolute growth rates between the weight groups decreased as weight increased. The equations derived for absolute growth rate in relation to food consumption rate for the smallest (4-30 g) and the largest (210-300 g) weight groups of fish were:

$$GW(c-4/30) = 1.1982(RC)^{0.1455} - C1 \quad (r^2=0.95, n=6) \quad (28)$$

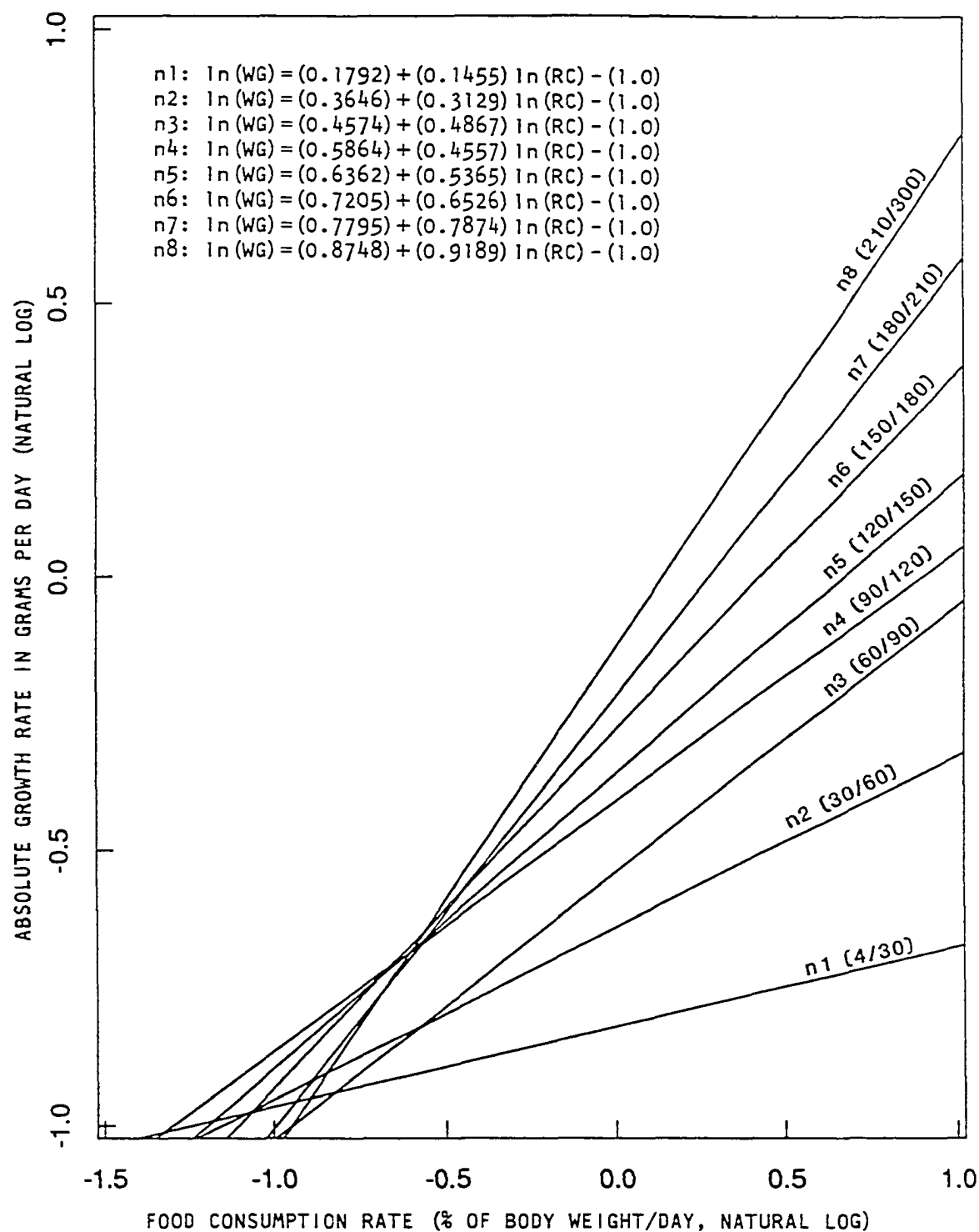
$$GW(c-210/300) = 2.5058(RC)^{0.9189} - C1 \quad (r^2=0.96, n=4) \quad (29)$$

where  $GW(c-4/30)$  and  $GW(Cc-4/30)$  represent the absolute growth rates of fish weighing 4.0 - 30.0 g and 210 - 300 g at the corresponding individual food consumption rate ( $RC$ , % of body weight/day) of fish fed the commercial diet respectively and  $C1$  is a correction constant ( $C1 = 1$ ). Though the number of the representative values in each sub-group (a component of matrix consisted of grouped food consumption rate and weight) were small ( $n=4-7$ ), the equations derived in each weight group showed good fitting to the real observations with the high values of determination



Figure 16.

Absolute growth rate versus food consumption rate within  
fixed weights (WG vs. RC / W) for fish fed commercial diet  
The 'n' number and number in parenthesis indicate group  
number of weight and range of weight of corresponding  
group (grams) (see Table 12a for details).



coefficients ( $r^2=0.85 - 0.99$ ,  $p(T)<0.01$ ) (see Table 12a). Since the averages of mean body weight and absolute growth rate of fish in each sub-group were used to derive the equation for each weight group, the best fitting of the equation for each weight group occurred at the average of mean body weight of each weight sub-group.

When the equations (absolute growth rate versus food consumption rate) obtained from eight weight groups were compared, some trends were found between the exponents and between the constants of proportionality of the equations (see Table 12a). The values of exponent and constant of proportionality of the equation for each group increased as group weight increased. A generalized equation was derived by expressing the exponents and the constants of proportionality as a linear function and power function of the weight respectively. The generalized expression was:

$$\ln WG(c) = \ln(A3) + (B3) \ln(RC) - C1 \quad (30)$$

$$A3 = 1.1541 + 0.005 (W) \quad (r^2=0.99, n=8)$$

$$B3 = 0.00916 W^{0.6984} \quad (r^2=0.97, n=8)$$

$$C1 = 1.0$$

where  $WG(c)$  is the absolute growth rate of the fish fed the commercial diet at the corresponding food consumption rate ( $RC$ , % of body weight/day) and mean body weight ( $W$ , grams). ' $A3$ ' and ' $B3$ ' are the constants of proportionality and the exponents, respectively and  $C1$  is the correction constant. The equation was expressed as a primary power function of food consumption rate and a secondary linear and power function of weight of fish. The constants of proportionality were described as a linear expression rather than a power function of the weight due to the better

fitting than the power function ( $r^2=0.94$ ). The overall relationship between the three equations are shown in Figure 17.

The estimated absolute growth rate in relation to food and weight using equation 30 should be justified by the weight-specific maximum food consumption rate (equation 26) as well as the generalized equation for instantaneous growth rate since no food consumption rate higher than the limit determined by the equation 26 was expected in this feeding condition. Therefore, the potential absolute growth rate estimated using equation 30 was also subjected weight-specific maximum food consumption rate.

The values estimated from the equation showed close fitting to the calculated values from the maximum growth rate of the fish (equation 19). The fish weighing 4.3 g and having maximum food consumption rate, 4.79 % of body weight per day revealed 0.23 g/day for the estimated absolute growth rate from equation 30 and 0.30 g/day for the calculated maximum absolute growth rate from the equation 19 respectively while 295.2 g fish had 2.69 g/day and 2.64 g/day for estimated growth rate at maximum food consumption rate ( $R_{Cest}=1.35$  % of body weight/day) and calculated maximum absolute growth rate at the weight respectively. The largest difference between the calculated and the estimated values (23 %) occurred for the smallest fish (4.3 g). The difference was less than 10 % in the weight range between 20 g and 210 g.

When instantaneous growth rate was estimated using the same method, the pattern was similar to that found in absolute growth rate related to food consumption rate for fixed weight groups. The instantaneous growth rate increased as food consumption rate increased, but the variation of

Figure 17.

Overall relationship between absolute growth rate (WG, g/day), food consumption rate (RCest, % of body weight/day) and weight (W, g) of fish fed commercial diet in three-dimensional array (see equation 30 for details) Dotted area indicates negative values of absolute growth rate.

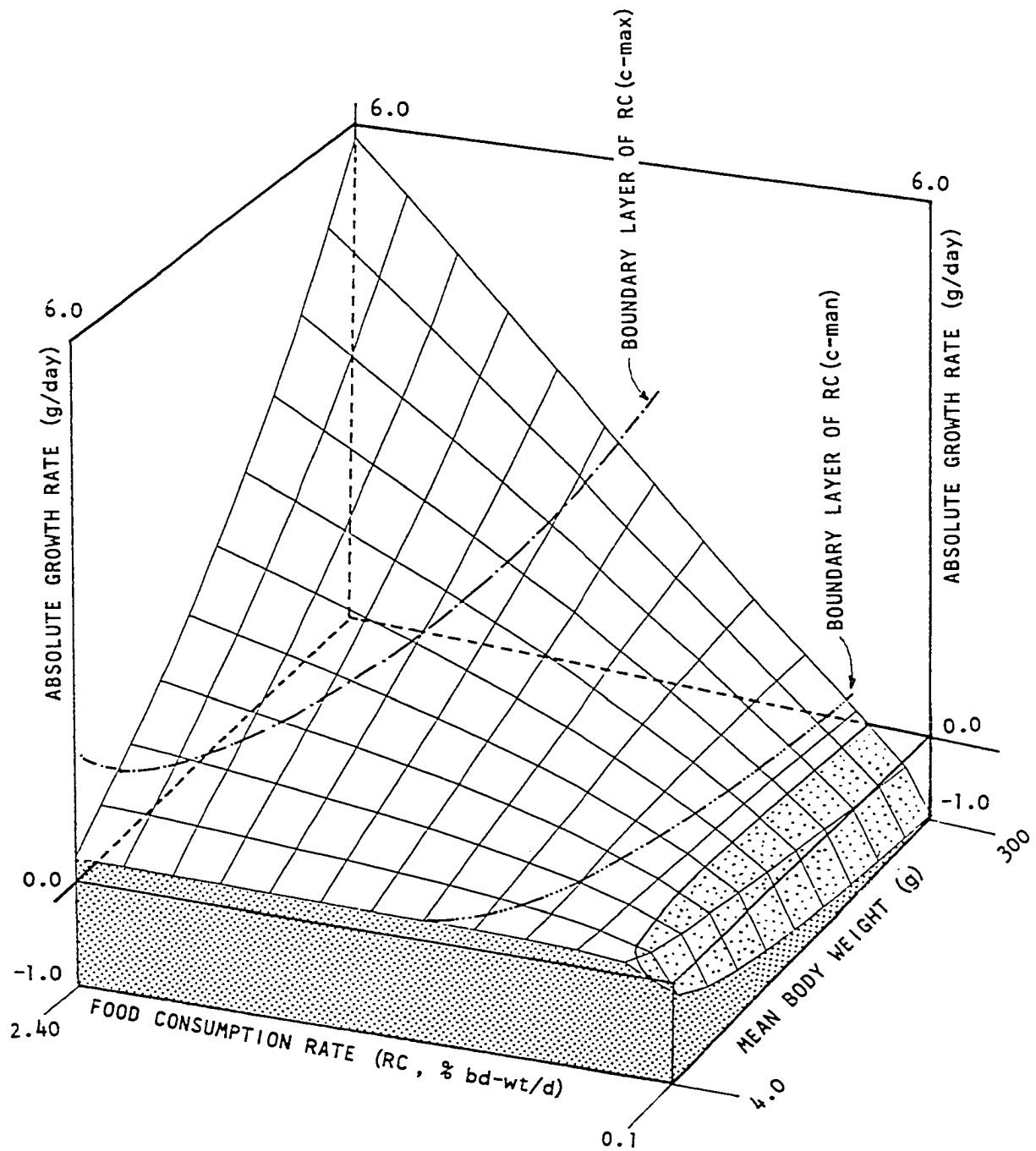
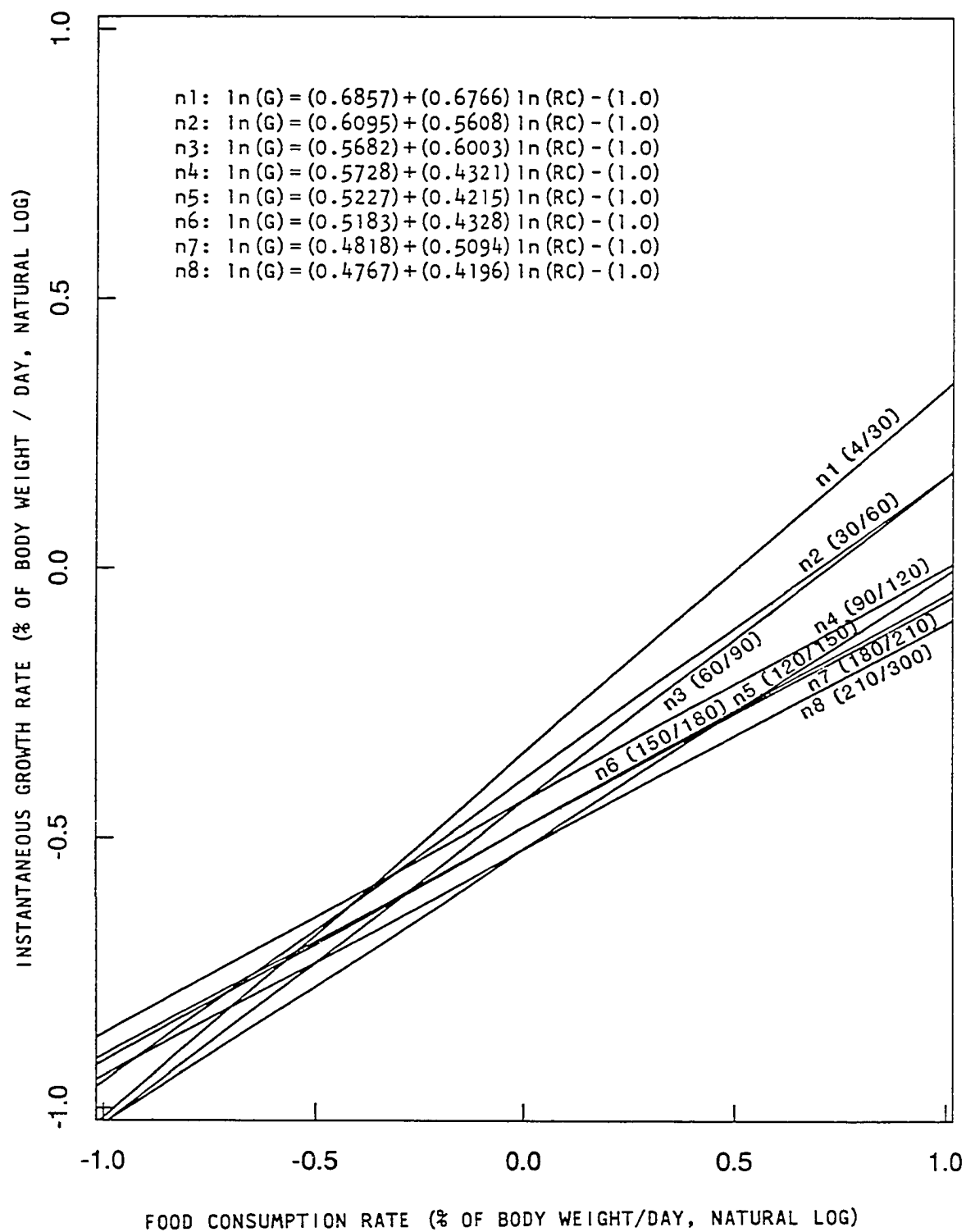


Figure 18

Instantaneous growth rate versus food consumption rate within fixed weights (G vs. RC / W) for fish fed commercial diet (n=1024). The 'n' number and number in parenthesis indicate group number of weight and the range of weight of corresponding weight groups (grams) (see Table 12b for details).





growth rate between the weight groups at the same food consumption rate was much less than that found in the absolute growth rate (see Figure 18). However, an opposite trend to the absolute growth rate was found in the instantaneous growth rates, in which the upper values of the growth rates were mostly obtained from the groups of small fish and the lower values were mostly obtained from the groups of large fish. The instantaneous growth rate tended to increase as the weight decreased at the high food consumption rate (above 0.9 % of body weight per day) but the tendency was not apparent when the food consumption rates were lower than 0.9 % of the mean body weight per day.

The equations derived for instantaneous growth rate in relation to food consumption rate (% of body weight /day) in the smallest weight group (4-30 g) and the largest weight group (210-300 g) of fish were:

$$G(c-4/30) = 1.932(RC)^{0.678} \quad (r^2=0.91, n=6) \quad (31)$$

$$G(c-210/300) = 1.611(RC)^{0.420} \quad (r^2=0.99, n=4) \quad (32)$$

where  $G(c-4/30)$  and  $G(c-210/300)$  are the instantaneous growth rates (% of body weight/day) of the fish weighing 4 - 30 g and 210 - 300 g respectively at the corresponding food consumption rate (RC) of fish fed the commercial diet (see Table 12b). The estimated instantaneous growth rate for the smallest fish (4.3 g) determined from the equation was 5.57 % of body weight/day at the maximum food consumption rate (4.79 % of body weight/day). This was 38 % lower than the value found in the maximum instantaneous growth rate calculated from the maximum growth rate (equation 20, 7.27 % of body weight/day). The estimated values showed close fitting to the calculated value for larger fish. The fish having

mean body weight of 295.2 g showed 6 % difference between the estimated and calculated values. No generalized equation was available since no uniform trends were found between the exponents and between the constants of proportionality of the equations obtained from eight weight groups ( $p(F) > 0.2$ ).

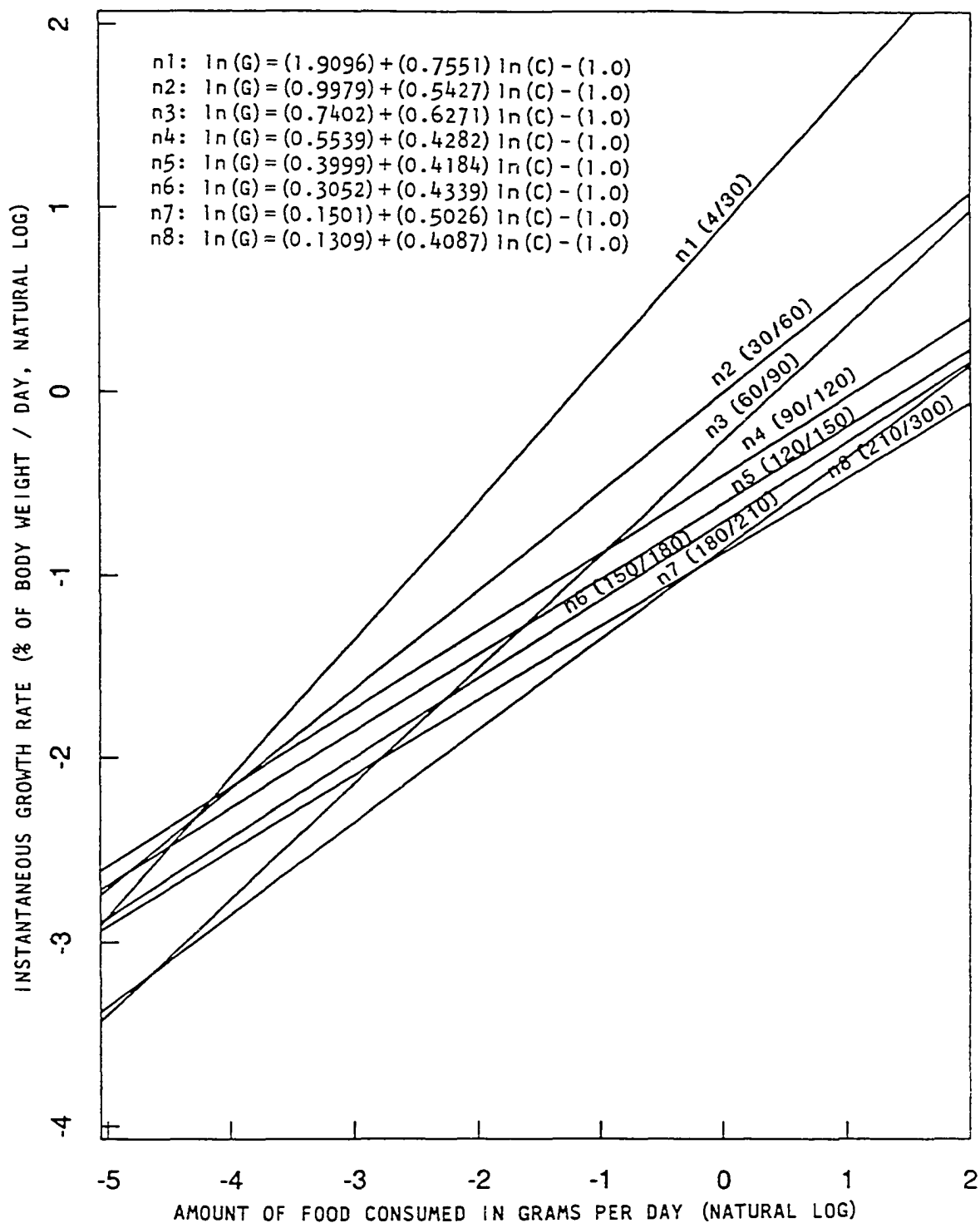
When instantaneous growth rate was related to the amount of the food consumed by individuals ( $C$ , g/day), the difference of the instantaneous growth rate between weight groups of fish increased as the amount of food consumed ( $C$ , g/day) increased as shown in Figure 19 and Table 12d. However, no consistent trend was found between weight groups in the instantaneous growth rates related to amount of food consumed (see Table 12d). The equations obtained from two weight groups ( $n_3$  and  $n_7$ ) showed higher values of exponents than those found from the rest of the weight groups resulting in more rapidly increasing rate of instantaneous growth as amount of food consumed by fish ( $C_{est}$ , g/day) increased. The equation derived in each weight group using group arrangement showed good fitting to the observed values with high values of determination coefficients ( $r^2 > 0.96$ ). However, a generalized equation could not be derived since no uniform trends were found between the exponents and between the constants of proportionality of the equations obtained from eight weight groups ( $p(F) > 0.05$ ) (see Table 12e).

#### Food Consumption for Maintenance

The level of the food consumption resulting in no weight gain or loss was regarded as the food consumption rate (% of body weight/day) for maintenance. It varied depending on the food type and the weight of the

Figure 19.

Instantaneous growth rate versus amount of food consumed within fixed weights (G vs. C / W) for fish fed commercial diet. The 'n' number and number in parenthesis indicate group number of weight and the range of weight of corresponding weight groups (grams) (see Table 12d for details).



fish. A total of 117 fish showed no weight changes during the growth experiments (n=1298, a total of 88 fish in the commercial diet experiments and 29 fish in the natural diet feeding experiments). Estimated individual food consumption rate (RCest, % of body weight/day) of fish showing no weight change tended to decrease as the weight of the fish increased. The equations derived from the observations for two food types using the group arrangement and regression analysis were:

$$RC(n\text{-man}) = 22.53 W^{-0.49} \quad (r^2=0.96, n=7) \quad (33)$$

and

$$RC(c\text{-man}) = 1.450 W^{-0.214} \quad (r^2=0.69, n=7) \quad (34)$$

where RC(n-man) and RC(c-man) represented the estimated individual food consumption rates (% of body weight/day) resulting in no weight change at the corresponding mean body weight of fish (W, grams) fed the natural diet and the commercial diet respectively. The equations indicated that the maintenance food consumption rate decreased faster in the natural diet feeding as the weight of the fish increased. At the same body weight fish fed the natural diet consumed more food than those fed the commercial diet by a factor of 3.2 - 8.8 to maintain their body weight over the observed weight range (4.3 - 295.2 g).

#### Food Conversion Rate

Food conversion rate (gross growth efficiency, Fm) is a comparative value between absolute growth rate (g/day) and the amount of food consumed by a fish (g/day) in producing the absolute growth rate. An alternative common expression for food conversion efficiency in feeding study of

aquaculture is a wet weight ratio between the amount of food consumed and the resulted absolute growth rate of fish ( $F_c = C : WG$ ).

Through the growth experiments, average food conversion rate of each experiment ranged from 0.06 to 0.92 ( $F_c = 16.8:1 - 1.1:1$ ). Poor food conversion rates were commonly observed in the natural diet feeding experiments ( $F_m = 0.06 - 0.23$  or  $F_c = 16.8:1 - 4.3:1$ ) where the average food consumption rate of each experiment ranged 1.9 - 5.0 % of body weight/day. The highest average food conversion rate ( $F_m = 0.23$ ) was observed in experiment 9b where the food consumption rate ( $RC_m$ ) was 2.5 % of body weight/day (see Table 4).

In the satiated commercial diet feeding experiments (experiment 5, 6, 7, 8, and 9c), food conversion rates ranged from 0.60 to 0.92 ( $F_c = 1.7:1 - 1.1:1$ ) while the average food consumption rate of each experiment ranged 0.9 - 1.5 % of body weight/day. Generally, much higher food conversion rates were recorded in the commercial diet over the test feeding level (see Appendix C). In reduced commercial diet feeding experiments (experiment 4, 12, and 9d), the food conversion rates of each experiment ranged from 0.52 - 0.92 ( $F_c = 2.0:1 - 1.1:1$ ) with the average the food consumption rates ( $RC_m$ ) ranging 0.8 - 1.0 % of body weight/day. The highest average food conversion rate was found in reduced commercial diet feeding (experiment 9d,  $F_m = 0.92$ ). The range of food conversion rate in each feeding condition showed in Table 5.

Negative correlations were found between average mean body weights of groups of fish ( $W_m$ ) and the average food conversion rates ( $F_m$ ) in seven of the nine experiments where fish were grouped by size (see Table 7). Highly significant and positive correlation coefficients were obtained

between the average instantaneous growth rate ( $G_m$ ) and the average food conversion rate ( $F_m$ ) in all experiments ( $r(G_m-F_m)=0.68 - 0.97$ ,  $p(D)<0.01$ ) except for experiment 9b.

The relations between the estimated individual food conversion rate and the estimated individual food consumption rate ( $R_{Cest}$ , % of body weight/day) of fish fed the commercial diet was shown in Figure 20. The food conversion rate, 0.0 was common at the food consumption rate below 0.4 % of body weight/day. As the food consumption rate increased, rapid increase of the food conversion rate was followed up to the food conversion rate approximately 0.8, then the increment was reduced until the maximum estimated individual food conversion rate was found ( $F_{est}=1.34$  or  $F_c=0.75:1$ ). In the commercial diet feeding the food conversion rates of individuals higher than 1.2 ( $F_c=0.8:1$ ) were mostly obtained from the fish smaller than 60 g and the estimated food consumption rate ( $R_{Cest}$ ) larger than 1.0 % of body weight per day.

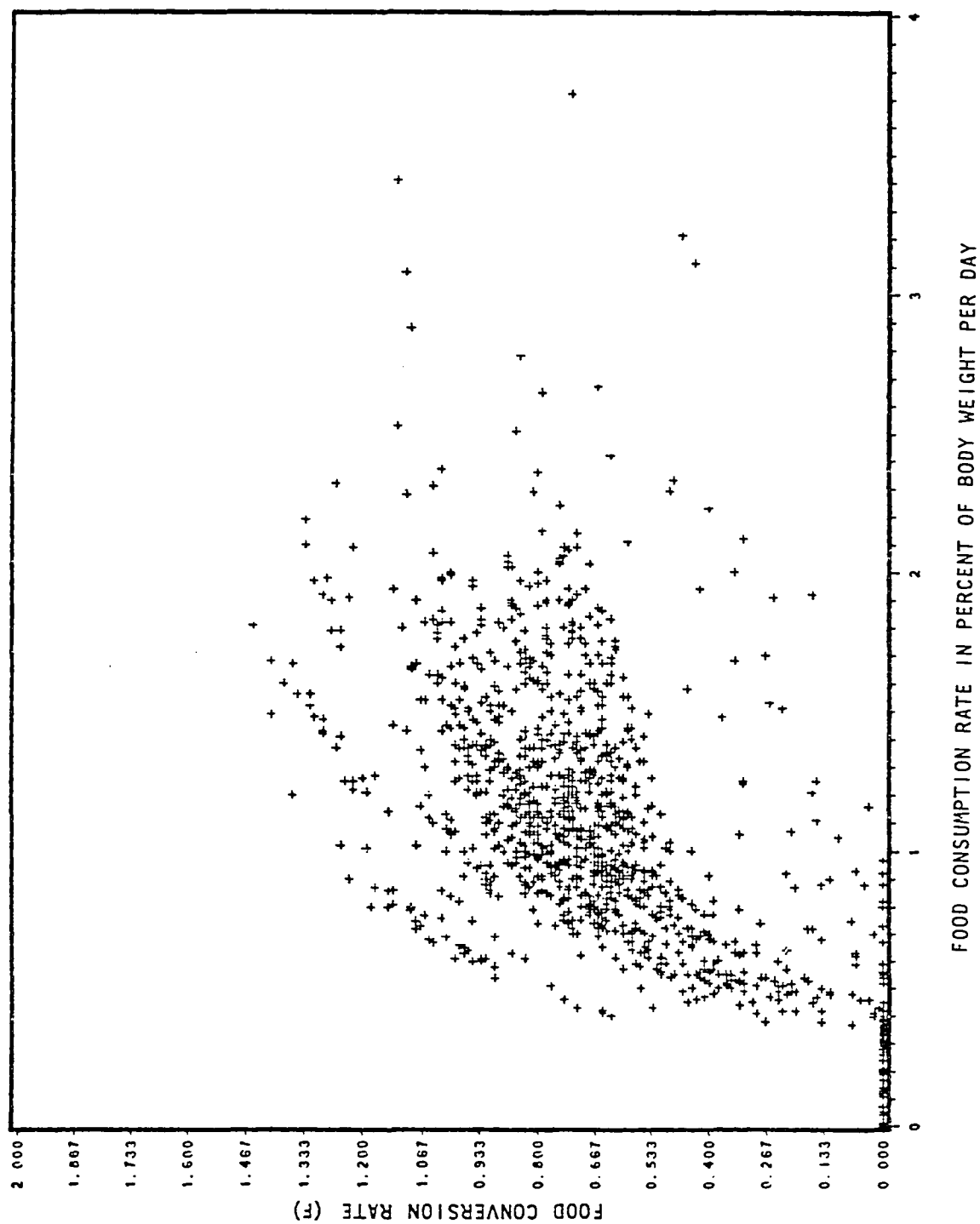
The groups of fish fed the commercial diets ( $n=109$ ) showed significantly positive relationship between the food consumption rate (% of body weight/day) and food conversion rate ( $r=0.61$ ,  $p(D)<0.01$ ). No significant correlation was found between food consumption rate and food conversion rate in the groups of fish fed the natural diet ( $n=10$ ,  $r=0.1$ ,  $p(D)>0.5$ ).

The food conversion rate of fish fed the commercial diet showed a significant relation to the instantaneous growth rate ( $n=989$ ,  $r=0.80$ ,  $p<0.01$ ). The instantaneous growth rate of the individuals tended to increase exponentially as the food conversion rate increased. The equation derived using regression analysis was:

Figure 20

Food conversion rate (Fest) versus food consumption rate (RCest, % of body weight/day) of fish fed the commercial diet (n=1022).





FOOD CONSUMPTION RATE IN PERCENT OF BODY WEIGHT PER DAY

FOOD CONVERSION RATE (F)

$$G = 1.32 (\text{Fest})^{1.57} \quad (r^2=0.80, n=989) \quad (35)$$

where G is instantaneous growth rate in percent of body weight per day and 'Fest' is the estimated food conversion rate of individual fish. The equation indicated that instantaneous growth rate rapidly increased as food conversion rate increased over the observed food consumption rate (0 - 1.34).

#### Condition Indices and Length-Weight Relationship

The cultured fish showed relatively uniform length-weight relationship (Figure 21). A typical exponential equation for weight-length relationship, which mean body weight was expressed as a power function of mean standard length, showed good fitting to the observations obtained from each experiment or overall experiments with the values of determination coefficients ( $r^2$ ) 0.95 - 0.99. The length-weight relationships obtained from fish in each experiment and in each feeding condition were listed in Table 13. The equation derived for weight-length relationship of all fish ( $n=1703$ ) was:

$$\ln(W) = -11.4122 + 3.1675 \ln(SL) \quad (r^2=0.98, n=1703) \quad (36)$$

where W is mean body weight in grams at the corresponding mean standard length in milli-meter. The equation showed that the weight-length relationship of all fish did not change significantly during the experimental period as the values of the exponent and the constant of proportionality of 3.1784 and 0.000001 for the beginning and 3.1860 and 0.000001 for the end of experiments respectively ( $p(F)>0.1$ ). The value of

Figure 21.

Weight-length relationship of all fish in growth  
experiments (n=1703).

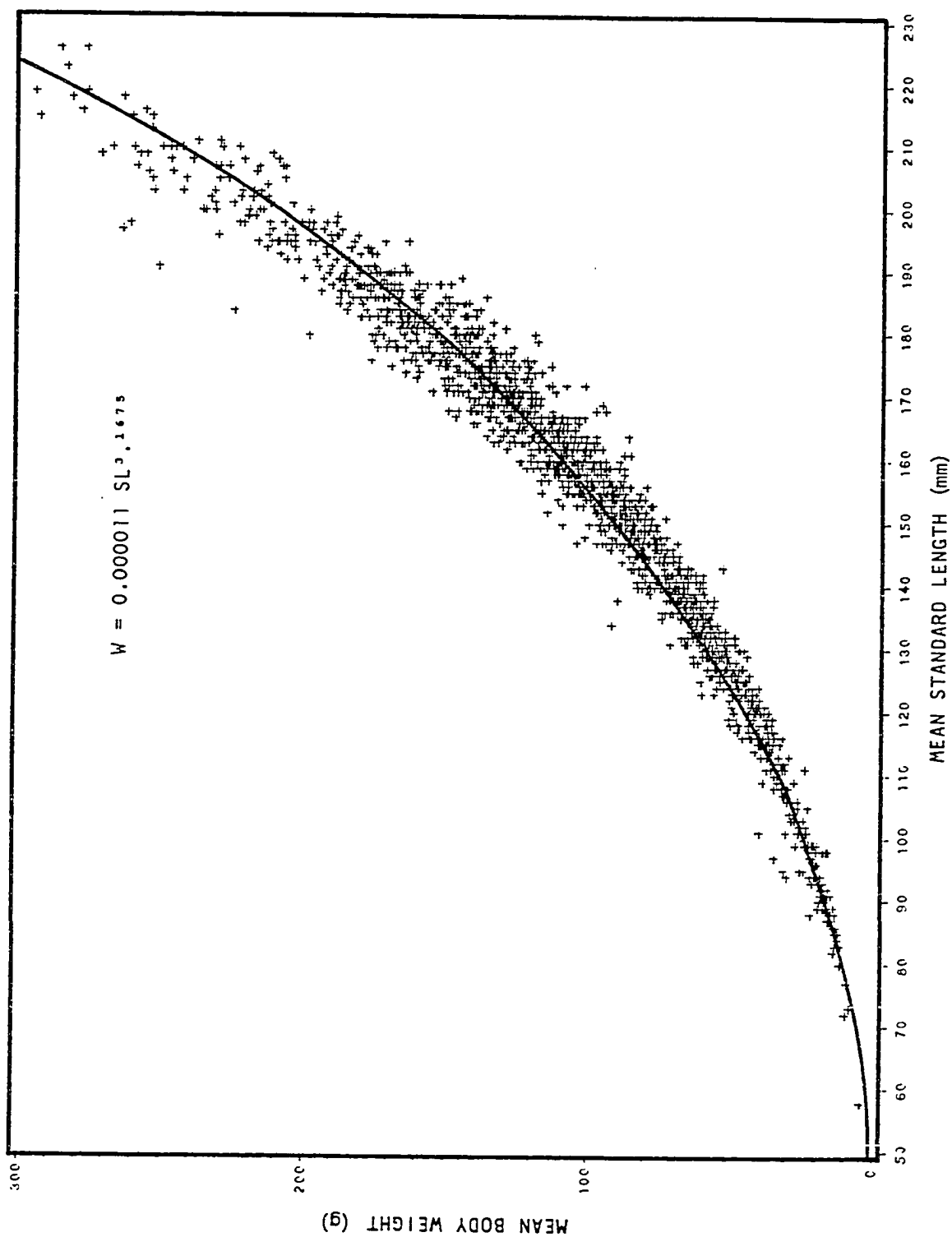


Table 13. Summary of regression analysis for length-weight relationship in each experiment.

| experiment.<br>number                              | number<br>of fish | constant of<br>proportion.<br>(A7) | exponent<br>(B7) | cceff. of<br>determinat.<br>(r <sup>2</sup> ) | p (T)<br>(Ho: B7=0) |
|--|-------------------|------------------------------------|------------------|---|---------------------|
| 1  | 75                | 0.000028                           | 2.9965           | 0.96  | p<0.0001            |
| 2  | 74                | 0.000017                           | 3.0892           | 0.98  | p<0.0001            |
| 3  | 74                | 0.000026                           | 2.9963           | 0.98  | p<0.0001            |
| 4  | 103               | 0.000015                           | 3.1007           | 0.97  | p<0.0001            |
| 5  | 180               | 0.000018                           | 3.0667           | 0.97  | p<0.0001            |
| 6  | 177               | 0.000012                           | 3.1532           | 0.97  | p<0.0001            |
| 7  | 187               | 0.000026                           | 3.008            | 0.95  | p<0.0001            |
| 8  | 186               | 0.000019                           | 3.0707           | 0.95  | p<0.0001            |
| 9  | 254               | 0.000007                           | 3.2672           | 0.99  | p<0.0001            |
| 10   | 263               | 0.000007                           | 3.2398           | 0.99  | p<0.0001            |
| 11   | 76                | 0.000009                           | 3.1886           | 0.95  | p<0.0001            |
| 12   | 54                | 0.000004                           | 3.3430           | 0.98  | p<0.0001            |
| Total<br>fish                                      | 1703              | 0.00001                            | 3.1675           | 0.98  | p<0.0001            |
| Starved<br>fish                                    | 212               | 0.00001                            | 3.2227           | 0.98  | p<0.0001            |
| Commercial<br>diet fish                            | 1161              | 0.00001                            | 3.2179           | 0.98  | p<0.0001            |
| Natural<br>diet fish                               | 330               | 0.000018                           | 3.080            | 0.98  | p<0.0001            |
| Equation ; $\log (W) = \log (A7) + (B7) \log (SL)$ |                   |                                    |                  |   |                     |

the exponent of the equation derived for weight-length relationship of fish in each experiment varied in a range of 2.9965 - 3.3430 . According to the equation, no significant change was found in length-weight relationship of fish during each experimental period. A trend was found between the exponent and the constant of proportionality of the equation obtained from each experiment for weight-length relationship: the constant of proportionality always changed inversely to the exponents in a range of 0.000004 - 0.000028. No significant difference was found between the fed fish and starved fish according to the equation for the lengthweight relationship ( $p(F) > 0.5$ ). Some individuals in each experiment showed rapid change of the length-weight relationship during the experimental period regardless of their growth rates. Most individuals showing the abrupt change of the weight-length relationship had the weight less than 50 g.

The values of the condition index (K) of the individuals ranged from 1.50 to 3.76 through all experiments, and the mean values of each experiment ranged from 2.21 to 2.84 with the average of 2.56 (see Table 14). Condition index did not show significant relationship with the mean body weight of the fish in all observations ( $p(D) > 0.05$ ). However, the changes of the condition index during each experimental period ( $dK$ ) showed significant relationship with absolute and instantaneous growth rates ( $r(G-dK) = 0.50-0.58$ ,  $r(WG-dK) = 0.52-0.64$ ,  $p(D) < 0.01$ ). This indicated that the growth of fish affected positively on the length-weight relationship of the fish.

The range of relative condition index (RK) was 0.653 - 1.670 at the beginning of each experiment and 0.636 - 1.801 at the end of the experiments. Except for the Experiment 12 in which all individuals ( $n=54$ )

Table 14. Summary of condition index and relative condition index in each experiment and each feeding condition.

| Number of exp.  | number of fish | average condition index (K) | avg. daily change of condition index (dK) | average relative condition index (RK) | avg. daily change of rel. cond. index (dRK) |
|-----------------|----------------|-----------------------------|---|---------------------------------------|---|
| 1               | 75             | 2.72                        | -0.25 (0.04)                              | 1.14                                  | -0.12 (0.02)                                |
| 2               | 74             | 2.57                        | -0.01 (0.02)                              | 1.05                                  | -0.01 (0.01)                                |
| 3               | 74             | 2.55                        | -0.04 (0.02)                              | 1.05                                  | -0.02 (0.02)                                |
| 4               | 103            | 2.45                        | 0.05 (0.01)                               | 1.02                                  | 0.02 (0.01)                                 |
| 5               | 180            | 2.52                        | 0.21 (0.01)                               | 1.03                                  | 0.07 (0.01)                                 |
| 6               | 177            | 2.63                        | 0.01 (0.01)                               | 1.06                                  | 0.00 (0.01)                                 |
| 7               | 187            | 2.67                        | 0.02 (0.01)                               | 1.07                                  | 0.00 (0.01)                                 |
| 8               | 186            | 2.71                        | 0.06 (0.01)                               | 1.08                                  | 0.02 (0.01)                                 |
| 9               | 254            | 2.58                        | -0.01 (0.01)                              | 1.04                                  | -0.01 (0.01)                                |
| 10              | 263            | 2.51                        | -0.08 (0.01)                              | 1.02                                  | -0.03 (0.01)                                |
| 11              | 76             | 2.46                        | -0.26 (0.02)                              | 0.97                                  | -0.11 (0.02)                                |
| 12              | 54             | 2.24                        | 0.08 (0.03)                               | 0.91                                  | 0.02 (0.03)                                 |
| <hr/>           |                |                             |   |                                       |   |
| total           | 1703           | 2.58                        | 0.00 (0.01)                               | 1.04                                  | -0.01 (0.01)                                |
| starved         | 212            | 2.41                        | -0.18 (0.01)                              | 0.96                                  | -0.08 (0.01)                                |
| natural diet    | 330            | 2.64                        | -0.08 (0.01)                              | 1.08                                  | -0.04 (0.01)                                |
| commercial diet | 1161           | 2.59                        | 0.05 (0.01)                               | 1.05                                  | 0.01 (0.01)                                 |

were previously exposed to long starvation periods up to 89 days, 72 % of the total fed fish ( $n=1437$ ) showed the values of the RK higher than 1.00 with the average value of 1.04, which was not significantly different from 1.00 ( $p(T)>0.1$ ).

The relative condition index and length-weight relationship of the cultured fish indicated that the fish did not differ significantly from the those in natural population (Mercer, 1978) in length-weight relationship. Therefore, the cultured fish were not inferior to that of the natural population in terms of relative heaviness or weight-length relationship.

Positive correlation coefficients ( $r=0.22 - 0.66$ ) were found between the change of condition index and the absolute growth rate in all experiments except two experiments (experiment 10 and 12). Significant correlation coefficients were obtained between the change of relative condition index and the instantaneous growth rate in each experiment ( $r=0.30 - 0.85$ ,  $p(D)<0.05$ ). This indicated that the condition index and the relative condition index could be also used as indice of growth of fish as well as condition indicators.



### Patterns of Energy Expenditure

In the previous section the potential quantitative growth of fish related to food type, food consumption rate, and body weight of fish was considered in terms of wet weight or percent of body weight from the aquacultural point of view. Since growth of fish primarily depends on the physiological processes, the basic pattern of energy transfer in each component of energetics of fish should be understood to extend the knowledge of the potential growth of fish. To detect the energy input in food consumption and the energy allocation for growth-related energetics of fish, the basic components of energetics of the cultured fish were examined as follows: (1) the energy expenditures for metabolism (standard, routine, and feeding metabolism), (2) energy input related to food consumption rate and type of food, (3) energy loss in excretion and defecation, and (4) energy deposition in growth. The energetic values of food, fish, excreta, and feces were primarily expressed as calories per unit weight (dry weight or wet weight) and the relationships expressed as mathematical forms were derived using regression analysis and group arrangement except for the simulated forms using more than one equation described in the previous section.

#### Standard Metabolism

Standard metabolism of fish is regarded as the basal energy expenditure of fish for normal existence in the condition of no external activities (feeding and locomotive activities). The standard metabolism of the cultured fish was assessed by measuring the oxygen consumption rate in the defined condition and by converting into caloric value using an

oxycaloric equivalent, 4.63 cal/ml-oxygen (Brett and Groves, 1979).

A total 105 tested individuals weighing 10.5 - 274.8 g showed a typical tendency that the total amount of oxygen consumed by a fish increased as weight of fish increased but the oxygen consumption rate per unit body weight decreased as weight of fish increased (see Figure 22). The equations for total oxygen consumed by a fish in a unit time (OCstd, ml-oxygen/min) and oxygen consumption rate per unit body weight per unit time (ORstd, ml-oxygen/g/min) in relation to mean body weight of fish (W, grams) were derived using group arrangement and regression analysis as follows:

$$OCstd = 0.00342 W^{0.8435} \quad (r^2=0.99, n=9) \quad (37)$$

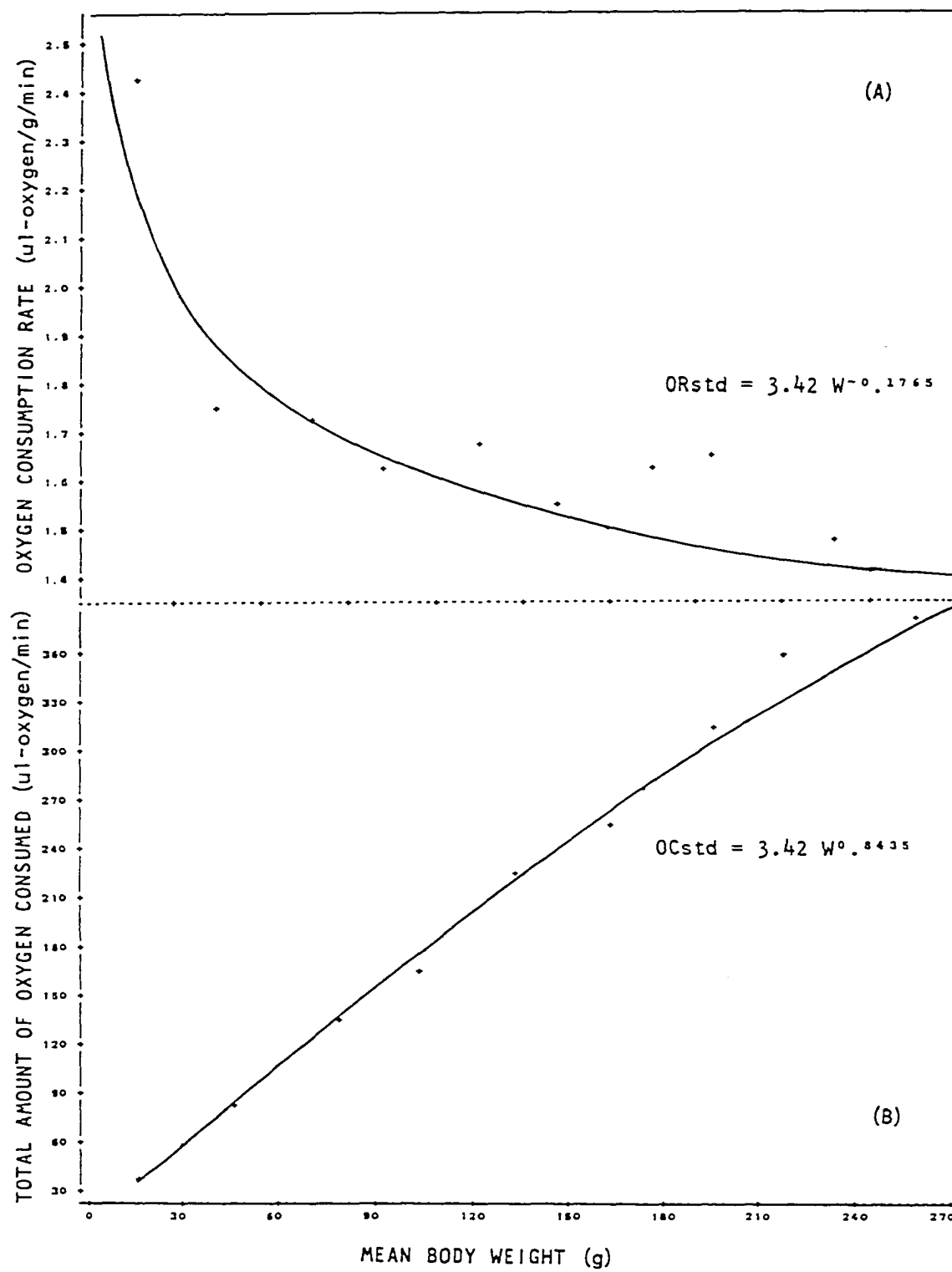
$$ORstd = 0.00342 W^{-0.1565} \quad (r^2=0.92, n=9) \quad (38)$$

where 'OCstd' and 'ORstd' indicate the total amount of oxygen consumed (ml-oxygen/min) and oxygen consumption rate per unit body weight (ml-oxygen/g/min) respectively at the corresponding body weight 'W' in grams. The exponent of equation 37 (0.8435), indicated that the total amount of oxygen consumed by fish increased rapidly following weight increase. The increasing rate of the weight-specific oxygen consumption was larger than any weight-specific growth rates found in the equations derived for weight-specific growth, where the exponents typically ranged between 0.3 and 0.7. Both equations indicated that the total amount of oxygen consumed by fish increased exponentially with weight but the oxygen consumption rate per unit body weight decreased exponentially as weight of fish increased.

Both equations showed good fitting to the values of observations

Figure 22

Weight-specific oxygen consumption rates of fish in standard metabolism (n=105): (A) oxygen consumption rate per unit body weight versus body weight ( $OR_{std}$  vs.  $W$ ), and (B) total amount of oxygen consumed versus body weight ( $OC_{std}$  vs.  $W$ ). Data-points indicate representative values of oxygen consumption in weight intervals and corresponding mean body weights in group arrangement. The number of weight groups is nine.



with the coefficients of determination, 0.99 and 0.92 respectively. Relatively large variation was found in the oxygen consumption rate per body weight in small fish and caused the lower  $r^2$  value in the equation for 'ORstd' than that for 'OCstd'. The results also showed that the variation of weight-specific oxygen consumption (ml-oxygen/g/min) for standard metabolism at the same body weight was much less than the variation found in weight-specific growth rate of the fed fish. The results were similar to those obtained from the starvation experiments, where individual variation of weight loss of fish at the same weight was much less than those found in the fed fish.

The results found in the equations could be converted into energy unit (cal/day) using 4.63 cal/ml-oxygen (Brett and Groves, 1979) and the daily energy expenditure for standard metabolism could be expressed as:

$$E(c\text{-std}) = 22.80 W^{0.8435} \quad (37-1)$$

$$E(r\text{-std}) = 22.80 W^{-0.1565} \quad (38-1)$$

where  $E(c\text{-std})$  and  $E(r\text{-std})$  represent the energy equivalent of the amount of oxygen consumed (OCstd) per day (cal/day) and the oxygen consumption rate per unit body weight (ORstd) per day (cal/g/day) of fish for standard metabolism expressed as calories per day at the corresponding body weight 'W' in grams.

### Waste Production

#### 1) Feces Production

A total of 112 samples were collected from all compartments of the

culture system in experiment 10. The results of the analysis revealed poor relationship between the weight or the food consumption rate and the feces production rates ( $r=0.03 - 0.14$ ,  $p(D)>0.10$ ). The dry weight of the feces produced during the experiment ranges from less than 0.01 g/day to 0.25 g/day for the fish fed the commercial diet ( $n=86$ ) and from 0.13 g/day to 2.90 g/day for fish fed natural diet ( $n=26$ ). The amount of food given to the fish ranged from 1.2 g/day to 13.9 g/day ( $n=86$ ) with the average of 6.7 g/day in the commercial diet feeding. The amount of the natural diet given to the fish ranged from 9.5 g/day to 69.2 g/day with the average of 21.6 g/day ( $n=26$ ).

The feces production rate of the fish fed the commercial diet was extremely low at 0.01 - 5.6 % of the dry weight of the food with the average of 2.2 % of dry weight of food. Approximately 72 % of the samples showed that the production rates were below 1 % of dry weight of food in the commercial diet feeding. A few samples ( $n=7$ ) showed the large amount of feces production in a range of 4.1- 5.6 % of dry weight of food. The feces production in the natural diet feeding was significantly higher than that of commercial diet feeding in the range from 0.2 % to 14.6 % of dry weight of food with the average of 6.9 % ( $p(T)<0.01$ ).

The collected feces in both diet feedings indicated no damage of feces during the collecting procedure as the typical round pellet shapes were preserved. Since the culture system was in abnormal condition due to high ammonia level (average of 0.06 ppm) during Experiment 10, food consumption rate of the fish was poor in all size. The amount of feces produced by the fish was also regarded to be abnormal due to the condition of the system during the experiment. Therefore, the data obtained from

this experiment were regarded to be not adequate to represent the normal feces production rate of the test fish.

## 2) Excretory Production

The fish maintained in the noncirculating water with a dark photoperiod varied greatly in ammonia production. The large variation occurred over the observed weight range (11.4 - 169.7 g with the average of 62.7 g). The amount of ammonia produced daily by the fish ranged from 0.06 mg to 37.4 mg with the average of 17.6 mg ( $n=49$ ,  $SE.=3.4$ ), which was equivalent to 86.1 cal/day in caloric values. The average energy expenditure per unit body weight was 1.4 cal/g-wet weight/day, which was too low compared to energy expenditure for standard metabolism : fish weighing 4.3 g and 295.2 g consumed 18.1 cal/g-wet weight/day and 9.4 cal/g-wet weight/day respectively. Since the condition of excretion experiments was regarded as routine metabolic state (including standard metabolism, feeding, and routine activities), the values obtained in this experiments were exceptionally low.

The correlation coefficient in the relationship between the weight of the fish and the ammonia production rate is 0.27 ( $p(D)<0.05$ ), which indicates that poor but significant change of ammonia production occurs with change of the weight of the fish. However, no regression line was calculated due to the low  $r^2$  values (0.37,  $p(T)>0.05$ ). Due to unacceptably low values in excretion rates, some experimental errors were regarded to be involved.

### Caloric Equivalents

The caloric values of the fish, food, and feces were measured using the direct method. The commercial diet, Rangen-Zeigler Soft-moist diet, revealed homogeneous and high caloric values. With the average moisture content 15.0 % ( $n=67$ ,  $se=0.01$ ), 33 samples of the commercial diet resulted in the average 5691 cal/g-dry weight with a range of 5625 - 5706 cal/g-dry weight ( 4827 - 4906 cal/g-wet weight with the average value of 4869 cal/g-wet weight). No significant difference in energy value was found between large and small pellets ( $p(T)>0.1$ ).

The natural diet, mole crabs, is characterized by low caloric content with large variation in caloric values between samples. A total of 45 samples of the natural diet revealed several different values between size and between the season of sampling. The lowest average caloric value, 3392 cal/g-dry weight, was found in the small size mole crabs caught on May 1986 ( $n=7$ ). The largest values, 3802 cal/g-dry weight, was found from the large size mole crabs caught in the same day ( $n=6$ ). Significant difference in caloric values was found between two sizes of mole crabs ( $p(T)<0.05$ ). The caloric values found from the mole crabs caught on November, 1985 showed relatively homogeneous values as 3467 - 3716 cal/g-dry weight with the mean of 3569 cal/g-dry weight ( $n=11$ ,  $se=11.7$ ). Mole crabs caught on April 1986 also showed homogeneous caloric values in a range of 3576 - 3754 cal/g-dry weight with the average of 3621 cal/g-dry weight ( $n=9$ ). Though the variation was significant in two sizes of the mole crabs caught on May 1986, the rest of the samples showed no significant difference between sizes and between sampling seasons. The average caloric value of all samples ( $n=33$ ) was 3629 cal/g-dry weight and the largest variation of the caloric values was approximately 9 % of the



average values.

The average water content of the mole crabs was 68.7 % ( $n=56$ ,  $se=0.02$ ) and the corrected value for moisture loss in frozen condition was 71.7 %. The average caloric value of the mole crabs in wet weight was 1027 cal/g-wet weight.

The feces produced by fish fed the commercial diet showed the caloric values in a range of 3631 - 3685 cal/g-dry weight with the average of 3655 cal/g-dry weight ( $n=5$ ). Since the caloric value of the feces were measured from the combined sample due to low feces production rate of the fish, the difference of caloric values in each group of the fish could not be measured.

The feces produced by fish fed the natural diet showed low caloric value with high ash content. Calorific values of the feces varied in a range of 962 - 1048 cal/g-dry weight with the average of 1009 cal/g-dry weight ( $n=12$ ). The average content of ash was 70.1 %. The relatively homogeneous caloric values of the feces was also caused by premixing before the measurement due to low production rate by the tested fish.

A total of 66 samples prepared from 22 fish showed a large variation in caloric value between samples and even between replicates. The range of the caloric values of the fish was 5431 - 7345 cal/g-dry weight. Approximately 65 % of the samples had values between 6400 - 6800 cal/g-dry weight. The average caloric value was 6537 cal/g dry weight ( $n=66$ ,  $se=29.7$ ). No significant relationship was found between the weight and the caloric values of fish ( $r=0.12$ ,  $p(D)>0.2$ ).

The caloric values of tissue (meat portion) of fish were lower than the samples prepared from the whole body. The average caloric value for

the meat was 6025 cal/g-dry weight ( $n=4$ ,  $se=69$ ). Four samples of fish scale showed relatively homogeneous values in a range of 2525 - 2648 cal/g-dry weight with the average value of 2536 cal/g-dry weight ( $n=4$ ).

The average caloric value of the whole body of fish in wet weight was calculated from the 33.3 % corrected moisture content and the average scale weight of 7.2 % of total weight. The estimated caloric equivalent of the fish was 2203 cal/g-wet weight. The ash content was negligible in all samples of fish body.

#### Energetics in Food Consumption and Growth

When food is consumed by a fish, the quantity and quality of food are directly reflected in total energy contents in the consumed food by the fish as gross energy input. Energy input related to food consumption as well as energy deposit on body tissues for growth is mainly related to the physiological activities of fish when abiotic environmental factors are constant and food is provided at satiation level. Using caloric equivalents of foods (4869 cal/g-wet weight for the commercial diet and 1027 cal/g-wet weight for the natural diet) and fish (2203 cal/g-wet weight), the equations derived as a function of weight (weight-specific maximum food consumption and growth, weight-specific maintenance food consumption, weight-specific weight loss in starvation) were converted into energetic forms and summarized in Table 15. The energy gain and the energy allocation in some energetic components were calculated for fish weighing 4.3 g and 295.2 g (minimum and maximum weight observed in this study) using the equations and summarized in Table 16.

When energy input related to maximum food consumption was compared between food types, 4.3 g fish fed the commercial diet consumed less

Table 15. Summary of equations for energetics transformed from the weight-specific food consumption, growth, and oxygen consumption.

| symbol of equation                                     | description                  | expression       | remark     |
|--|------------------------------|------------------|------------|
| <u>I. Energy in Total Growth and Food Consumption*</u> |                              |                  |            |
| <u>A. Natural Diet</u>                                 |                              |                  |            |
| Ewg(n-max)   | maximum growth               | $41 W^{0.701}$   | *** (17-1) |
| Ec(n-max)  | maximum food consumption     | $1109 W^{0.411}$ | (23-1)     |
| Ec(c-max)  | maintenance food consumption | $231 W^{0.513}$  | (33-1)     |
| <u>B. Commercial Diet</u>                              |                              |                  |            |
| Ewg(c-max)   | maximum growth               | $319 W^{0.512}$  | (19-1)     |
| Ec(c-max)  | maximum food consumption     | $340 W^{0.709}$  | (24-1)     |
| Ec(c-man)  | maintenance food consumption | $71 W^{0.786}$   | (34-1)     |
| <u>C. Starved Condition</u>                            |                              |                  |            |
| Ewg(stv)   | weight loss                  | $41 W^{0.675}$   | (21-1)     |
| E(c-std)   | standard metabolic rate      | $23 W^{0.844}$   | (38-1)     |

I. Energy in Growth and Food Consumption per Body Weight\*\*

|                             |                              |                   |        |
|-----------------------------|------------------------------|-------------------|--------|
| <u>A. Natural Diet</u>      |                              |                   |        |
| Eg(n-max)                   | maximum growth               | $41 W^{-0.300}$   | (17-2) |
| Erc(n-max)                  | maximum food consumption     | $1109 W^{-0.509}$ | (23-2) |
| Erc(n-man)                  | maintenance food consumption | $231 W^{-0.487}$  | (33-2) |
| <u>B. Commercial Diet</u>   |                              |                   |        |
| Eg(c-max)                   | maximum growth               | $319 W^{-0.488}$  | (19-2) |
| Erc(c-max)                  | maximum food consumption     | $340 W^{-0.191}$  | (24-2) |
| Erc(c-man)                  | maintenance food consumption | $71 W^{-0.214}$   | (34-2) |
| <u>C. Starved Condition</u> |                              |                   |        |
| Eg(stv)                     | weight loss                  | $41 W^{-0.325}$   | (21-2) |
| E(r-std)                    | standard metabolic rate      | $23 W^{-0.156}$   | (38-2) |

\* Equations were directly transformed from originals by applying energy equivalent values (unit: cal/day).

\*\* Equations were derived from the upper equations dividing by weight: (unit: cal/g-wet weight/day).

\*\*\* Equation number: first number indicates the number of original equation.

Table 16 Calculated energy intake, energy consumption, energy deposit for growth with energy allocation over total energy input in two diet types (weights are minimum and maximum weights of fish observed in this study).

| symbol  | description                         | natural diet      |                     | commercial diet   |                     |
|---|-------------------------------------|-------------------|---------------------|-------------------|---------------------|
|   |                                     | weight<br>(4.3 g) | weight<br>(295.2 g) | weight<br>(4.3 g) | weight<br>(295.2 g) |
| I <u>Energy Input and Allocation for Growth and Metabolism*</u> |                                     |                   |                     |                   |                     |
| Eg (max)  | energy gain in maximum growth       | 26.5              | 7.5                 | 156.2             | 19.7                |
| Erc (man)   | maintenance energy expenditure rate | 113.1             | 14.3                | 52.2              | 20.9                |
| Erc (max)   | maximum energy intake rate          | 469.1             | 38.7                | 222.7             | 65.3                |
| Estv  | energy loss in weight loss          | 25.3              | 6.4                 | 25.3              | 6.4                 |
| Er (std)  | standard metabolism                 | 18.1              | 9.4                 | 18.1              | 9.4                 |
| E (atv) **  | energy expenditure for activity     | 94.8              | 4.9                 | 26.9              | 14.5                |
| E (phy) ***   | physiologically available energy    | 139.6             | 21.8                | 208.1             | 40.6                |
| -----   |                                     |                   |                     |                   |                     |
| II <u>Energy Allocation over Total Input****</u>                |                                     |                   |                     |                   |                     |
| Eg (max) /Erc (max)   | gross growth efficiency             | 6                 | 19                  | 70                | 30                  |
| Erc (man) /Erc (max)  | metabolic expenditure               | 24                | 37                  | 23                | 32                  |
| $\frac{Eg (max) + Erc (man)}{Erc (max)}$                        | physiological energy                | 30                | 56                  | 93                | 62                  |

\* Unit: cal/g-wet weight/day or cal/g-body weight/day.

\*\* Energy expenditure for activities (feeding and locomotion): the values were obtained by the equation:  $E (atv) = Erc (man) - Er (std)$ .

\*\*\* Energy available for growth and metabolism (physiological energy): The values were obtained by the equation:  $E (phy) = Erc (man) + Eg (max)$ .

\*\*\*\* Unit: percent of gross energy.

energy (cal/g-body weight/day) than those fed the natural diet (223 cal/g-body weight/day and 469 cal/g-body weight/day respectively). At 295.2 g body weight, the tendency was opposite as fish fed the commercial diet consumed more energy than those fed the natural diet (65.3 cal/g-body weight/day and 38.7 cal/g-body weight/day). The energy consumption for maintenance showed the same pattern.

When energy allocation in energetic components was considered, fish consumed 23 - 37 % of the gross energy for maintenance, when no weight gain in body tissues occurred. Small fish consumed less energy (cal/g-body weight/day) for maintaining body weight than large fish. When maximum food consumption and maximum growth rate were combined at the same body weight, fish fed the commercial diet showed more energy deposit into the body tissues for growth (30 - 70 % of gross energy) than those fed the natural diet (6 - 19 % of gross energy). Energy consumption during starvation, which was represented as routine metabolism (standard metabolism and routine activities without feeding) indicated that small fish consumed certain amounts of energy for activities over the energy expenditure for standard metabolism but large fish abnormally consumed less energy for routine metabolism than for standard metabolism. Caloric estimation in weight loss of starved fish was regarded to be erratic due to body composition change as noted by Brett and Groves (1979).

When gross growth efficiency was compared in each experiment and in each feeding condition from an energetic point of view, fish fed the natural diet generally showed poor gross growth efficiency with a range of 0.16 - 0.17 except for one experiment (experiment 9b). In experiment 9b, where the highest growth rate of fish was observed among the natural diet

experiment, the highest gross growth efficiency, 0.47, was obtained among all experiments. Fish fed the commercial diet at satiated feeding level showed similar values between experiments in a range of 0.29 - 0.37 (average 0.32). The gross growth efficiency over 0.4 was observed in two reduced feeding experiments (experiment 4 and 9d) and the lowest gross growth efficiency (0.23) was obtained from the fish in experiment 12, where fish were starved for long periods (41 - 83 days) before the experiment. No consistent trend was found between gross growth efficiency and energy input related to food consumption.

When the result obtained from experiment 9b were compared with 9d, the energy gains in growth of fish fed the natural diet at satiated feeding level (1740 cal/day) showed the similar value to that obtained from the fish fed the commercial diet at reduced level (1850 cal/day). Fish in both experiments showed the similar values for energy intake (3697 and 4382 cal/day respectively). The results indicated that the growth of fish was rather related to the quantity of energy in food than the quality of diets used for this study. Therefore, the qualities of two diets used for this study were regarded to be similar in terms of growth production. However, the volume of the natural diet was much larger than that of the commercial diet for the same energetic values and resulted in less energy intake of fish fed the natural diet than that of fish fed the commercial diet due to limited stomach capacities at satiated feeding level. No significant trend was found between energy input in food consumption and gross growth efficiency.

#### Growth Potential in Maximum Food Intake

As found in the previous section, growth, food consumption rate, and

the energy consumption can be expressed as a function of weight (see equation 15 through 24, and Table 15). To roughly estimate the potential growth of fish fed the commercial diet in relation to maximum food consumption following common expression (see equation 14), the equations derived for weight-specific maximum food consumption and maintenance food consumption were transformed into the equations expressed as energy equivalent units as shown in Table 15. The equations are:

$$\text{Erc(c-max)} = 340 W^{-0.292} \quad (24-2)$$

$$\text{Erc(c-man)} = 71 W^{-0.214} \quad (34-2)$$

where  $\text{Erc(c-max)}$  is the energy equivalent in cal/g-body weight/day obtained at maximum food consumption rate,  $\text{Erc(c-man)}$  is the energy equivalent in cal/g-body weight/day in maintenance feeding level (amount of food consumed for no weight change under normal activities and feeding condition), and 'W' is mean body weight. Both equations represent the maximum gross energy obtained by a fish having a weight 'W' and energy consumption for maintenance of a fish having a weight 'W' respectively.

To estimate the physiologically available energy for metabolism and growth, waste energy in defecation, excretion, and anabolic processes should be determined. Since feces and excreta production were unacceptably low in the experiments, the energy losses were estimated from the reference values (Brett and Groves, 1979) considering the results found in gross growth efficiency of satiated commercial diet feeding experiments. The average gross growth efficiency found in the satiated commercial diet feeding in this study (0.32) was similar to those found from other carnivorous fishes (0.29) and thus the applied assumption was

that total energy loss for feces, excreta, and anabolic processes was 48 % of gross energy following Brett and Groves (1979) (20 % energy loss for feces, 7 % energy loss for excreta, 14 % energy loss for anabolic processes, and 7 % energy loss for feeding excitation). The rest of the gross energy (52 %) was regarded as physiologically available energy for growth and metabolism. As the metabolic energy expenditure can be represented by energy expenditure for maintenance ( $E_{rc(c-man)}$ ), the weight-specific maximum growth potential in an energetic term can be expressed as:

$$P = 0.52 (340 W^{-0.292} - 71 W^{-0.214}) \quad (39)$$

where 'P' is maximum growth potential (cal/g-body weight/day) at the corresponding weight 'W'.



## CHAPTER IV

## DISCUSSION

Although growth of fish is readily observed and easily measured, it is a resultant of complex processes of living phenomena. The physiological and behavioral activities related to growth of a fish make up various interactions between a fish and its environments. Among various environmental factors, temperature and food are known to be critical factors determining the physiological process involved in growth of fish.

When fishes are cultured in artificial environments, manipulating their natural environments is a typical and primary method in providing adequate abiotic or hydrological conditions for growth of fish. The difficulties of culturing fishes are that, even though environments are well defined as adequate conditions for fish to grow, individual-specific physiological conditions of fish, which determine the pattern of internal energy transfer, may not allow the fish to grow. Between individuals having the same morphological and ecological conditions, the variation of individual growth related to physiological characteristics of fish is, therefore, frequently large enough to hide the general pattern of growth of the fish in relation to well known environmental factors.

Numerous studies have been conducted to investigate the growth of fish in relation to abiotic and biotic factors: major concerns are (1) quantity and quality of dietary sources, (2) growth-related physiological and behavioral activities, (3) effects and regulating mechanism of environmental factors on growth, and (4) energy transfer and growth in

natural populations.

Despite the great volumes of literatures in the studies of growth of fish, adequate information for practical culture of fish, especially for enhancing growth, is hardly obtainable due to (1) limit of information to species-specific levels, (2) specified approaches resulting in little flexibility to apply the knowledge for other purposes including practical fields, (3) few attempts to investigate overall pattern of growth at energetic level, and (4) difficulties in culturing live fish in large scale for growth study. Feeding and nutritional studies of fish, which are typical approaches found in aquaculture, result in not only providing limited intraspecific information but also frequently neglecting essential physiological processes regulating growth of fish. Focusing growth on enzymatic activities in physiological processes does not permit understanding overall pattern of growth of fish at individual or at ecological levels. Studying growth of fish in natural population provides information about general pattern of species-specific growth but frequently ignores the differentiation of individual growth related to its physiological and behavioral peculiarity as well as specific growth potential in modified environments.

The interaction between environmental factors and growth of fish at individual level of fish has been investigated under the term of 'bioenergetics', since Ivlev (1939) established the general pattern of energetics of a fish. The general objectives of bioenergetic studies are to understand the pattern of energy allocation in growth-related physiological processes in relation to environmental factors. However, the ultimate goals of this kinds of studies are focused on growth of fish.

To improve the understanding of growth of fish it is necessary to investigate the important environmental factors affecting growth from an ecological point of view as well as internal energy transfer mechanism from an energetic point of view. changes of fish.

#### Culture of Black Sea Bass

Little information has been accumulated on culture of marine fishes. Compared to the large number of freshwater species involved in extensive researches and commercial cultures worldwide, only a few marine species have been subjected to commercial culture. Due to complicated requirement and restricted circumstances, culturing marine fishes was often avoided in researches except for some commercially important species (i.e., salmon, mullet, seabream, plaice, milkfish, yellowtail, etc.).

When marine fishes are classified by temperature preference, warm water species dominate cold water counterparts in number of species and in geographic distribution in nature. Nevertheless, warm water marine fishes have been almost excluded from aquaculture historically compared to cold water species such as salmonoid fish, for which tremendous amounts of information have been accumulated for several decades (Parker and Davis, 1979). Most warm-water species have been ignored in their cultural potential due to (1) variety of species resulting in less information for each species, (2) minor importance in commercial fisheries, (3) underdeveloped species-specific culture technology, and (4) difficulties in larvae culture associated with complicated food and habitat requirements.

The intensive culture of marine fish in closed culture system is extremely difficult as Spotte (1979) and Brett and Sutherland (1970)

pointed out. Aside from the essential biological and ecological information of cultured fish, sophisticated facilities and equipment as well as intensive, time-consuming care are always required to provide adequate culture condition even in small scale culture (Parker and Davis, 1979). Water quality deterioration is commonly found in marine culture systems due to lack of proper and generalized feasible technology.

Inadequate or unbalanced culture systems frequently result in serious culture failure with poor growth and mass mortality as found in an experiment of this study. In experiment 10 the low growth rates and the low food consumption rates were found in all size groups of fish. In the commercial diet feeding (experiment 10c and 10d) the lowest growth rates were found among all commercial diet experiments as less than 0.4 g/day for the average absolute growth rate and 0.4 % of body weight/day for the average instantaneous growth rate. In experiment 10c two of the ten groups even showed negative average group growth rate despite satiated feeding. Food consumption rates of fish were relatively low (less than two third of other satiated feeding) in both natural and commercial diet feedings.

During the experiment the culture system was in serious failure due to power outage. Severe damages in the bio-filter units were observed with poor water quality of the system. Poor growth of the cultured fish in the experiment was attributed to the high nitrogen compound levels, especially ammonia originating from the system failure. Monitoring ammonia level of the system for 24 hours revealed that the normal ammonia level (0.06 ppm) increased to over 0.1 ppm three or four hours after feeding, remained more than 8-10 hours, and then decreased to normal level

four or five hours before next feeding. The ammonia level in the experiment was much higher than the rest of the experiments where the ammonia levels ranged between 0.01 - 0.03 ppm.

Typical ammonia disease syndrome was found in many cultured fish in the experiment. Reddish color spread near the base of all dorsal and pectoral fins with changed body color to pale greenish from black. Abnormal behaviors were also frequently observed by swimming near the surface water instead of normal swimming behavior around near the bottom.

Colt and Armstrong (1981) pointed that water quality-associated ammonia syndrome of cultured marine fish was not rare in intensive culture. Growth inhibition of salmonoid fish by high ammonia level was reported by Brett and Zala (1975). The cultured black sea bass also showed the tendency with reduced feeding response at ammonia level above 0.05 ppm. However, the low mortality (less than 1 %) during the experiment indicated that the ammonia level of the culture system did not reach lethal levels. Since the test fish (n=346) were repeatedly involved in several experiments, approximately 80 % of all fish had been exposed to the culture condition for more than ten months. Though no apparent growth inhibition was found in the rest of the experiments where the ammonia and nitrate levels fluctuated in a range of 0.01 - 0.03 ppm and 20 - 60 mg/l respectively, the water quality of the culture system might have affected the growth of the test fish. Considering the critical effects of water quality on growth of fish, the variation of growth and feeding response between individuals and between groups may have been affected also by the water quality of the culture system. The water quality deteriorated by ammonia was regarded as a possible source of error for growth experiment.

When fish are cultured in modified environment, some behavioral changes of fish often occur depending on the culture conditions (Brown, 1957, Peter, 1979). In experiment 1 through 4 where fish were not sorted by size group, abnormally slow growth rates were observed for small fish despite good water quality of the system. During the experiments large fish frequently showed aggressive behaviors toward small fish in feeding. Even in a group of fish having similar weight and size, some behaviors of social hierarchy were observed, which did not necessarily depend on size or weight. When a niche was unintentionally provided, (e.g., outlet pipe of the culture system) a specific fish occupied the space and frequently attacked other fish. When the aggressive fish was removed, sooner or later another fish occupied the space and showed the same behavior. Groups of fish which occupied the middle compartments of the rearing tank, where no shelter-like structure existed, always showed the best growth and feeding response without social hierarchy even in the crowded conditions as the loading density of 1500 - 1800 g/ 30 liter. This phenomenon was found in all middle compartments of three rearing tanks (12 compartments) regardless of size of the cultured fish.

Brown (1957) found the size hierarchy effect in brown trout fry. Peter (1979) and Brett (1979) reported the growth dominance of large size teleost fish in a social hierarchy. In intraspecific competition of teleost fish large fish dominate small fish to a certain degree when food or space is not provided evenly. The result was that large fish grew faster and small fish grew slowly in a term of instantaneous growth rate, which was inverse pattern of natural growth. However, the amount of aggression and the growth by the dominants is reduced when the density of

fish increases above a certain level. In nature black sea bass is regarded to have behavior for securing a feeding territory (Kendall, 1977). The variation of growth of fish in a size group might have been caused due to this food and space competition evoked by behavioral characteristics, especially in reduced feeding experiments, where food was regarded to be an objective of severe competition for survival and social dominance.

When starved fish were fed, active feeding responses were found regardless of size mixing and aggressive behavior of dominants. Among them some individuals revealed extreme drop of condition index by fast growing in length without weight increment. This pattern was more frequently found in groups of small fish. Isometric growth in weight and length is normal growth pattern found in natural populations of black sea bass (Mercer, 1978). However, under specific conditions such as intensive cultivation of fish, the competition for survival may result in patterns different from isometric growth of weight and length. No previous studies were found in the strategy of growth in morphologically selective situation, where either length or weight increment should proceed to another.

The black sea bass cultured for this study generally showed good growth and condition even in the small space and the hardy culture conditions with an exception of the reduced growth in high ammonia levels (over 0.05 ppm). The applied culture conditions were regarded to be appropriate for normal living and growth of black sea bass. Some large fish fed the commercial and the natural diets at satiated feeding level also showed good growth of gonads during the experiments regardless of

natural spawning cycle. Some males (approximately larger than 250 mm) showed full maturation of the gonads by producing milt during measurement procedures. The growth of reproductive organs may effect negatively on somatic growth, which may cause the growth variation of larger fish as observed during the experiments (see Figure 3 and 4).

The closed culture system was regarded to be adequate in providing an artificial environment for mass culture of this species though the scale of culture was not large. Expansion of the system for large scale cultivation for researches or for practical commercial culture of black sea bass seems to be possible with a little modification. However, periodic water change (every 2 - 4 weeks) may be necessary to maintain the system in good conditions without nitrogen compound accumulation. Based on the results of growth and feeding response, the recommended levels of nitrogen compounds for culturing black sea bass are (1) ammonia: less than 0.02 ppm, (2) nitrite: less than 0.01 ppm, and (3) nitrate: less than 30 mg/l.

### Growth

Growth of fish is a matter of survival for a population or a species as well as for an individual. Good growth of fish in nature means success in intra- and inter-species competition and environmental adaptation. As far as individual fish are concerned, growth is generally evaluated as somatic increment (Ricker, 1979). Some authors prefer to express the growth of fish as changes of body chemicals or energetic values of body tissues to find substantial growth associated with nutritional or energetic inputs in dietary sources (Gerking, 1956a, Elliott, 1975b, 1976c; Brett and Groves, 1979). Whether growth is expressed



morphologically, physiologically, or biochemically, body dimensional changes almost always accompanys growth of fish as a final resultant.

Growth of fish is the most important issue in aquaculture. Ultimate purposes of most aquacultural studies are related to improve survival and growth of culture animals. When proper diets are developed for a species or for a specific life stage of a species, various maneuvers are applied to obtain optimum or maximum growth of the culture organisms. Since growth is the resultant of the combined effects of nature and animals, the strategy to optimize growth in culture is primarily to provide the adequate environmental conditions for the culture animals to grow, especially food and hydrological factors.

The primary purpose of this study was to evaluate black sea bass for aquacultural potential, especially maximum growth potential in artificial culture conditions. To enhance the growth of black sea bass, optimum hydrological conditions were provided as defined in nature by Musik and Mercer (1977). Since food is the most important factor related to growth of fish in an optimized hydrological condition, selecting adequate quality of diet is an essential preliminary in evaluating the growth diversity associated with quantity of the diet.

In nature black sea bass is characterized as an opportunistic carnivore. Chee (1977) reported that seasonal variation and abundance of food in habitats were directly reflected by the diets of black sea bass. Crabs and molluscs were regarded as prime dietary sources while gammarids, caprellids, shrimps, fishes, and other miscellaneous foods were occasionally found in the stomachs of black sea bass from season to season. The fish collected in May 1986 at Chesapeake Bay Bridge Tunnel

pier (4.3 - 31.6 g body weight) showed extensive consumption of caprellids while various crabs, molluscs, annelids and fishes were eaten by the fish caught at Rudee Inlet in August and September 1985 (11.3 - 89.6 g body weight).

In selecting experimental diets for black sea bass, nutritional quality was considered to satisfy the minimal nutritional requirements for the black sea bass, as no direct mortality or chronic nutritional diseases were caused by nutritional deficiency of diets. Mole crabs used as 'natural diet' for this study were frequently found in the diet of captured samples. Black sea bass stocked for preliminary test in the culture system for three to eight months revealed the normal development of most male gonads and a few female gonads when mole crabs were fed as a sole dietary source. Despite the lower dietary energy contents of the mole crabs in the caloric values, mole crabs resulted in good growth for the cultured black sea bass in some satiated feeding conditions. Considering the dietary items and feeding behavior found in natural population, other dietary items for enforcing the caloric values in total food intake may be necessary for long-term experiment.

Harpster et al. (1977) investigated the growth and food conversion of juvenile southern black sea bass, C. melana, using the four selected commercial and semi-natural diets in the laboratory. Trout chow resulted in good growth and survival rate for the juveniles of southern black sea bass. High protein diets were recommended for the species in culture. Considering the common utilization of the Oregon Moisture Pellet type diets for commercial salmonoid fish culture, the commercial diet was selected for this study as an representative artificial diet. The

nutritional quality and high protein level of this diet were regarded to satisfy the minimal nutritional requirements for normal growth of black sea bass. The results of the study showed that the commercial diet originally developed for cold water species produced good growth of black sea bass and could be a substitutional diet for other warm water species which require high protein diet in culture as well as for black sea bass. High food conversion efficiency over 0.8 ( $FC=1.3:1$ ) was commonly observed from the test fish in good growing condition for 6 - 11 months without resulting in any nutritional deficiency syndrome. The caloric values of the commercial diet obtained from the caloric analysis indicated that the energetic content of the diet (4869 cal/g-wet weight) was much higher than those used in the previous energetic studies for other fishes (normally 2000 - 3500 cal/g-wet weight) despite higher moisture content than other commercial dry diets as 15 % (typical commercial dry diets have 8 - 12 % of weight in moisture contents) (Brett and Groves, 1979; Krueger et al., 1968; Marais and Kissil, 1977).

The growth of the cultured black sea bass in satiated feeding conditions for this study was much higher than those found in the natural population regardless of the applied diet type. According to the weight of black sea bass calculated by Cupka et al. (1977) for each age of southern natural population, average daily growth rate (WG) was 0.12 g/day between age 0 and age 1 and increased to 0.28 g/day between age 2 and age 3 of which average body weight reached to 233.6 g. The corresponding instantaneous growth rates were 1.04 % of body weight/day and 0.15 % of body weight/day respectively. The average absolute and instantaneous growth rates between age 1 and age 3 was 0.26 g/day and 0.49 % of body

weight/day respectively while the average body weight of fish increased from 45.2 g at age 1 to 233.6 g at age 3.

The fish in the northern natural population showed growth rates similar to southern population according to Mercer (1978): the absolute and the instantaneous growth rates were 0.04 g/day and 0.76 % of body weight/day respectively between age 0 and age 1, and 0.35 g/day and 0.20 % of body weight/day respectively between age 2 and age 3 with the average absolute and instantaneous growth rates between age 1 and age 3 as 0.31 g/day and 0.37 % of body weight/day (average body weights were 15.9 g and 240.6 g for age 1 and age 3 respectively). These growth rates were much lower than those found in the cultured fish fed the commercial diet at satiated feeding level (average absolute growth rate, 0.90 g/day; average instantaneous growth rate, 0.88 % of body weight/day; average body weight, 115.1 g; weight range, 11.9 - 291.6 g) (see Table 3).

When the highest average growth rates of the cultured fish observed in experiment 9c (WG=1.32 g/day, G=1.16 % of body weight/day, Wm=13.4 g, and range of body weight=11.9 - 291.6 g) was compared to that of the northern natural population, the culture fish grew faster by a factor of 4.3 for absolute growth rate, and 3.1 for instantaneous growth rate. The fish fed the mole crabs as test natural diet in experiment 9b also showed higher average growth rates than the natural population by a factor of 2.5 for absolute growth rate and 1.6 for instantaneous growth rate. However, the lowest average growth rate observed from the cultured fish fed the natural diet at satiated feeding level without size-sorting (experiment 1, 2, 3) showed the similar growth rate to natural population (see Table 3). The overall results indicated that the cultured fish grew much faster in

the commercial diet feeding than the natural population, and the growth rates of the cultured fish fed the natural diet were also prompted at satiated feeding level.

Kendall (1977) reported that black sea bass cultured in the laboratory grew from 265 g to 880 g over 9 months. The calculated average absolute and instantaneous growth rates for the fish were 2.24 g/day and 0.44 % of body weight/day respectively, which were typical values found in many large fish in good growing condition under the satiated commercial diet feeding regime (see Table 3 and Appendix C). These growth rates were also much higher than that found in the natural population by Mercer (1978) by a factor of 4.1 for absolute growth rate and 4.9 for instantaneous growth rate respectively.

The results of this study and Kendall's report indicated that 3 - 5 times higher growth rate of the cultured fish than that of natural population was obtainable in artificial cultivation. The calculated values of the absolute and the instantaneous growth rates from weight-specific maximum growth rate in this study (see equation 19 and 20) showed higher values by a factor of approximately one and a half of Kendall's results, which indicated that the growth rate of cultured black sea bass could be enhanced potentially as much as 7 - 8 times the natural growth rate.

Harpster et al (1977) reported the survival and growth of young C. melana in satiated feeding condition using the fish produced by artificial spawning technique. Initial body weight of the cultured fish, 9.0 g increased to approximately 25.0 g after 69 days. The calculated daily growth rates for the fish were 0.24 g/day for absolute rate (WG) and 1.45

% of body weight for instantaneous rate (G). These average growth rates were much lower than those observed from the fish in the smallest size groups (4.3 - 30 g) under satiated feeding condition (0.34 - 0.37 g/day and 1.99 - 2.08 % of body weight/day (see Appendix C, experiment 9c, group 8-1 and 8-2). Many of the cultured fish in good growing condition showed much higher growth rate in this study (the average of 10 % highest values among individual growth rates found from the fish weighing 4.3 - 30 g was 0.48 - 0.66 g/day for absolute growth rate and 2.72 - 3.79 % of body weight/day).

Harpster et al (1977) reported in their study that the ammonia level did not exceed 0.071 mg/l, which was regarded to be the regime where growth prohibition might occur. If the cultured fish by Harpster et al (1977) were exposed to the high level of ammonia near the observed upper level, the growth of the cultured fish might be much reduced. The growth rates of the southern black sea bass recorded in Harpster et al's study were also much lower than the typical high instantaneous growth rates found in many cultured young fishes at the size (3 - 10 % of body weight/day) (Brett, 1979).

The pattern of weight and food-specific growth was similar to the results reported in most previous growth studies for other fishes. Brett (1979) deserves credit for his extensive review of growth of fish in relation to environmental factors. Though the magnitude of growth of fish is not comparable due to species-specific growth rate, the general pattern of growth in relation to weight and food in the previous studies showed that the results obtained in this study were not exceptional in (1) positive exponential growth pattern in weight-specific absolute growth and

weight-specific food consumption, and (2) negative exponential growth pattern in weight-specific instantaneous growth.

Through this study, most experimental equations showed good fitting to the observations with high values of determination coefficients when group arrangement was performed. In group arrangement of this study, most frequent observations (more than 99 %) were made in the six weight intervals ranging from 10 g to 180 g and few were obtained from one weight group ranging 180 - 295 g. Since the upper 10 % highest values of all observations in each weight group were selected for group arrangement, some lower values may be included when few observations were found in each weight interval. This might result in the representative values in each weight group (arithmetic mean of selected values) being biased and might affect calculation of the values of exponents for maximum weight-specific growth rate or maximum-weight specific food consumption in both diets. However, even in equations having been biased in exponents, the constants of proportionality normally compensate the biased exponent values under least squares method, and relatively good fittings to observations might be found.

The results of this study in weight-specific patterns of growth for the cultured fish were similar to the previous studies in salmonoid and sparid fishes (Elliott, 1976b; Brett, 1976b; Kerr, 1982; Kitchell et al., 1983; Neill and Seidman, 1983). The exponent, -0.49, for the maximum instantaneous growth rate coincided with the values typically found in salmonoid fish (Brett, 1979), of which the range was from -0.33 to -0.69 with common values between -0.4 and -0.5. The tendency found in other weight-specific growth and food consumption patterns, which were indicated

by exponents of the exponential equations, also coincided with the typical results of many previous studies.

In multivariate analysis for growth in relation to food and weight, the effects and the relationships between two influential factors and the resultant growth rate were clearly found as shown in Figure 15 and 17. Weight and food consumption were primarily separated variables but, as shown in equation 21 - 24, the maximum food consumption was dependent on weight of fish. Therefore, the growth rate related to maximum food consumption rate could be expressed only by weight variable in generalized equations by converting the food consumption rate as function of weight and weight-specific growth as function of weight.

When food and weight were simultaneously related to growth, the weight-specific growth rate was frequently obscured by the interference of food effect on growth. According to the results of this study, the interference between variables was severe when growth (dependent variable) was expressed in different units of independent variables. For example, if dependent variable was instantaneous growth rate (G) expressed as percent of body weight per day independent variable was better expressed by the variable using the same unit such as food consumption rate (RC, % of body weight/day) instead of amount of food consumed by fish (C, g/day). When amount of food consumed (C, g/day) was related to both instantaneous and absolute growth rate, the weight-specific variation in growth was more apparent in the absolute growth rate (WG, g/day) than in the instantaneous growth rate (% of body weight/day).

The generalized equations corrected by the correction curves were regarded to be more useful to predict growth rate than the equations



obtained before calculation. Since the equation derived from each weight or food consumption group might be biased by (1) experimental errors from measurement, (2) errors in assumption, (3) group arrangement, and (4) error in mathematical expression itself, an overall calibration was necessary to show the general tendency of growth pattern.

When the calculated maximum instantaneous growth rate is used in the equation developed by Elliott (1976b), fish weighing 4.3 g will be 300 g after 190 days and 1000 g after 375 days respectively.

Through this study, a general pattern of growth was found for the cultured black sea bass under the applied culture conditions. The results of all growth experiments, and the equations derived or simulated from the large number of observations ( $n=1496$ ) showed apparent relationships between the growth of cultured fish and influential factors (food and weight of fish) as shown in Figure 15 and 17. However, the results of this study also indicated that the individual variation of growth almost always occurred in the same applied condition regardless of extensive controls of experimental conditions. Single experiments on small numbers of fish may give misleading results due to (1) experimental errors associated to cultural and analytical methods, and (2) behavioral and physiological differences between individuals over genetic variations. To minimize experimental errors for growth study, it is recommended to (1) use fish having physiologically, genetically, and morphologically identical characteristics, (2) define the growth variation of individuals related to behavioral and physiological differences, (3) consider genetic variation of individuals or populations to obtain the generalized patterns for a species, and (4) include all critical biotic and abiotic factors affecting

growth (weight, food, temperature, etc.).

### Food and Energetics

Studies of ration level or food consumption in relation to growth and energetics for marine fishes are relatively rare. Among warm water species, some sparid, serranid and pleuronectid fishes, for which commercial aquaculture techniques have already been established to a certain degree, were intensively studied in growth-related food quality. Energetic studies of fish were rarely found in warm water marine species. The species previously studied for partial or overall energetics were sea bream (Davis, 1963; Marais and Kissil, 1979; Neill and Seidman, 1983), turbot (Adron et al., 1969), drum (Roberts et al., 1977, 1978; Jones and Strawn, 1985), plaice (Edwards, 1968; Edwards et al., 1970, 1971; Jobling, 1981), cod (Kohler, 1964; Edwards et al., 1972; Jones, 1978), speckled trout (Graham, 1949; Job, 1960), mullet (Kutty, 1969a, 1969b; Kuo, 1972), sablefish (Sullivan and Smith, 1982), tuna (Gooding et al., 1981), and atlantic menhaden (Durbin et al., 1981; Durbin and Durbin, 1981).

Food consumption and bioenergetics of fish as well as growth are rather species-specific. However, some authors described the generalized patterns of energetics of fish depending on feeding behaviors. Brett and Groves (1979) described a generalized model for energy allocation pattern for carnivorous fish. Among total energy input (gross energy, 100%), digestible energy is 80 % (20 % energy loss in defecation and 0.8 assimilation efficiency). Metabolizable energy is 73 % after subtracting 7 % non-fecal energy loss in excretion (mostly ammonia). Only 59 % of gross energy is net energy available for growth and metabolism due to 14 % extra energy loss as heat in anabolic processes. Metabolic expenditure

and growth are alternative energy allocation of net energy. Normally, 7 % of gross energy is required for standard metabolism ( $R_s$ ) and extra 7 % is used for feeding activities (apparent SDA). Therefore, maximum available energy for growth is 45 % of total energy input. Extra energy expenditures for other activities reduce the available energy for growth. Generally, 29 % of the total energy input links to growth (including reproductive and secretory products). Though this general pattern of energy allocation was derived from freshwater species or cold water marine species such as salmonoid fishes, many warm water marine species involved in the previous energetic studies showed the similar patterns in energy allocation with some variations in metabolic expenditures depending on feeding and activities.

Since the energy deposited in tissues as energy gain is part of the physiologically available energy, the energetic value of unit body weight in weight gain (positive weight increment) is regarded to be equal to that in weight loss for routine metabolism during starvation except for the extra energy loss for feeding activities (apparent SDA) to obtain positive weight gain. Since energy expenditures for feeding activities are generally negligible in culture due to short feeding periods, the equation 12 was regarded to be a proper expression to estimate the individual food consumption rate from group feeding.

In this study the food consumption rates obtained from the groups of fish fed the commercial diet were mostly low in a range of 0.4 - 2.0 % of body weight/day while much higher values were collected from the fish fed the natural diet (0.9 - 5.1 % of body weight/day). The feeding response of the fish fed the natural diet was almost always better than the fish

fed the commercial diet. The daily food consumption rate of the fish fed the natural diet showed less fluctuation than that of the fish fed the commercial diet in satiated feeding regimes. Feeding time required for satiation was normally short as less than 10 minutes. Extra foods provided 20 - 30 minutes after initial feeding to confirm satiation were rarely consumed. Though the highest food consumption rate found from the fish fed the commercial diet was much lower than those found in the studies for salmonoid fish (6 - 12 % of dry-body weight/day), the estimated individual food consumption rate showed that some small fish consumed approximately 4 % of body weight /day at the maximum food consumption rate. According to the study by Fange and Groves (1979), 1.0 - 3.0 % of dry body weight per day are the values of food consumption rate commonly found in satiated feeding for fish used for gastric evacuation tests. When the average caloric content of the foods was compared, the commercial diet (4869 cal/g-wet weight) had much higher energy contents than the natural diet (1027 cal/g-wet weight).

It has been well known that fish consuming low dietary energy food sources increase food consumption until they meet the physiological minimum requirements (Gerking, 1956; Pandian, 1967; Halver, 1970; Cowey and Sargent, 1979). Peter (1979) described the behavior of feeding of some teleost fish, in which food intake was directly related to growth and the energy requirements for growth was the fundamental parameter controlling feeding behavior. Marais and Kissil (1979) reported in their feeding study using seabream that food consumption was inversely proportional to energy content. The magnitude of food consumption rates of Kissil's tested fish was similar to that observed in this study.

However, they obtained abnormal results in that the low energy diet resulted in better growth without significant difference in food conversion rate between the diets. They used the diets for which the energy difference between the highest energy-content diet and the lowest energy-content diet was less than 10 %.

The differences found between the tested commercial and the natural diet used in this study were ash contents (19.4 - 25.9 % for the natural diet and less than 1.0 % for the commercial diet) and energetic values (1027 cal/g-wet weight for the natural diet and 4869 cal/g-wet weight for the commercial diet), which showed that the natural diet was inferior to the commercial diet in terms of food conversion rate and growth rate. Though the energetic value in true physiologically available energy of food was not estimated by direct measurement, the inferiority of the natural diet was indicated from the growth rates of fish fed the natural diet and their poor food conversion rate. The maximum daily feeding frequency was twice during the experiments. Fish fed the natural diet at satiated feeding level showed good feeding response and apparent maximum food consumption at each feeding. However, in the second daily feeding the fish fed the natural diet almost always dominated the fish fed the commercial diet. The fish fed the natural diet in satiated feeding level were regarded to consume the maximum amount of food as their stomach capacities were allowed. Therefore, the maximum energy input of fish was also affected by the stomach capacity limiting the maximum food intake as well as the energetic contents of the food itself.

During the experiments feces production rate was extremely low compared to the values found in the previous energetic and digestion

studies for other fishes. The value, 2.2 % of fecal production rate, is far below the values from salmonoid fishes (Bryan, 1974; Elliott, 1976b; Brett, 1976b), Megalops (Pandian, 1967), gilthead seabream (Neill and Seidman, 1983), largemouth bass (Beamish, 1972), Perch (Solomon and Brafield, 1972). However, some authors (Edwards et al., 1972; Wallace, 1973) reported the values similar in magnitude to this study (1.3 - 4.0 % of total food consumption). High density of the fish in small space during my experiments may contribute to destruction of the fecal products into small particulates or dissolved forms by the activities of the fish. The feces collecting devices were also not able to measure the dissolved fecal materials or the particulates less than 10  $\mu$ m and might cause underestimation of the actual production rate. The possibility was not also neglectable that the fecal pellets might be reconsumed by fish, especially when food was not provided enough and competition was severe. The experimental condition of experiment 10 was also abnormal due to high ammonia level in culture system, the feces production rate of the cultured fish was regarded to be abnormal and erratic results.

The excretion rate, which was evaluated by ammonia production rate was also abnormal during the experiments. Since the ammonia levels in collected water samples were much higher than the upper limit allowed by the analytical method, the samples were diluted 10 times. However, some samples showed high levels of ammonia even after dilution resulting in erratic values in excretion rate. The values obtained from the experiments were regarded to be unacceptable due to the lower values than the standard metabolic energy expenditure, of which energy level was supposed to be lower than the values obtained from the ammonia experiments

represented as routine metabolism.

Another abnormal phenomenon found in the energy expenditure in the present study was the reversed energy expenditure rate between the standard metabolism obtained from respiration experiments and the routine metabolism related to starved condition. As the term indicates, standard metabolism is a part of routine metabolism, which energy expenditure for standard metabolism should be always less than the routine metabolism. Since the values for routine metabolism were estimated from the weight loss in starvation and caloric equivalent for fish, either one might be misled to the estimation.

Elliott (1975c, 1976a) reported the body composition change of brown trout during starvation period. When starved condition prevailed fish consumed available lipids first and the water content in the body tissues increased to compensate weight loss. Therefore, the energetic value of fish body actually decreased than the values estimated from weight loss. Several authors reported the same pattern of water lipid exchange in body tissues during starvation from various species. The abnormal low values of energy loss during starvation in this study was also attributed to the water content increment in body tissues though no energetic comparison had been attempted between the tissues of starved fish and fed fish.

The energy expenditure found in this study coincided with the values in many references (Brett and Zala, 1974; Pentelow, 1968; Fry, 1978; Neill and Seidman, 1983; Elliott, 1976). The exponent,  $-0.1565$  found in the weight and oxygen consumption relationship was little higher than the values found in the several researches in cold water species ( $-0.18$  -  $-0.50$ ). However, Brett (1979) pointed out that the standard metabolism

was primarily species-specific within a range. The value found in this study was regarded to be acceptable for a typical sluggish marine fish in normal behavior, in which much less energy was consumed for maintenance compared to continuous swimmers such as salmon and tuna.

The energy gain in growth of fish in satiated commercial diet feeding (0.32) showed the similar values to those found in cold water carnivorous fishes (29 % of total energy input). Brett and Groves (1979) reported that the value can be increased if extra energy expenditure competing with growth (extra feeding cost, activity-related energy consumption, etc.) can be reduced. Since most species resulting in the similar values were more or less continuous swimmers, fish having less active behaviors such as black sea bass may show higher values in good growing condition.

The weight-specific energy intake and energy consumption for maintenance showed relatively large variation between food type. The pattern of energy transfer as well as magnitude was irregular in relation to weight. Since the equations were originally derived for calculating weight-related food consumption pattern based on estimated food consumption rate, some assumption was involved. However, the determination coefficients of the equations derived from the fish fed the natural diet were relatively low with small number of representative values for weight groups ( $n=4$ ). Poor fitting at small independent values may bias the calculated magnitude or even the weight-specific pattern between food type.

The overall results in energetic study indicated that the energy input in food and energy consumption for metabolism of black sea bass were



generally similar to the results obtained in the previous energetic study but large variation also occurred in magnitude and pattern depending on weight, fish, and food type.

To obtain better results, precise measurements should be conducted in each energetic component with few assumption.

#### Comparison between natural population and cultured fish

The fish cultured for growth tests initially belonged to the natural population since they were captured from wild stocks. When fish are cultured in artificial environments, morphological abnormality related to poor growth is often found in unfavorable culture conditions (Cowey et al., 1972; Blaxter, 1975). Nutritional disease caused by poorly balanced diets (nutritionally or energetically) is a serious obstacle in establishing culture technology for historically unknown species for aquaculture. Generally, growth of fish is acutely or chronically reduced when nutritional diseases or poor water qualities are involved in culture (Elliott, 1975c; Brett and Groves, 1979; Girin, 1983). To examine overall quality of culture conditions applied for this study, especially food and water quality, morphological differentiation of the cultured fish from natural population was evaluated in a term of relative heaviness using condition factors (K and RK) and length-weight relationship as well as growth rate of the fish.

Condition index is expressed as a relative relationship between weight and standard length of the fish in this study. The average value 2.57 of the condition index of the cultured black sea bass was much lower than that observed from the natural southern population of black sea bass by Cupka et al., (1977). In the natural southern population the

condition index fluctuated from 2.85 to 3.09 depending on season. During the experiments of this study less than 1.0 % of the cultured fish showed the values of condition index higher than 2.80 after the second experiment. When the average value of the condition index of cultured fish is compared to the values obtained by Cupka et al. (1977) from the natural southern population of black sea bass, the cultured fish seemed to be inferior to the natural population in any culture conditions in terms of 'relative heaviness'.

The relative condition index is a indicator used to compare the relative heaviness of the cultured fish to the natural northern population of black sea bass described by Mercer (1978). As far as relative condition index was concerned, all fish fed the natural or the commercial diet showed slightly but significantly heavier weight (4 % in average) than the natural population at the same standard length ( $p(T) < 0.05$ ). The average value of condition index increased to 1.06 for fed fish ( $n=1391$ ) indicating that the fed fish were heavier 6 % in relative weight than the natural population.

Correlation analysis between the condition index and the relative condition index of all fish ( $n=1703$ ) showed a significantly high and positive value of correlation coefficient ( $r=0.91$ ,  $p(D) < 0.01$ ). The value of the correlation coefficient increased to 0.99 when changes of the condition index ( $dK$ ) were related to changes of relative condition index ( $dRK$ ) of fish during the experiments. The results indicated that both condition index and relative condition index functioned identically as indicators of morphological index. Nevertheless, a controversy was found between two condition factors in comparing the cultured fish to natural

populations: the condition index indicated the cultured fish having less weights than those in natural population at the same standard length while the relative condition index indicated the cultured fish having heavier weights than those in natural population at the same standard length.

Mercer (1978) and Cupka et al. (1977) respectively examined the different populations of the black sea bass separated by location and migratory behavior. If the condition index and the relative condition index of this study identically represent the condition of fish as shown in the correlation analysis, two natural population may have different conditions in a term of relative heaviness.

The exponential equations for length-weight relationship derived from each natural population by Cupka et al. (1977) and Mercer (1978) showed a difference in the exponents, which 3.1798 and 2.9108, were obtained from the northern population and the southern counterpart respectively. According to the results of 12 experiments of this study, a negative correlation coefficient value ( $r=-0.75$ ) was obtained between the exponent of the equation in weight-length relationship and the relative condition index for fish in each experiment. The exponents of the equations tended to decrease as the relative condition index increased. If this tendency is applicable to natural population, the southern population having lower value of exponent in length-weight equation may be heavier than northern population at the same standard length. However, no direct comparison between two population was done in relative heaviness, though Mercer (1978) reported that northern population grew faster than southern population in a factor of time.

Through overall experiments the relationship between growth rates

and condition indices varied from individual to individual. Theoretically, growth simultaneously occurs in both length and weight in positive weight gain. In isometric growth both length and weight increase at the same ratio and thus the condition factors should be constant regardless of growth rate. Since the growth rate and condition factor were expressed as weight change and length-weight relationship respectively, both variables were regarded to be totally separated independent variables. However, the correlation coefficients obtained between two types of growth rates (WG and G) and two types of condition indices (K and RK) showed significant relationships in a range of 0.50 - 0.63 ( $p(D) < 0.01$ ). This indicated that condition indices can be also used for growth index in a certain degree as well as for relative heaviness of fish.

In different feeding conditions both condition factors may be used more properly for starved fish in a term of relative weight indicators since weight loss occurs continuously for starved fish as an expense of energy consumption for living while length is unchangeable due to bony structure. Therefore, the condition index may well reflect the condition of starved fish by degree of differentiation from the normal relative heaviness as shown in this study (see Table 14).

During the experiments abnormally high and low values of condition index were found from ten fish. Two fish involved in the four preliminary experiments showed no growth in length due to tagging damages but normal weight increment occurred like other fish resulting in maximum value of condition index (4.15) during the experiments. On the other hand, six of eight fish died in the last two experiments showed the condition index as

low as 1.30 with the average values of 1.45. Since no external and internal damages were not found, those fish were regarded to have died by starvation. Generally, most fish reared in the growth experiments showed the values of condition index between 2.20 - 3.00. Both normal and abnormal values of condition index found in this study indicate that certain lower and higher limits of condition index might exist for black sea bass in normal growing condition as Ricker (1979) suggested for salmonoid fish.

As long as growth occurs, the value of condition index is changed in a certain range depending on individual morphological growth patterns as observed in the experiments. In normal circumstance it seems to be unlikely adequate to express the overall condition of fish by using either condition factor in a term of relative heaviness due to (1) its small range of variation in relation to large variation of somatic changes, and (2) continuous and simultaneous changes in both length and weight of fish. To define the proper relative heaviness of fish, it seems to be more desirable to use degree of saturation, which is a relative comparison between the value of current condition index and maximum obtainable values of the condition index of fish in a normal growth pattern.

#### Future Objectives

Through this study, basic patterns of the growth and the energy allocation in some bioenergetic components of black sea bass were examined in relation to a representative commercial and natural diet, and weight of fish. However, some important factors concerned with growth and energetics, especially abiotic factors such as temperature were not investigated unfortunately due to limited laboratory facilities and

labors. To understand overall pattern of growth of fish in interaction between nature and fish, the effects of those factors on growth should be investigated in further studies to establish a reliable bioenergetic model applicable for practical aquaculture or other ecological and physiological studies.

The weight range of the test fish during this study (4.3 - 295.2 g) showed that most fish were sexually unmatured juveniles and young fish, in which complicated energy allocation related to reproduction can be negligible. As Brett (1979) indicated, weight and life stage of fish play important roles in determining growth and bioenergetic patterns. Though other size of fish (except for 4.3 - 295.2 g) was not examined in this study, the growth and the energetic patterns of the test fish may be, therefore, different from large adults or from small ones in postlarval stages. Many growth stanza resulting in different growth patterns could be found during the life span of fish and especially in early life stages of fish. It indicates that the application of the results of current study to interpret the general pattern of growth the black sea bass is limited not only by involvement of other environmental factors but also by the differentiated growth patterns originated from different life stages of the black sea bass. Therefore, as suggested by many authors in growth and energetic studies, one should be cautious applying this result to other environmental conditions or life stage of fish in intraspecies level as well as interspecies level. However, this study is meaningful to provide primary information of growth potential of black sea bass for aquaculture.

Another important information obtained from this study is that the

commercial diet developed for cold water species can be utilized an excellent substitutional diet for mass culture of black sea bass. Considering that feeding is one of the most important factor determining the success of commercial culture, availability of ready-to-use commercial diet is often an important determinant to establish a mass culture of historically unknown species in commercial scale. The lack of proper diet developed for warm water marine fishes in culture may cause a major obstacle for evaluating a species in potential culture. The growth rate and feeding response of black sea bass fed the commercial diet showed the great potential that the commercial diet can be directly usable as a effective diet for black sea bass without modification.

To improve the application of the results obtained from this study for aquaculture or bioenergetic studies, the growth pattern related to temperature, energy expenditure related to main components of catabolic processes (especially, waste production related to temperature and activity), and nutritional aspects of the fish should be solved in future.

## SUMMARY AND CONCLUSIONS

1. Black sea bass, Centropristis striata was cultured in pilot scale for the first time to find aquacultural potential.
2. The growth rates of fish were significantly related to both weights and food consumption rates of fish regardless of feeding levels or food types.
3. The maximum instantaneous and absolute growth rates, the maximum food consumption rate, the maintenance food consumption rate, and the weight loss in starvation of fish were exponentially related to weight of fish.
4. The average daily weight gain and food consumption of fish (grams per day) exponentially increased with body weight of fish while the average daily weight gain and food consumption per unit body weight of fish (percent of body weight per day) exponentially decreased as weight of fish increased.
5. The commercial diet (moisture pellets, trout chow) having high caloric contents was significantly superior to the natural diet (mole crabs) in terms of growth produced and food conversion rates (wet-weight comparison) of black sea bass.
6. The natural diet (mole crabs) having low caloric contents showed low food conversion rates (wet-weight comparison) with high food consumption rates and good feeding responses of the cultured fish.
7. Two generalized equations were developed to predict the potential



growth rates of fish at given body weights and food consumption rates.

The instantaneous growth rates predicted by the equation showed close fitting to observations than the predicted absolute growth rates over the observed weight range.

8. The cultured fish were not significantly different from the natural population in terms of relative heaviness.

9. The oxygen consumption rate for standard metabolism was exponentially related to body weight of fish: a total amount of oxygen consumed daily by a fish increased exponentially with weight of fish and oxygen consumption rate per unit body weight decreased exponentially as weight of fish increased.

10. Black sea bass has good potential for aquaculture:

- a) Growth rates of culture fish were prompted four to five times faster than those of natural population using the commercial diet with satiated feeding regimes.
- b) Food conversion rates of the commercial diet were mostly less than 2.0 (food given/growth in wet weight) and less than 1.2 in good conditions for fish to grow.
- c) Commercially available diet for cold water species was effective for black sea bass on growth promotion in mass culture conditions.

## LITERATURE CITED

- Adron, J. W., A. Blair, C. B. Cowey, and A. M. Shanks, 1969  
Effects of dietary energy level and dietary energy source on growth, feed conversion and body composition of turbot (Scophthalmus maximus L.). Aquaculture 7: 125-132.
- Andrew, J. W., and R. R. Stickney, 1972  
Interactions of feeding rates and environmental temperature on growth, food conversion and body composition of channel catfish. Trans. Am. Fish. Soc., 101 : 94-99.
- Bailey, R. M., Chairman, 1970  
A list of common and scientific names of fishes from the United States and Canada. 3rd. ed., Am. Fish. Soc. Spec. Pub., No. 6 Washington D. C. 128pp.
- Baldwin, N. S., 1957  
Food consumption of brook trout at different temperatures. Trans. Am. Fish. Soc., 87: 323.
- Bardach, J. E., J. H. Ryther, and W.O. McLarney, 1972  
Aquaculture. Wiley Interscience. New York, 868 pp.
- Basu, S. P., 1959  
Active respiration of fish in relation to ambient concentrations of oxygen and carbon dioxide. J. Fish. Res. Bd. Can., 16: 175-212.
- Beamish, F. W. H., 1964a  
Respiration of fishes with special emphasis on standard oxygen consumption . II. Influence of weight and temperature on respiration on several species. Can. J. Zoo., 42: 177-188.
- Beamish, F. W. H., 1964b  
Influence of starvation on standard and routine oxygen consumption. Trans. Am. Fish. Soc., 93: 103-107.
- Beamish, F. W. H., 1964c  
Seasonal changes in the standard rate of oxygen consumption of fishes. Can. J. Zoo., 42: 189-194.
- Beamish, F. W. H., 1970  
Oxygen consumption of largemouth bass, Micropterus salmoides in relation to swimming speed and temperature. Can. J. Zool., 48: 1221-1228.
- Beamish, F. W. H., 1972  
Ration size and digestion in largemouth bass Micropterus salmoides Lacepede. Can. J. Zool., 50: 153-164
- Beamish, F. W. H., 1974  
Apparent specific dynamic action in largemouth bass, Micropterus

- salmoides. J. Fish. Res. Bd. Can., 31: 1763-1769.
- Beamish, F. W. H. and L. M. Dickie, 1967  
Metabolism and biological production in fish. In: The biological basis of freshwater fish production (S. D. Gerking ed.) p 215-242. Blackwell Scientific Publ., Oxford and Edinburgh.
- Beamish, F. W. H. and P. S. Mookherjee, 1964  
Respiration of fishes with special emphasis on standard oxygen consumption. Trans. Am. Fish. Soc., 93: 103-107.
- Beamish, F. W. H., A. J. Niimi, and P. F. K. P. Lett, 1975  
Bioenergetics of teleost fishes: Environmental influence. In: Comparative physiology-Functional aspects of structural materials (L. Bolis, H. P. Maddrell and K. Schmidt-Nielsen, eds.) pp 187-209. North-Holland Publ., Amsterdam.
- Bertalanffy, L. von, 1951  
Metabolic types and growth types. Amer. Nat., 85: 115-119.
- Bertalanffy, L. von, 1957  
Quantitative laws in metabolism and growth. Q. Rev. Biol. 32, 217-231
- Birkett, L., 1969  
The nitrogen balance in plaice, sole and perch. J. Exp. Biol., 50: 375-386.
- Blaxter, J. H. S., 1975  
Reared and wild fish- How do they compare ? In: Proceeding of the 10th European symposium on marine biology vol. 1. Mariculture (P. Persoone, and E. Jaspers, eds.) pp 11-26. Bredene, Belgium.
- Blazka, P., 1958  
The anaerobic metabolism of fish. Physiol. Zool., 31: 117-128.
- Blazka, P., M. Volf, and M. Cepela, 1960  
A new type of respirometer for the determination of the metabolism of fish in an active state. Physiol. Bohemoslov., 9: 553-558.
- Bortone, S. A., 1977  
Osteological notes on the genus Centropristis (Pisces: Serranidae). Northeast Gulf Sci. 1(1): 23-33
- Boulekbache, H., 1981  
Energy metabolism in fish development. Am. Zool., 21: 377-389.
- Brafield, A. E., and D. J. Solomon, 1972  
Oxycalorific coefficients for animal respiring nitrogenous substrates. Comp. Biochem. Physiol., 43A: 837-841.
- Brett, J. R., 1963

Some considerations in the study of respiratory metabolism in fish particularly salmon. J. Fish. Res. Bd. Can., 19: 1025-1038.

Brett, J. R., 1964

The respiratory metabolism and swimming performance of young sockeye salmon. J. Fish. Res. Bd. Can., 21: 1183-1226.

Brett, J. R., 1965

The relation of size to rate of oxygen and sustained swimming speed of sockeye salmon (Oncorhynchus nerka). J. Fish. Res. Bd. Can., 22: 1491-1501.

Brett, J. R., 1970a

Fish - The energy cost of living. In: Marine aquaculture (W. J. M. Neill ed.), pp. 37-52. Oregon State Univ. Press, Corvallis.

Brett, J. R., 1970b

Station time, appetite, and maximum food intake of sockeye salmon, Oncorhynchus nerka. J. Fish. Res. Bd. Can., 28: 409-415.

Brett, J. R., 1970c

Growth responses of young sockeye salmon (Oncorhynchus nerka) to different diets and planes of nutrition. J. Fish. Res. Bd. Can., 28: 1635-1643.

Brett, J. R., 1971

Energetic response of salmon to temperature. Study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (Oncorhynchus nerka). Am. Zool., 11: 99-113.

Brett, J. R., 1972

The metabolic demand for oxygen in fish, particularly salmonoids, and a comparison with other vertebrates. Respir. Physiol., 14: 151-170.

Brett, J. R., 1974

Tank experiments on the culture of pan-size sockeye salmon (Oncorhynchus nerka) and pink salmon (O. gorbuscha) using environmental control. Aquaculture 4: 341-352.

Brett, J. R., 1976a

Scope for metabolism and growth of sockeye salmon, Oncorhynchus nerka, and some relate energetics. J. Fish. Res. Bd. Can., 33: 307-313.

Brett, J. R., 1976b

Feeding metabolic rates of sockeye salmon, Oncorhynchus nerka, in relation to ration levels and temperature. Envir. Can. Fish. Mar. Ser. Tech. Rep. No. 675, 18 pp.

Brett, J. R., 1979

Environmental factors and growth. In Fish physiology (W. S. Hoar, D.

- J. Randall, and J. R. Brett, eds.) vol. 8. Bioenergetics and growth, pp 599-677, Academic Press, New York, San Francisco, London.
- Brett, J. R., 1983  
Life energetics of sockeye salmon, Oncorhynchus nerka. In: Behavioral energetics: Vertebrate costs of survival (W. P. Aspey, and S. I. Lustwick, eds.) pp 29-63, Ohio State Univ. Press, Columbus, Oh.
- Brett, J. R., and J. M. Blackburn, 1978  
Metabolic rate and energy expenditure of spiny dogfish, Squalus acanthias. J. Fish. Res. Bd. Can., 35: 816-827.
- Brett, J. R., and N. R. Glass, 1973  
Metabolic rates and critical swimming speeds of sockeye salmon (Oncorhynchus nerka) in relation to size and temperature. J. Fish. Res. Bd. Can., 30: 379-387.
- Brett, J. R., and D. D. Groves, 1979  
Physiological energetics. In: Fish physiology (W. S. Hoar, D. J. Randall, and J. R. Brett, eds.) vol 8. Bioenergetics and growth, p 280-352, Academic Press, New York.
- Brett, J. R., J. E. Shelbourn, and C. T. Shoop, 1969  
Growth rate and body composition of fingerling sockeye salmon, Oncorhynchus nerka, in relation to temperature and ration size. J. Fish. Res. Bd. Can., 26: 2363-2394.
- Brett, J. R., and D. B. Sutherland, 1965  
Respiratory metabolism of pumpkinseed (Lepomis gibbosus) in relation to swimming speed. J. Fish. Res. Bd. Can., 22:405-409.
- Brett, J. R., and D. B. Sutherland, 1970  
Improvement in the artificial rearing of sockeye salmon by environmental control. Fish. Res. Bd. Can. Gen. Ser. Circ. No. 89.
- Brett, J. R., and C. A. Zala, 1975  
Daily pattern of nitrogen excretion and oxygen consumption of sockeye salmon (Oncorhynchus nerka) under controlled conditions. J. Fish. Res. Bd. Can., 32: 2479-2486.
- Briggs, P. T., 1978  
Black sea bass in New York waters. N. Y. Fish and Games J. 25(1): 45-48.
- Brody, A., 1945  
Bioenergetics and growth with special reference to the efficiency complex in domestic animals. Reinhold Publishing Co., New York, 1129 pp.
- Brown, M. E., 1946  
The growth of brown trout (Salmo trutta L.) II. The growth of two-

- year-old trout at a constant temperature of 11.5 C. J. Exp. Biol., 22: 130-144.
- Brown, M. E., 1951  
The growth of brown trout (salmo trutta L.). IV. The effect of food and temperature on the survival and growth of fry. J. Exp. Biol. 28: 473-491.
- Brown, M. E., 1957  
Experimental studies on growth. In: The physiology of fishes (M. E. Brown, ed.) vol. 1. pp. 361-400, Academic Press, New York.
- Brusle, J., 1981  
Food and feeding of grey mullet. In: Aquaculture of grey mullets (O. H. Oren, ed.), pp. 185-218, IBP Handbook, No. 26, Cambridge Univ. Press, Cambridge. London, New York, New Rochelle, Melbourne, Sydney.
- Bryan, P. G., 1975  
Food habits, functional digestive morphology and assimilation efficiency of the rabbitfish, Siganus spinus (Pisces, Siganidae) on Guam, Pac. Sci. 29: 269-277.
- Buddington, R. K., 1979  
Digestion of an aquatic macrophyte by Tilapia zilli (Gervais). J. fish. Biol., 15: 449-455.
- Burnabe, G., 1974  
Mass rearing of the bass, Dicentrarchus labrax. In: Report of the international symposium on the early life history of fish. FAO Fish. Rept. No. 141, 58pp
- Chee, P. K., 1977  
Feeding ecology of black sea bass, Centropristis striata on an artificial reef off Virginia (Perciformes, Serranidae). M. S. Thesis, Old Dominion Univ., 28 pp.
- Cho, C. Y., H. S. Bailey, and S. J. Slinger, 1974  
Partial replacement of herring meal with soybean meal and other changes in a diet for rainbow trout (Salmo gairdneri). J. Fish. Res. Bd. Can., 31: 1523-1528.
- Cho, C. Y., H. S. Bailey, and S. J. Slinger, 1976  
Influence of level and type of dietary protein and of level of feeding on food utilization by rainbow trout. J. Nutr. 106: 1547-1556.
- Choubert, G. Jr., J. de la Noue, and P. Luquet, 1981  
Continuous quantitative automatic collector for fish feces. Prog. Fish-Cult., 41(2): 64-67.
- Cochran, P. A., 1979  
Comments on some recent methods for estimating food consumption by

- fish. J. Fish. Res. Bd. Can., 36: 1018.
- Cochran, P. A., and J. A. Rice, 1971  
Studies on the nutrition of marine flatfish. Growth of the plaice, Pleuronectes platessa on diets containing proteins derived from plants and other sources. Mar. Biol., 10: 145-153.
- Cochran, P. A., and J. A. Rice, 1972  
Studies on the nutrition of marine flatfish. The protein requirement of plaice, Pleuronectes platessa. Br. J. Nutr., 28: 447-456.
- Cochran, P. A., and J. A. Rice, 1979  
Nutrition. In: Fish physiology (W. S. Hoar, D. J. Randall, and J. R. Brett, eds.) vol. 8. Bioenergetics and growth, pp 1-70, Academic Press, New York, London.
- Cochran, P. A., and J. A. Rice, 1982  
A comparison of bioenergetics and field estimates of cumulative food consumption by largemouth bass (Micropterus salmoides). In: Gutshop '81 (G. Calliet, and C. Simenstad, eds.), pp. 88-96, Univ. Washington Sea Grant Pub., Seattle, Wa.
- Colt, J. E., and D. A. Armstrong, 1981  
Nitrogen toxicity to crustaceans, fish, and Molluscs. In: Bio-engineering symposium for fish culture. (L. J. Allen and E. C. Kinney eds.) Am. Fish. Soc. Fish Cul. Sec. Publ. No. 1: 34-47.
- Cowey, C. B., J. Adron and A. Blair, 1972  
Studies on the nutrition of marine flatfish. The protein requirement of plaice, Pleuronectes platessa. Br. J. Nutr., 28: 447- 456.
- Cowey, C. B., and J. R. Sargent, 1979  
Nutrition. In: Fish physiology (W. S. Hoar, D. J. Randall, and J. B. Brett, eds.) Vol. 8. Bioenergetics and growth, pp 1- 70, Academic Press, New York, London.
- Cupka, D. M., R. K. Dias, and J. Tucker, 1976  
Biology of the black sea bass, Centropristis striata (Pisces: Serranidae) from south Carolina water. South Carolina Res. Wild. Life Serv. Publ.
- Cutter, G. A., 1985  
Analytical method for chemical oceanography. Old Dominion Univ. 38pp.
- Daan, N., 1973  
A quantitative analysis of the food intake of North Sea cod, Gadus morhua. Neth. J. Sea. Res., 6: 479-517.
- Davis, P. M. C., 1963

- The energy relations of Carassius auratus L. I. Food input and energy extraction efficiency at two experimental temperatures. *Comp. Biochem. Physiol.*, 12:67-79.
- Davis, P. M. C., 1966  
The energy relations of Crassius auratus. II. The effect of food, crowding and darkness on heat production. *Comp. Biochem. Physiol.*, 17(3): 983-995.
- Davis, P. M. C., 1967  
The energy relations of Crassius auratus. III. Growth and the overall balance of energy. *Comp. Biochem. Physiol.*, 23(1): 59-63.
- Dawes, B., 1930a  
Growth and maintenance in the plaice (Pleuronectes platessa L.). I. *J. Mar. Biol. Ass. U. K.*, 17: 103-174.
- Dawes, B., 1930B  
Growth and maintenance in the plaice (Pleuronectes platessa L.). II. *J. Mar. Biol. Ass. U. K.*, 17: 877-895.
- Dowgiallo, A., 1975  
Chemical composition of an animal's body and of its food. In: *Methods for ecological bioenergetics* (W. Grodzinski, R. Z., Klekowski, and A. Duncan, eds.), pp. 160-200, IBP Handbook No. 24, Blackwell Scientific Publications, Oxford, London, Edinburgh, Melbourne, 367 pp.
- Duncan, A., and R. Z. Klekowski, 1975  
Parameters of an energy budget. In: *Methods for ecological bioenergetics* (W. Grodzinski, R. Z. Klekowski, and A. Duncan, eds.), IBP Handbook, pp. 97-148, Blackwell Scientific Publ., Oxford.
- Durbin, E. G. and A. G. Durbin, 1981  
Assimilation efficiency and nitrogen excretion of a filter-feeding planktivore, the atlantic menhaden, Brevoortia tyrannus (Pisces, Clupeidae). *Fish. Bull.* Vol. 79 : 601-615.
- Durbin, A.G., E.G. Durbin, P.G. Verity, and T.J. Smayda, 1981  
Voluntary swimming speeds and respiration rates of a filter-feeding planktivore, the atlantic menhaden, Brevoortia tyrannus (Pisces: Clupeidae). *Fish. Bull.* 78 (4): 877-895.
- Edwards, R. R. C., 1968  
Estimation of the respiratory rate of young plaice (Pleuronectes platessa L.) under natural conditions, using zinc-65. *Nature* (London), 216: 1335-1337.
- Edwards, R.R.C., J.H.S. Blaxter, U.K. Gopalan, and C.V. Mathew, 1970  
A comparison of standard oxygen consumption of temperate and tropical bottom-living marine fish. *Comp. Biochem. Physiol.*, 34: 491-495.



- Edwards, R. R. C., J. H. S. Blaxter, and U. K. Gopalan, 1971  
Feeding, metabolism and growth of tropical flatfish. *J. Exp. Mar. Biol. Ecol.*, 6: 279-300.
- Edwards, R. R. C., D. M. Finlayson, and J. H. Steele, 1972  
An experimental study of the oxygen consumption, growth, and metabolism of the cod (Gadus morhua L.). *J. Exp. Mar. Biol. Ecol.*, 8: 299-309.
- Elliott, J. E., 1969  
The oxygen requirement of chinook salmon. *Prog. Fish. Cult.*, 31: 67-73.
- Elliott, J. M., 1975a  
The growth rate of brown trout, Salmo trutta L., fed on maximum rations. *J. Anim. Ecol.* 44: 805-821.
- Elliott, J. M., 1975b  
The growth rate of brown trout (Salmo trutta L.) fed on reduced rations. *J. Anim. Ecol.*, 44: 823-842.
- Elliott, J. M., 1975c  
Weight of food and time required to satiate brown trout, Salmo trutta L. *Freshwat. Biol.*, 5: 51-64.
- Elliott, J. M., 1975d  
Number of meals in a day, maximum weight of food consumed in a day and maximum rate of feeding for brown trout, Salmo trutta L. *Freshwat. Biol.*, 5: 287-303.
- Elliott, J. M., 1976a  
Energy losses in the waste products of brown trout (Salmo trutta). *J. Anim. Ecol.*, 45: 561-580.
- Elliott, J. M., 1976b  
The energetics of feeding, metabolism and growth of brown trout (Salmo trutta) in relation to body weight, water temperature, and ration size. *J. Anim. Ecol.*, 45: 923-948.
- Elliott, J. M., 1979  
Comments on some recent methods for estimating food consumption by fish. *J. Fish. Res. Bd. Can.*, 36: 1018-1019.
- Elliott, J. M., and W. Davison, 1975  
Energy equivalents of oxygen consumption in animal energetics. *Decologia* 19: 195-201.
- Fänge, R., and D. Grove, 1979  
Digestion. In: *Fish physiology* (W. S. Hoar, D. J. Randall, and J. R. Brett, eds.), vol. 8. Bioenergetics and growth, P. 162-260, Academic Press, New York.

- Foster, R. P., and L. Goldstein, 1969  
Formation of excretory products. In: Fish physiology (W. S. Hoar and D. J. Randall, eds.) vol. 1., pp 313-350, Academic Press, New York, London.
- Fromm, P. O., and J. R. Gillet, 1968  
Effect of ambient ammonia on blood ammonia and nitrogen excretion of rainbow trout (Salmo gairdneri). Comp. Biochem. Physiol., 26: 887-896.
- Fry, F. E. J., 1947  
Effects of the environment on animal activity. Univ. Toronto Stud. Biol. Ser. 55, Ontario, Res. Lab. No. 68, pp 5-62.
- Fry, F. E. J., 1957  
The aquatic respiration of fish. In: The physiology of fishes (M. E. Brown, ed.) vol. 1. pp 1-63, Academic Press, New York.
- Fry, F. E. J., 1971  
The effect of environmental factors on the physiology of fish. In: Fish physiology (W. S. Hoar and D. J. Randall, eds.), vol. 6, pp 1-93, Academic Press, New York.
- Fry, F. E. J., and J. S. Hart, 1948  
The relation of temperature to oxygen consumption in the goldfish. Biol. Bull. (Woods Hole), 94: 66-77.
- Gerking, S. D., 1952  
The protein metabolism of the sunfishes of different ages. Physiol. Zool., 25: 358-372.
- Gerking, S. D., 1955a  
Endogenous nitrogen excretion of bluegill sunfish. Physiol. Zool., 28: 283-289.
- Gerking, S. D., 1955b  
Influence of rate of feeding on body compositions and proteins metabolism of bluegill sunfish. Physiol. Zool., 28: 267-282.
- Gerking, S. D., 1962  
Production and food utilization in a population of bluegill sunfish. Ecol. Monogr., 32: 31-78.
- Gerking, S. D., 1971  
Influence of rate of feeding and body weight on protein metabolism of bluegill sunfish. Physiol. Zool., 44: 9-19.
- Girin, M., 1979  
Some solution to the problem of producing juvenile marine finfishes for aquaculture. European Mariculture Soc. Spe. Publ. No. 4: 199-210.

- Girin, M., 1983  
Cultivation of marine fishes in the world., J. Word. Mar. Soc. 13: 9-17
- Gooding, R. M., W. H. Neill, and A. E. Dizon, 1981  
Respiration rates and low-oxygen tolerance limits in skipjack tuna, Katsuwonus pelamis. Fish. Bull. 79(1): 31-48.
- Graham, J. M., 1949  
Some effects of temperature oxygen pressure in the metabolism and activity of the speckled trout, Salvelinus fontinalis. Can. J. Res. Sect. D., 27: 207-288.
- Grodzinski, W., R. Z. Klekowski, and A. Duncan, 1975  
Methods for ecological bioenergetics (eds.). IBP Handbook No 24, Blackwell Scientific Publications, Oxford, London, Edinburgh, Melbourne.
- Halver, J. E., 1971  
Nutritional requirements of salmon and trout. Proc. Georgia Nutr. Conf. Feed. Manuf., 128 pp.
- Halver, J. E., 1972  
Fish nutrition. Academic Press, New York, 581 pp.
- Harpster, B. V., D. E. Jr. Roberts, and G. E. Bruger, 1977  
Growth and food conversion in juvenile southern sea bass, Centropristis melana (Ginsburg) fed commercial and seminatural diets. Florida Dept. Nat. Resource Mar. Res. Lab. Cont. No. 288, 23pp.
- Hoff, F. H. Jr., 1970  
Artificial spawning of the black sea bass, Centropristis striatus melanus Ginsberg, aided by chorionic gonadotrophic hormones. Fla. Dept. Nat. Resources Mar. Res. Lab. Spec. Sci. Rep. No. 25, 17 pp.
- Holme, W. N., and E. M. Donaldson, 1969  
Excretion, ionic regulation and metabolism. In: Fish physiology (W. S. Hoar and D. J. Randall, eds.) vol. 1, pp. 1-89, Academic Press, New York.
- Huges, G. M., 1964  
Fish respiratory homeostasis. Symp. Soc. Exp. Biol., 18: 81-107.
- Huisman, E. A., 1976  
Food conversion efficiencies at maintenance and production levels of carp, Cyprinus carpio L., and rainbow trout, Salmo gairdneri Richardson. Aquaculture, 9: 259-273.
- Hunt, B. P., 1960  
Digestion rate and food consumption of Florida gar, warmouth, and

- largemouth bass. Trans. Am. Fish. Soc., 89: 206-210.
- Ivlev, V. S., 1939  
Energy balance in the carp. Zool. Zh., 18: 303-318.
- Job, S. V., 1955  
The oxygen consumption of Salvelinus fontinalis. Univ. Toronto Stud. Biol. Ser., 61: 1-39.
- Job, S. V., 1960  
Growth and calorific approximation in the speckled trout (Salvelinus fontinalis). Indian J. Fish., 7: 129-136.
- Jobling, M., 1981  
Some effects of temperature, feeding and body weight on nitrogenous excretion in young plaice, Pleuronectes platessa L.. J. Fish. Biol., 18: 87-96.
- Johnson, M. G., and W. H. Charlton, 1960  
Some effects of temperature on metabolism and activity of largemouth bass, Micropterus salmoides. Prog. Fish. Cult., 22(4): 155-163.
- Jones, D. R., 1971  
Theoretical analysis of factors which may limit the maximum oxygen uptake of fish: The oxygen cost of the cardiac and bronchial pumps. J. Theor. Biol., 341-349.
- Jones, D. R., 1978  
Estimates of the food consumption of haddock (Melanogrammus aeglefinus), and cod (Gadus morhua). J. Cons. Cons. Int. Explor. Mer., 38: 18-27.
- Jones, R., and J. R. G. Hipslop, 1978  
Further observations on the relation between food intake and growth of gadoids in captivity. J. Cons. Cons. Int. Explore. Mer., 38: 244-251.
- Kaushik, S. J., 1980  
Influence of nutritional status on the daily patterns of the nitrogen excretion in carp (Cyprinus carpio L.) and the rainbow trout (Salmo gairdneri R.). Reprod. Nutr. Dev., 20: 1751-1765.
- Kelso, J. R. M., 1972  
Conversion, maintenance, and assimilation for walleye, Stizostedion vitreum, as affected by size, diet, and temperature. J. Fish. Res. Bd. Can., 29: 1181-1192.
- Kendall, A. W. Jr., 1972  
Description of black sea bass Centropristis striata (L.) larvae and their occurrences north of Cape Lookout, North Carolina in 1966. Fish. Bull., U. S. 70: 1243-1260.

- Kendall, A. W. Jr., 1977  
Biological fisheries data on black sea bass, Centropristis striata (L.). Sandy Hook Lab. Northwest Fish. Center. National Mar. Fish. Serv. NOAA. Tech. Ser. Rep. No. 7, 29 pp.
- Kerr, S. R., 1971a  
Analysis of laboratory experiments on growth efficiency of fishes. J. Fish. Res. Bd. Can., 28: 801-808.
- Kerr, S. R., 1971b  
Prediction of fish growth efficiency in nature. J. Fish. Res. Bd. Can., 28: 809-814.
- Kerr, S. R., 1971c  
A simulation model of lake trout growth. J. Fish. Res. Bd. Can., 28: 815-819.
- Kerr, S. R., 1982  
Estimation of the energy budgets of actively predatory fishes. Can. J. Fish. Aquat. Sci. 39(3): 371-379.
- Kinne, O., 1960  
Growth, food intake and food conversion in an euryplastic fish exposed to different temperature and salinities. Physiol. Zool., 33: 288-317.
- Kitchell, J. F., 1983  
Energetics. In: Fish biomechanics (P. W. Webb, and D. Weihs, eds.), pp. 312-338, Praeger Publisher, CBS Inc., 398 pp.
- Kitchell, J. F., and D. J. Stewart, 1977  
Application of bioenergetics model to yellow perch (Perca flavescens) and walleye (Stizostedion vitreum vitreum). J. Fish. Res. Bd. Can., 34: 1922-1935.
- Kitchell, J. F., and J. E. Breeck, 1980  
Bioenergetics model and foraging hypothesis for sea lamprey (Petromyzon marinus). Can. J. Fish. Aquat. Sci., 37: 2159-2168.
- Kitchell, J. F., J. F. Koonce, R. V. O'Neill, H. H. Shugart, J. J. Magnuson, and R. S. Booth, 1974  
Model of fish biomass dynamics. Trans. Am. Fish. Soc., 103: 786-798.
- Kleiber, M., 1961  
The fire of life - an introduction to animal energetics. (ed.). John Wiley and Sons Inc., New York, 454 pp.
- Kohler, A. C., 1964  
Variations in the growth of Atlantic cod (Gadus morhua L.). J. Fish. Res. Bd. Can., 21: 57-100.
- Korringa, P. 1976

- Farming marine organisms low in the food chain. Development in aquaculture and fisheries science. 4. Farming marine fishes and shrimps. publ. Elsevier, Amsterdam., 180 pp.
- Krueger, H. M., J.B. Saddler, C.A. Chapman, I.J. Tinsley, and R.R. Lowry, 1968 Bioenergetics, exercises and fatty acid of fish. Am. Zool., 8: 119-129.
- Kutty, M. N., 1968a  
Influence of ambient oxygen on the swimming performance of goldfish and rainbow trout. Ca. J. Zool., 46: 647-653.
- Kutty, M. N., 1968b  
Respiratory quotients in goldfish and rainbow trout. J. Fish. Res. Bd. Can., 25: 1689-1728.
- Kutty, M. N., 1969a  
Anaerobiosis in fish with special reference to respiratory quotient and ammonia excretion. Indian Biologist, 1: 239-242.
- Kutty, M. N., 1969b  
Oxygen consumption in the mullet, Liza macrolepis, with special reference to swimming velocity. Mar. Biol., 4: 239-242.
- Kutty, M. N., 1972  
Respiratory quotient and ammonia excretion in Tilapia mossambica. Mar. Biol. 16: 126-133.
- Kutty, M. N., 1981  
Energy metabolism in mullet. In: Aquaculture of grey mullets (O. H. Oren, ed.) pp. 219-264, IBP Handbook No. 26, Cambridge Univ. Press, Cambridge, London, New York, New Rochelle, Melbourne, Sydney.
- Kutty, M. N., and M. P. Mohamed, 1971  
Modification of Fry's fish activity counter and respirometer. Ind. J. Exp. Biol., 9: 218-222.
- Kutty, M. N., and M. P. Mohamed, 1975  
Metabolic adaptation of mullet, Rhinomugil corsula, (Hamilton) with special reference of energy utilization. Aquaculture, 5: 253-270.
- Lavenda, N., 1949  
Sexual differences and normal protogynous hermaphroditism in the Atlantic sea bass, Centropristis striatus. Copeia, 1949 (3):185-194.
- LeBrasseur, R. J., 1969  
Growth of juvenile chum salmon (Oncorhynchus keta) under different feeding regimes. J. Fish. Res. Bd. Can., 26: 1631-1645.
- Majkowski, J. and W. S. Hearn, 1984  
Comparison of three methods for estimating the food intake of a

- fish. Can. J. Fish. Aquat. Sci. 41: 212-215
- Marais, J. F. K., and G. W. Kissil, 1979  
The influence of energy level on the food intake, growth, food conversion and body composition of Sparus aurata. Aquaculture, 17(3): 203-219.
- Menzel, D. W., 1960  
Utilization of food by a Bermuda reef fish, Epinephelus guttatus. J. Cons. Cons. Perm. Int. Explor. Mer. 25: 216-222
- Mercer, L. P., 1978  
The reproductive biology and population dynamics of black sea bass, Centropristis striata. Ph. D. Diss., College of William and Mary., 196 pp.
- Miller, R. J., 1959  
A review of the seabasses of the genus Centropristes (Serranidae). Tulane Stud. Zool., 7:36-68.
- Murray M. W., J. W. Andrew, and H. L. DeLoach, 1977  
Effects of dietary lipid, dietary protein and environmental temperatures on growth, food conversion and body composition of channel catfish. J. Nutr. 107: 272-280.
- Musik, J. A., and L. P. Mercer, 1977  
Seasonal distribution of black sea bass, Centropristis striata, in the Mid-Atlantic Bight with comments on the ecology and fisheries of the species. Trans. Amer. Fish. Soc., 106(1): 12-25.
- Neill, W. H. and E. R. Seidman, 1983  
Bioenergetic limits on the growth of Gilthead seabream (Sparus aurata). In: Proceedings of the warmwater fish culture workshop. Spec. Publ. No. 3 (R. R. Stickney and S. P. Meyers eds.) Publ. Louisiana State Univ. (Div. Conti. Ed.) Baton Rouge, Li. pp 172-190.
- Niimi, A. J., and F. W. H. Beamish, 1974  
Bioenergetics and growth of largemouth bass (Micropterus salmoides) in relation to body weight and temperature. Can. J. Zool., 52: 447-456.
- Nose, T., 1967  
On the metabolic fecal nitrogen in young rainbow trout. Bull. Freshwater Fish. Res. Lab., 17: 97-106.
- Paloheimo, J. E., and L. M. Dickie, 1965  
Food and growth of fishes. I. A growth curve derived from experimental data. J. Fish. Res. Bd. Can., 22: 521-542.
- Paloheimo, J. E., and L. M. Dickie, 1966a  
Food and growth of fish. II. Effects of food and temperature on the relation between metabolism and body weight. J. Fish. Res. Bd.

- Can., 23: 89-908.
- Paloheimo, J. E., and L. M. Dickie, 1966b  
Food and growth of fishes. III> Relations among food, body size and growth efficiency. J. Fish. Res. Bd. Can., 23(8): 1209-1248.
- Pandian, T. J., 1967a  
Food intake, absorption and conversion in the fish Ophiocephalus striatus. Helgol. Wiss. Meeresunters., 15: 637-647.
- Pandian, T. J., 1967b  
Intake digestion absorption and conversion of food in the fishes, Megalops cyprinoides and Ophiocephalus striatus. Mar. Biol., 1: 16-32.
- Pandian, T. J., 1970  
Transformation of food in the fish Limanda limanda exposed to different temperatures. Mar. Biol., 5: 1-17.
- Paulson, L. J., 1980  
Model of ammonia excretion for brook trout (Salvelinus fontinalis) and rainbow trout (Salmo gairdneri). Can. J. Aquat. Sci., 37: 1421-1425.
- Pentelow, F. T. K., 1939  
The relationship between growth and food consumption in brown trout (Salmo trutta). J. Exp. Biol., 16: 446-473.
- Phillips, A. M. Jr., and R. F. Duma, 1969  
Nutrition, digestion and energy utilization. In: fish physiology (W. S. Hoar and D. J. Randall, eds.) vol. 1, pp. 351-432, Academic Press, New York.
- Pierce, R. J., and T. E. Wissing, 1974  
Energy cost of food utilization in the bluegill (Lepomis macrochirus). Transact. Am. Fish. Soc., 103: 38-45.
- Rao, G. M. N., 1968  
Oxygen consumption of rainbow trout (Salmo gairdneri) in relation to activity and salinity. Can. J. Zool., 46: 781-786.
- Reinboth, R., 1965  
Sex reversal in the black sea bass, Centropristis striatus. Anat. Rec., 151: 403.
- Reinitz, G., 1983  
Relative effect of age, diet and feeding rate on the body composition of young rainbow trout (Salmo gairdneri). Aquaculture 35: 19-27.
- Reinitz, G., and F. Hitzel, 1979  
Formulation of practical diets for rainbow trout based on desired



- performance and body composition. *Aquaculture*, 19(3): 243-252.
- Ricker, W. E., 1957  
Handbook of computations for biological statistics of fish population. *Bull. Fish. Res. Bd. Can.*, No 119.
- Ricker, W. E., 1971  
Methods for assessment of fish production in freshwaters. (2nd edn.). IBP Handbook No 3, Blackwell Scientific Publ., Oxford.
- Ricker, W. E., 1979  
Growth rate and models. In: *Fish physiology* (W. S. Hoar, D. J. Randall, and J. R. Brett, eds.), vol. 8. Bioenergetics and growth, pp. 678-748, Academic Press, New York.
- Roberts, D. E., Jr., B.V. Harpster, W.K. Haven, and K.R. Halscott, 1977  
Facilities and methodology for culture of the southern sea bass, Centropomus melana. *Proceeding World Mariculture Society*, 7: 163-198.
- Roberts, D. E. Jr., B. V. Harpster, and G. E. Henderson, 1978  
Conditioning and induced spawning of the red drum (Sciaenops ocellata) under varied conditions of photoperiod and temperature. *Proceeding World Mariculture Society*,
- Rychly, J., and B. A. Mariana, 1977  
The ammonia excretion during a 24 hours period. *Aquaculture*, 11: 173-178.
- Saunders, R. L., 1963  
Respiration of the Atlantic cod. *J. Fish. Res. Bd. Can.*, 20(2): 373-386.
- Savitz, J., 1969  
Effects of temperature and body weight on endogenous nitrogen excretion in the bluegill sunfish (Lepomis macrochirus). *J. Fish. Res. Bd. Can.*, 26: 1813-1821.
- Savitz, J., 1971  
Nitrogen excretion and protein consumption of the bluegill sunfish (Lepomis macrochirus). *J. Fish. Res. Bd. Can.*, 28: 449-451.
- Savitz, J., E. Albanese, M. J. Evinger, and P. Kolasinski, 1977  
Effect of ration level on nitrogen excretion, nitrogen retention and efficiency of nitrogen utilization for growth in largemouth bass (Micropterus salmoides). *J. Fish. Biol.*, 11: 185-192.
- Schalles, J. F., and T. E. Wissing, 1976  
Effects of dry pellet diets on the metabolic rates of bluegill (Lepomis macrochirus). *J. Fish. Res. Bd. Can.*, 33: 2443-2449.
- Smith, C. L., 1959

- Hermaphroditism in some serranid fishes from Bermuda. Pap. Mich. Acad. Sci: Art, Letters, 44: 111-118.
- Smith, H., 1965  
Some experiments on the oxygen consumption of goldfish (Carassius auratus L.) in relation to swimming speed. Ca. J. Zool., 43: 623-633.
- Smith, K. L. Jr., 1973  
Energy transformation by the sargassum fish, Histrio histrio (L.). J. Exp. Mar. Biol. Ecol., 12: 219-227.
- Smith, M. A. K., and A. Thorpe, 1976  
Nitrogen metabolism and trophic input in relation to growth in freshwater and saltwater. Biol. Bull. (Woods Hole, Mass), 150: 139-151.
- Smith, R. R., 1971  
A method for measuring digestability and metabolizable energy of feeds. Prog. Fish-Cult., 33(3): 132-134.
- Smith, R. R., 1976  
Studies on the energy metabolism of cultured fish. Ph. D. Diss. Cornell. Univ. Ithaca, New York.
- Smith, R. R., G. L. Rumsey, and M. L. Scott, 1978  
Heat increment associated with dietary protein, fat, carbohydrate and complete diets in salmonoids: comparative energy efficiency. J. Nutr., 108: 1025-1032.
- Solomon, D. J., and A. E. Brafield, 1972  
The energetics of feeding, metabolism and growth of perch (Perca fluviatilis L.). J. Anim. Ecol., 41: 699-718.
- Steffens, W., 1981  
Protein utilization by rainbow trout (Salmo gairdneri) and carp (Cyprinus carpio): A brief review. Aquaculture, 23: 337-345.
- Stewart, D. J., D. Weininger, D. V. Rottiers, and T. A. Edsall, 1983  
An energetic model for lake trout, Salvelinus nanaycush: h application to the Lake Michigan population. Can. J. Fish. Aquat. Sci. 40: 681-698.
- Stillwell, C. E., and N. E. Kohler, 1982  
Food, feeding habits, and estimates of daily ration of the shortfin mako (Isurus oxyrinchus) in the northwest Atlantic. Can. J. Fish. Aquat. Sci. 39: 407-414.
- Strickland, J. D. H., and T. P. Parsons, 1972  
A practical handbooks of seawater analysis (2nd edn.). Fish. Res. Bd. Can. Bull. No. 167. 310pp.

- Sullivan, K. M., and K. L. Jr. Smith, 1982  
Energetics of sablefish, Anoplopoma fimbria, under laboratory conditions. Can. J. Fish. Aquat. Sci., 39: 1012-1020.
- Sumner, F. B., and U. N. Lanham, 1942  
Studies of the respiratory metabolism of warm and cool spring fishes. Biol. Bull., 82: 313-327.
- Swift, D. R., 1964  
The effect of temperature oxygen on the growth rate of the windermere char (Salvelinus alpinus Willughbii). Comp. Biochem. Physiol., 12: 179-183.
- Tandler, A., and F. W. H. Beamish, 1979  
Mechanical and biochemical components of apparent specific dynamic action in largemouth bass, Micropterus salmoides Lacepede, J. Fish. Biol., 14: 343-350.
- Tandler, A., and F. W. H. Beamish, 1980  
Specific action and diet in largemouth bass, Micropterus salmoides (Lacepede). J. Nutr., 750-764.
- Tandler, A., and F. W. H. Beamish, 1981  
Apparent specific dynamic action (SDA), fish weight and level of caloric intake in largemouth bass, Micropterus salmoides Lacepede. Aquaculture, 23: 231-242.
- Tarr, R. J. Q., and B. Hill, 1978  
Oxygen consumption, food assimilation and energy contents of southern Africa elver (Anguilla sp.). Aquaculture, 15: 141-150.
- Taylor, C. C., 1962  
Growth equations with metabolic parameters. J. Cons. Cons. Per. Int. Exp. Mer., 27(3): 270-286.
- Tucker, J. W. Jr., 1983  
Utilization in Bay anchovy and black sea bass eggs and larvae contrasting ecological roles. Ph. D. Diss. College of William and Mary., 85pp.
- Turner, D. T., and C. E. Bower, 1982  
Removal of ammonia by bacteriological nitrification during the simulated transport of marine fishes. Aquaculture, 29: 347 - 357.
- Wallace, J. C., 1973  
Observations on the relationship between the food consumption and metabolic rate of Blennius pholis L. Comp. Biochem. Physiol., 45A: 293-306.
- Ware, D. M., 1978  
Bioenergetics of pelagic fish: Theoretical changes in swimming speed and ration with body size. J. Fish. Res. Bd. Can., 35: 220-228.

- Warren, C. E., and G. E. Davis, 1967  
Laboratory studies on the feedings, bioenergetics and growth of fishes, pp. 174-214. In: Biological basis of freshwater fish production (S. D. Gerking, ed.). Blackwell Scientific Publ., Oxford.
- Weihs, D., 1973  
Optimal fish swimming speed. *Nature*, 245: 48-50.
- Weihs, D., 1974  
Energetic advantages of burst swimming of fish. *J. Theor. Biol.* 48: 215-229.
- Wells, N. A., 1935  
Variation in the respiratory metabolism of the Pacific killfish, Fundulus parvipinnis, due to size, season and continued constant temperature. *Physiol. Zool.*, 8: 318-335.
- Winberg, G. G., 1956  
Rate of metabolism and food requirement of fish. *Fish. Res. Bd. Can. Transl. Ser.* 194.
- Winberg, G. G., 1961  
New information on metabolic rate in fishes. *Fish. Res. Bd. Can. Transl., Ser.*, 362.
- Windell, J. I., J. W. Foltz, and J. A. Sarokan, 1978a  
Methods of fecal collection and nutrient leaching in digestability studies. *Prog. Fish-Cult.*, 40(2): 51-55.
- Windell, J. I., J. W. Foltz, and J. A. Sarokan, 1978b  
Effect of body size, temperature and ration size on the digestability of a dry pelletized diet feed to rainbow trout, Salmo gairdneri. *Trans. Am. Fish. Soc.* 107: 415-423.
- Wood, J. D., 1958  
Nitrogen excretion in some marine teleosts. *Can. J. Biochem. Physiol.*, 36: 1237-1242.

## APPENDIX A

### Layout and Details of Culture System

Figure A-1.

Schematic diagram of culture system

SCHEMATIC DRAWING OF CULTURE SYSTEM

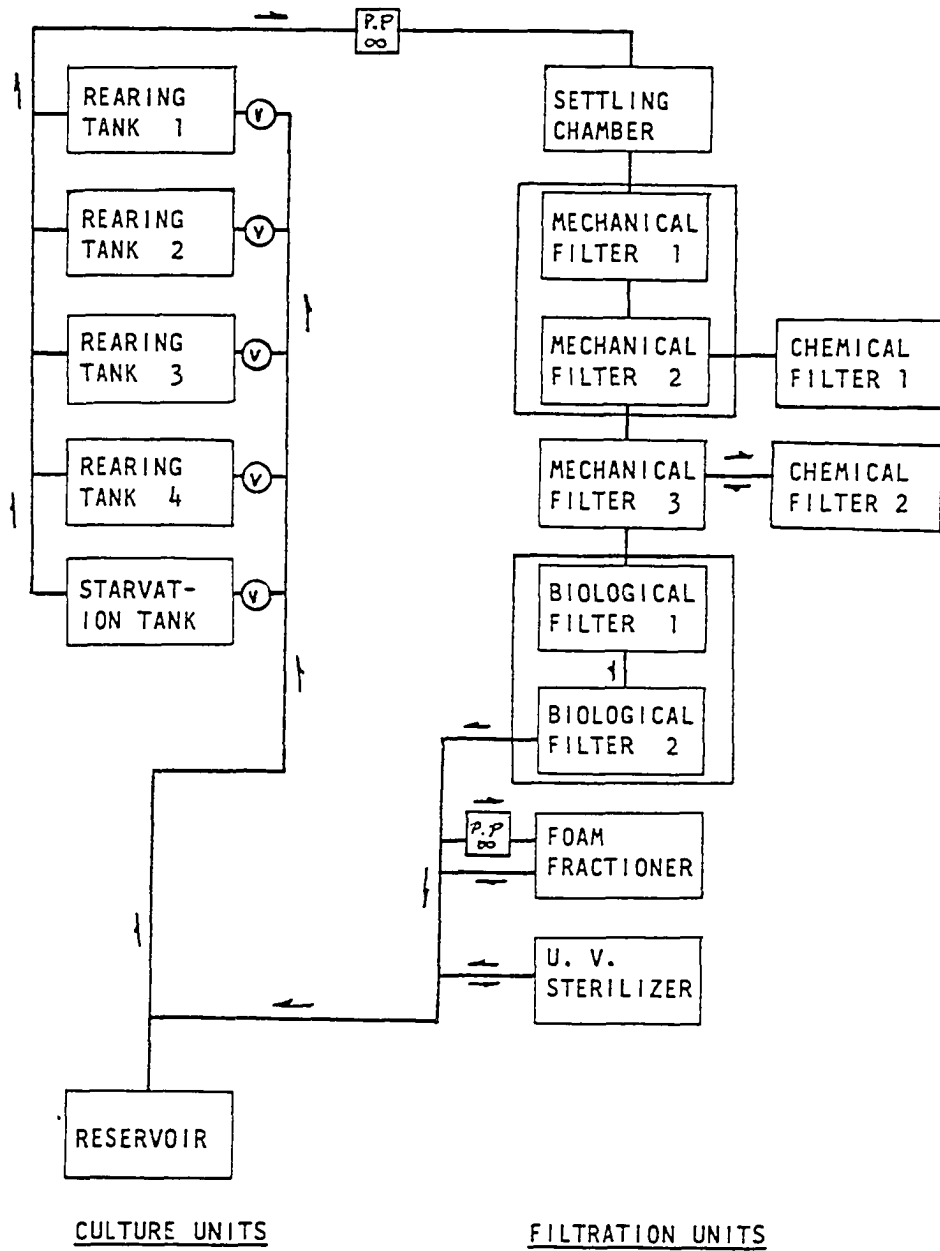


Figure A-2.

Layout of culture system.



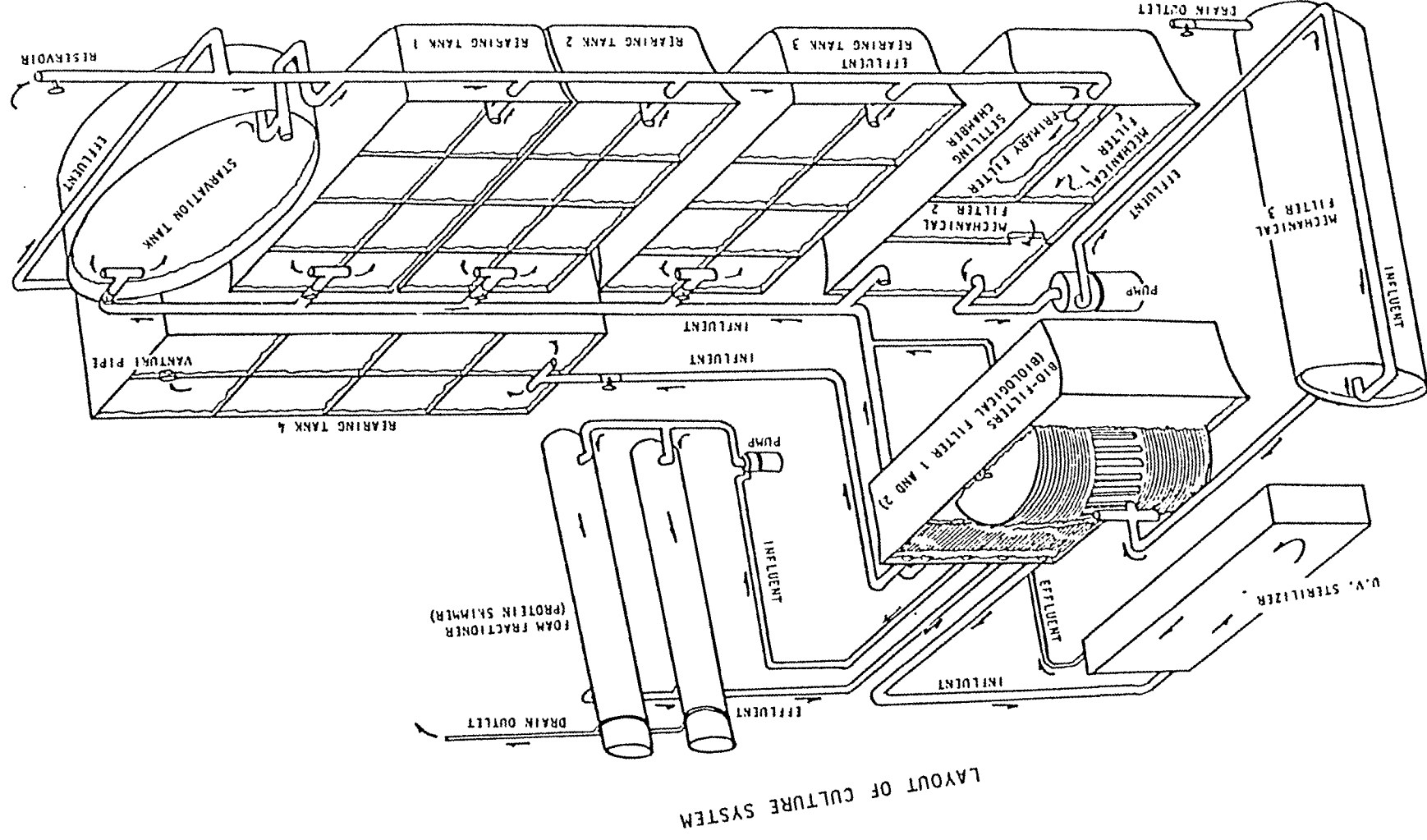
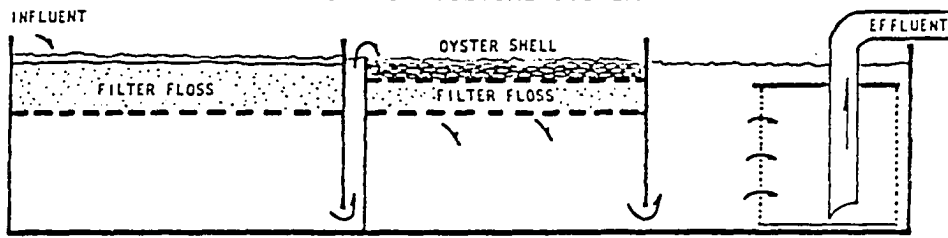
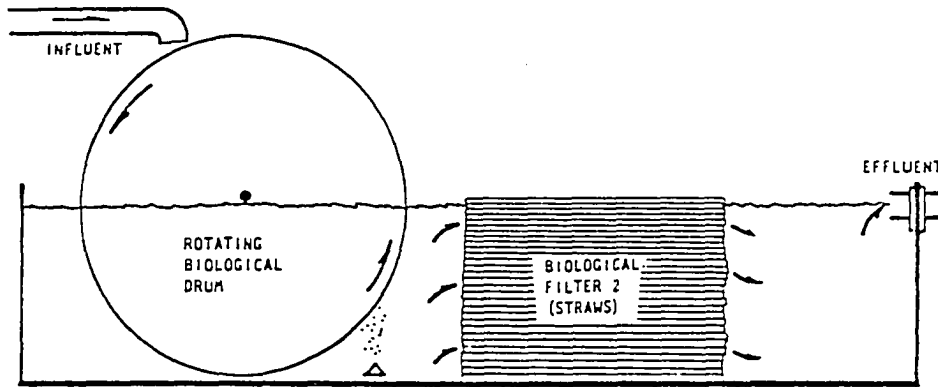


Figure A-3.

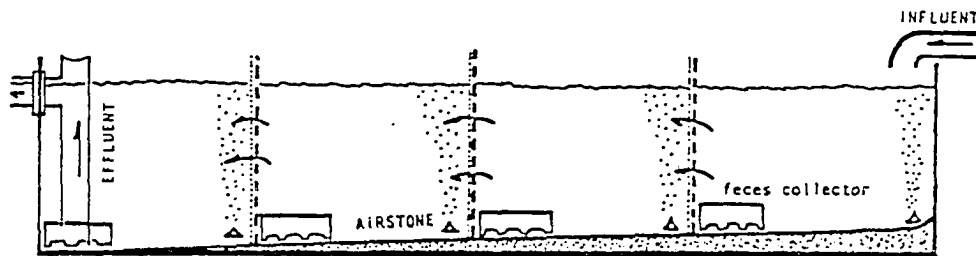
Details of each functional unit of culture system: (A) side view of mechanical filter 1 and 2, (B) side view of biological filters (biological filter 1 and 2), (C) side view of rearing tank, (D) side view of mechanical filter 3, and (E) side view of foam fractioner.



(A) SIDE VIEW OF MECHANICAL FILTER 1



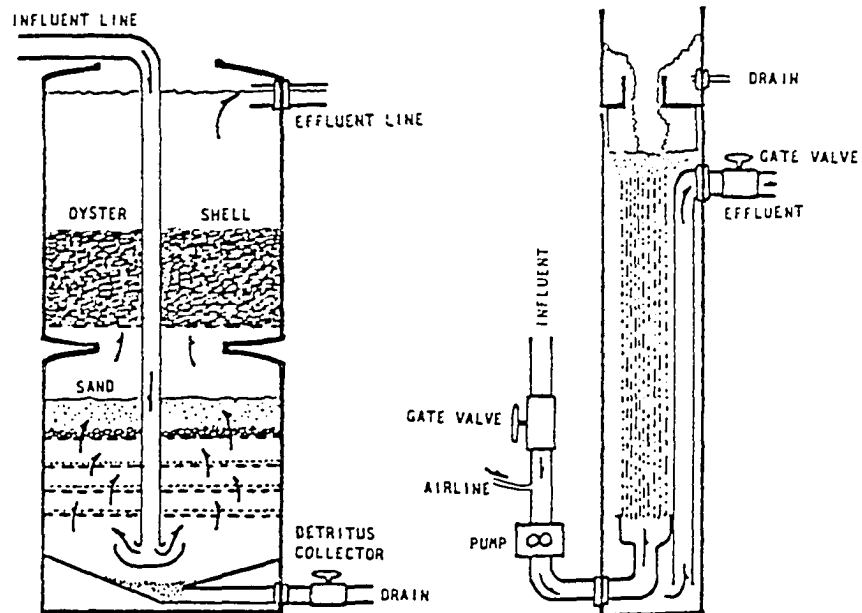
(B) SIDE VIEW OF BIOLOGICAL FILTER



(C) SIDE VIEW OF REARING TANK

(D) SIDE VIEW OF MECHANICAL FILTER 3

(E) SIDE VIEW OF FOAM FRACTIONER



## APPENDIX B

### Layout and Details of Respirometer

Figure B-1

Schematic diagram of respirometer.

## SCHEMATIC DIAGRAM OF RESPIROMETER

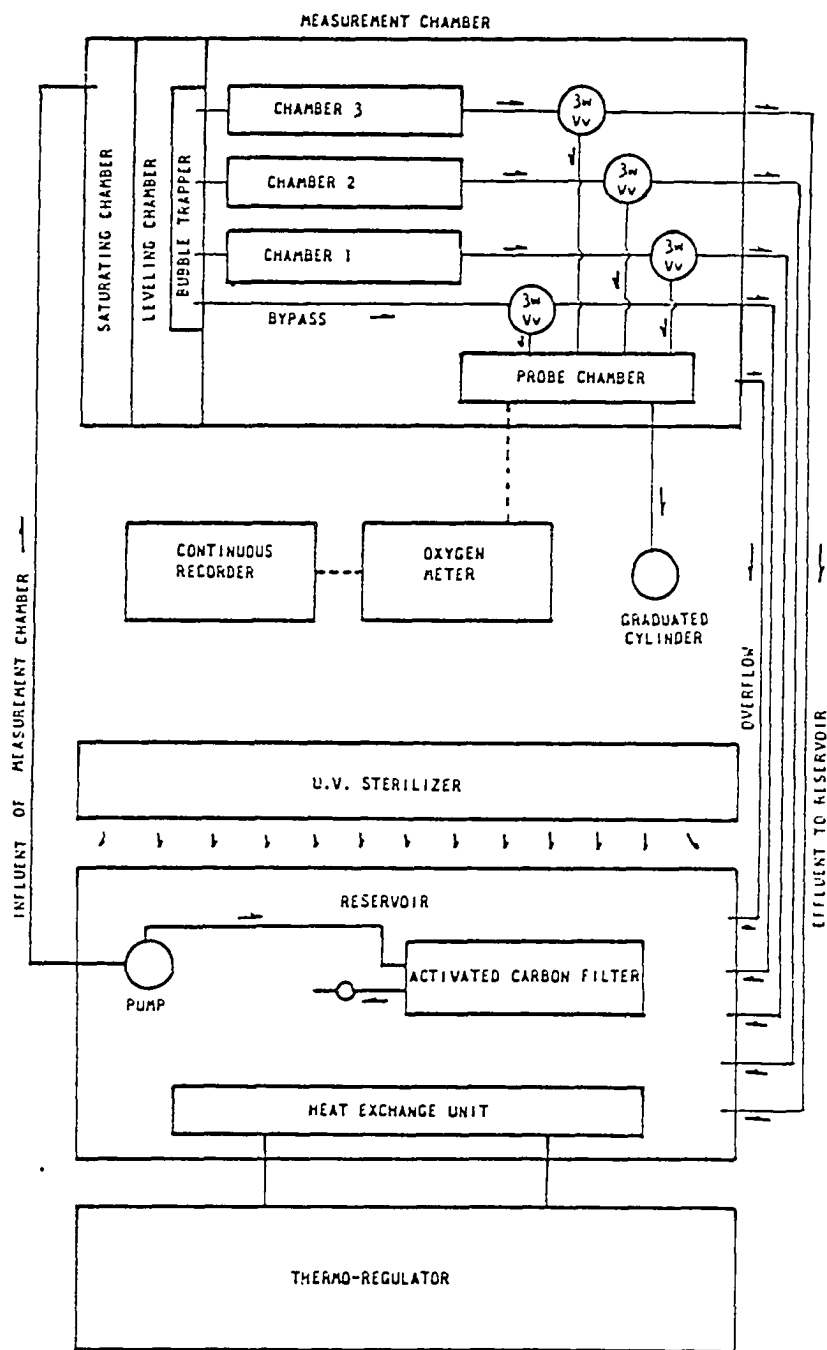
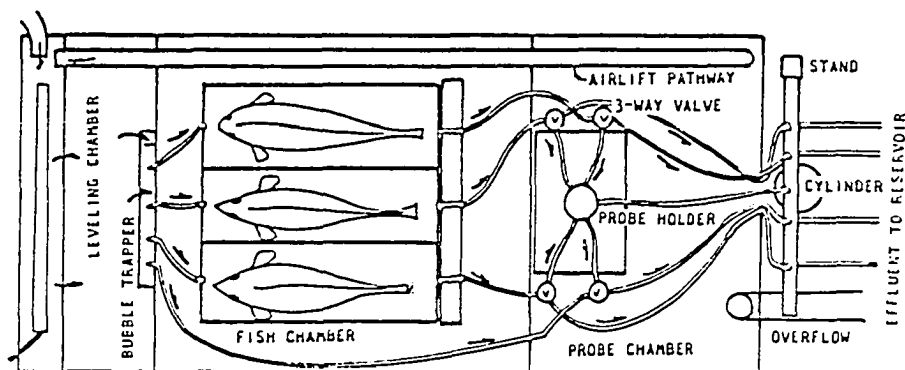


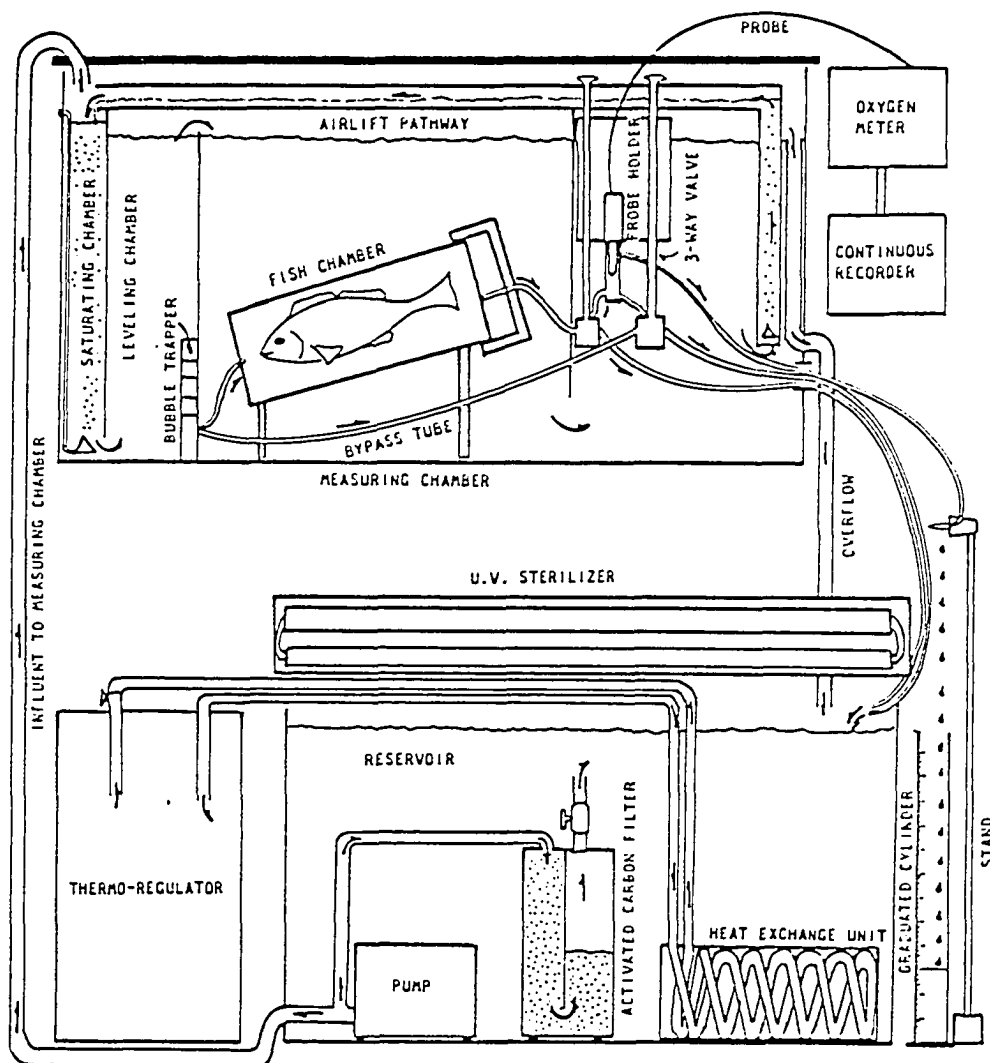
Figure B-2

Details of respirometer: (A) top view of measuring chamber, and (B) side view of respirometer (including measuring chamber, reservoir, thermo-regulator, U.V. sterilizer, oxygen meter and recoder).

(A) TOP VIEW OF MEASURING CHAMBER



(B) SIDE VIEW OF RESPIROMETER





## APPENDIX C

### Group Data of Each Experiment

Table C Averages of mean body weight, absolute and instantaneous growth rates, food consumption rate, and food conversion rate of each group of fish in each experiment.

Experiments 1, 2, 3, 4, and 5

| Exp. No. | Group Id.*<br>(Fish No.) | average<br>mean<br>body<br>weight<br>(Wm, g) | average<br>absolute<br>growth<br>rate (WGm,<br>g/day) | average<br>instant.<br>growth<br>rate (Gm,<br>% bw/day) | average<br>food com-<br>sumption<br>rate (RCm,<br>% bw/day) | average<br>food co-<br>nversion<br>rate<br>(Fm) |
|----------|--------------------------|--|---|---|---|---|
| 1        | 1-1 (75)                 | 63.9 (3.52) **                               | 0.24 (0.03) **  | 0.32 (0.04) **  | 5.08  | 0.06  |
| 2        | 1-1 (74)                 | 77.6 (4.48)                                  | 0.29 (0.03)   | 0.37 (0.03)   | 4.40  | 0.08  |
| 3        | 1-1 (74)                 | 85.3 (4.70)                                  | 0.26 (0.03)   | 0.45 (0.06)   | 4.81  | 0.07  |
| 4        | 1-1 (103)                | 63.6 (2.29)                                  | 0.53 (0.04)   | 0.86 (0.06)   | 1.00  | 0.84  |
| 5        | 1-1 (14)                 | 50.2 (1.73)                                  | 0.86 (0.06)   | 1.73 (0.08)   | 1.37  | 1.27  |
| 5        | 1-2 (14)                 | 45.7 (2.23)                                  | 0.71 (0.08)   | 1.53 (0.11)   | 1.50  | 1.03  |
| 5        | 2-1 (19)                 | 66.0 (1.23)                                  | 0.96 (0.06)   | 1.47 (0.09)   | 1.52  | 0.96  |
| 5        | 2-2 (19)                 | 62.4 (1.49)                                  | 0.84 (0.06)   | 1.35 (0.09)   | 1.53  | 0.87  |
| 5        | 3-1 (17)                 | 80.4 (1.71)                                  | 0.98 (0.09)   | 1.22 (0.11)   | 1.75  | 0.69  |
| 5        | 3-2 (19)                 | 79.5 (2.18)                                  | 0.84 (0.07)   | 1.06 (0.08)   | 1.56  | 0.68  |
| 5        | 4-1 (18)                 | 100.5 (2.12)                                 | 1.31 (0.07)   | 1.31 (0.06)   | 1.59  | 0.82  |
| 5        | 4-2 (17)                 | 99.5 (2.53)                                  | 1.14 (0.07)   | 1.15 (0.06)   | 1.54  | 0.74  |
| 5        | 5-1 (12)                 | 121.8 (3.58)                                 | 1.22 (0.11)   | 1.01 (0.09)   | 1.48  | 0.68  |
| 5        | 5-2 (11)                 | 123.4 (3.59)                                 | 1.30 (0.13)   | 1.05 (0.09)   | 1.62  | 0.65  |
| 5        | 6-1 (12)                 | 156.0 (5.45)                                 | 1.42 (0.09)   | 0.91 (0.05)   | 1.53  | 0.59  |
| 5        | 6-2 (8)                  | 161.6 (5.26)                                 | 1.44 (0.16)   | 0.89 (0.09)   | 1.48  | 0.60  |

\* group id: size class-replicate (number of fish)

\*\* Numbers in parenthesis are standard errors.

Table C Continued.

## Experiment 6

| Exp. No. | Group Id.* |      | average mean body weight (Wm, g) | average absolute growth rate (WGm, g/day) | average instant. growth rate (Gm, % bw/day) | average food consumption rate (RCm, % bw/day) | average food conversion rate (Fm) |
|----------|------------|------|----------------------------------|---|---|---|-----------------------------------|
|          |            |      | **                               | **  | **  |   |                                   |
| 6        | 1-1        | (7)  | 66.9 (4.6)                       | 0.81 (0.12)                               | 1.18 (0.12)                                 | 1.53  | 0.79                              |
| 6        | 1-2        | (6)  | 64.4 (3.4)                       | 0.75 (0.10)                               | 1.17 (0.11)                                 | 1.78  | 0.66                              |
| 6        | 1-3        | (7)  | 55.5 (4.6)                       | 0.80 (0.13)                               | 1.39 (0.19)                                 | 1.89  | 0.76                              |
| 6        | 1-4        | (7)  | 66.3 (5.4)                       | 0.87 (0.16)                               | 1.25 (0.22)                                 | 1.57  | 0.83                              |
| 6        | 2-1        | (10) | 82.4 (1.5)                       | 0.65 (0.04)                               | 0.79 (0.04)                                 | 0.98  | 0.80                              |
| 6        | 2-2        | (9)  | 83.9 (3.3)                       | 0.73 (0.06)                               | 0.87 (0.06)                                 | 1.14  | 0.76                              |
| 6        | 2-3        | (9)  | 80.6 (3.5)                       | 0.78 (0.06)                               | 0.96 (0.06)                                 | 1.16  | 0.83                              |
| 6        | 2-4        | (10) | 75.8 (3.2)                       | 0.63 (0.07)                               | 0.81 (0.08)                                 | 1.13  | 0.74                              |
| 6        | 3-1        | (9)  | 97.5 (2.4)                       | 0.83 (0.07)                               | 0.84 (0.06)                                 | 1.05  | 0.81                              |
| 6        | 3-2        | (8)  | 101.9 (6.5)                      | 1.03 (0.19)                               | 0.96 (0.17)                                 | 1.13  | 0.90                              |
| 6        | 3-3        | (10) | 93.5 (4.5)                       | 0.92 (0.08)                               | 0.99 (0.07)                                 | 1.00  | 0.99                              |
| 6        | 3-4        | (9)  | 101.5 (3.5)                      | 1.00 (0.07)                               | 0.98 (0.05)                                 | 1.02  | 0.97                              |
| 6        | 4-1        | (9)  | 125.4 (4.1)                      | 1.09 (0.11)                               | 0.87 (0.08)                                 | 1.23  | 0.71                              |
| 6        | 4-2        | (9)  | 122.9 (4.6)                      | 0.86 (0.06)                               | 0.69 (0.04)                                 | 1.14  | 0.61                              |
| 6        | 4-3        | (8)  | 122.1 (4.4)                      | 1.04 (0.13)                               | 0.86 (0.10)                                 | 1.36  | 0.63                              |
| 6        | 4-4        | (8)  | 123.0 (4.3)                      | 0.92 (0.13)                               | 0.75 (0.10)                                 | 1.16  | 0.65                              |
| 6        | 5-1        | (12) | 142.2 (4.3)                      | 0.70 (0.06)                               | 0.49 (0.05)                                 | 0.87  | 0.56                              |
| 6        | 5-2        | (4)  | 144.7 (5.5)                      | 0.55 (0.12)                               | 0.38 (0.07)                                 | 0.83  | 0.45                              |
| 6        | 5-3        | (6)  | 146.2 (8.7)                      | 0.63 (0.20)                               | 0.43 (0.13)                                 | 0.84  | 0.51                              |
| 6        | 6-1        | (12) | 181.0 (6.8)                      | 0.96 (0.13)                               | 0.52 (0.07)                                 | 0.85  | 0.63                              |
| 6        | 6-2        | (4)  | 195.7 (7.4)                      | 1.41 (0.13)                               | 0.72 (0.05)                                 | 1.04  | 0.70                              |
| 6        | 6-3        | (4)  | 180.8 (12.1)                     | 0.91 (0.14)                               | 0.50 (0.05)                                 | 0.89  | 0.56                              |

\* group id: size class-replicate (number of fish)

\*\* Numbers in parenthesis are standard errors.

Table C Continued.

## Experiment 7

| Exp. No. | Group Id.*<br>(Fish No.) | average<br>mean<br>body<br>weight<br>(Wm, g) | average<br>absolute<br>growth<br>rate (WGm,<br>g/day) | average<br>instant.<br>growth<br>rate (Gm,<br>% bw/day) | average<br>food com-<br>sumption<br>rate (RCm,<br>% bw/day) | average<br>food co-<br>nversion<br>rate<br>(Fm) |
|----------|--------------------------|--|---|---|---|---|
|          |                          | **   | **  | **  |   |   |
| 7        | 1-1 (7)                  | 73.2 (5.3)                                   | 0.61 (0.09)   | 0.82 (0.08)   | 0.97  | 0.86  |
| 7        | 1-2 (7)                  | 72.9 (2.9)                                   | 0.46 (0.09)   | 0.62 (0.11)   | 0.92  | 0.68  |
| 7        | 1-3 (7)                  | 67.1 (5.1)                                   | 0.60 (0.12)   | 0.86 (0.16)   | 1.14  | 0.78  |
| 7        | 1-4 (7)                  | 76.7 (7.0)                                   | 1.04 (0.21)   | 1.32 (0.27)   | 1.37  | 0.99  |
| 7        | 2-1 (10)                 | 98.5 (3.1)                                   | 1.23 (0.17)   | 1.22 (0.14)   | 1.29  | 0.96  |
| 7        | 2-2 (10)                 | 95.7 (3.1)                                   | 1.00 (0.17)   | 1.01 (0.16)   | 1.24  | 0.84  |
| 7        | 2-3 (10)                 | 94.3 (2.3)                                   | 0.68 (0.10)   | 0.70 (0.10)   | 0.98  | 0.73  |
| 7        | 2-4 (10)                 | 93.2 (2.1)                                   | 0.54 (0.15)   | 0.56 (0.15)   | 0.87  | 0.66  |
| 7        | 3-1 (9)                  | 113.6 (3.6)                                  | 0.67 (0.14)   | 0.57 (0.11)   | 0.91  | 0.64  |
| 7        | 3-2 (9)                  | 124.5 (3.5)                                  | 1.29 (0.10)   | 1.05 (0.10)   | 1.14  | 0.91  |
| 7        | 3-3 (9)                  | 112.3 (5.8)                                  | 0.93 (0.14)   | 0.81 (0.10)   | 1.03  | 0.81  |
| 7        | 3-4 (9)                  | 114.1 (4.2)                                  | 0.81 (0.20)   | 0.67 (0.13)   | 1.04  | 0.68  |
| 7        | 4-1 (7)                  | 138.2 (4.4)                                  | 0.78 (0.12)   | 0.56 (0.08)   | 0.98  | 0.58  |
| 7        | 4-2 (7)                  | 140.5 (6.2)                                  | 1.22 (0.16)   | 0.85 (0.09)   | 1.10  | 0.79  |
| 7        | 4-3 (8)                  | 143.0 (5.1)                                  | 0.99 (0.20)   | 0.67 (0.12)   | 0.98  | 0.71  |
| 7        | 4-4 (8)                  | 141.1 (4.0)                                  | 1.09 (0.15)   | 0.77 (0.09)   | 1.14  | 0.68  |
| 7        | 5-1 (7)                  | 152.6 (6.5)                                  | 0.41 (0.20)   | 0.25 (0.13)   | 0.58  | 0.46  |
| 7        | 5-2 (7)                  | 158.2 (3.0)                                  | 0.44 (0.19)   | 0.28 (0.12)   | 0.53  | 0.53  |
| 7        | 5-3 (6)                  | 167.5 (7.7)                                  | 0.85 (0.18)   | 0.50 (0.10)   | 0.73  | 0.70  |
| 7        | 5-4 (5)                  | 146.1 (6.3)                                  | 0.74 (0.13)   | 0.50 (0.08)   | 0.77  | 0.66  |
| 7        | 6-1 (5)                  | 210.1 (11.6)                                 | 0.69 (0.32)   | 0.32 (0.14)   | 0.76  | 0.43  |
| 7        | 6-2 (5)                  | 212.3 (8.7)                                  | 0.96 (0.23)   | 0.45 (0.11)   | 0.75  | 0.60  |
| 7        | 6-3 (4)                  | 214.7 (7.5)                                  | 1.10 (0.12)   | 0.52 (0.06)   | 0.78  | 0.66  |
| 7        | 6-4 (4)                  | 200.8 (8.5)                                  | 0.55 (0.23)   | 0.27 (0.11)   | 0.60  | 0.46  |
| 7        | 7-1 (10)                 | 54.9 (2.8)                                   | 0.46 (0.06)   | 0.82 (0.10)   | 0.76  | 1.09  |

\* group id: size class-replicate (number of fish)

\*\* Numbers in parenthesis are standard errors.

Table C Continued.

## Experiment 8.

| Exp. No. | Group | Id.* | average mean body weight (Wm, g) | average absolute growth rate (WGm, g/day) | average instant. growth rate (Gm, % bw/day) | average food consumption rate (RCm, % bw/day) | average food conversion rate (Fm) |
|----------|-------|------|----------------------------------|---|---|---|-----------------------------------|
|          |       |      | **                               | **  | **  |   |                                   |
| 8        | 1-1   | (8)  | 91.2 (1.3)                       | 0.62 (0.09)                               | 0.68 (0.10)                                 | 1.01  | 0.67                              |
| 8        | 1-2   | (7)  | 90.9 (1.7)                       | 0.57 (0.08)                               | 0.62 (0.08)                                 | 0.96  | 0.65                              |
| 8        | 1-3   | (6)  | 77.8 (1.4)                       | 0.39 (0.08)                               | 0.49 (0.09)                                 | 0.90  | 0.56                              |
| 8        | 1-4   | (10) | 73.4 (2.2)                       | 0.58 (0.09)                               | 0.78 (0.11)                                 | 1.08  | 0.73                              |
| 8        | 2-1   | (9)  | 106.3 (2.8)                      | 0.70 (0.11)                               | 0.65 (0.10)                                 | 1.10  | 0.60                              |
| 8        | 2-2   | (7)  | 108.9 (3.1)                      | 0.78 (0.14)                               | 0.70 (0.12)                                 | 1.20  | 0.60                              |
| 8        | 2-3   | (9)  | 106.9 (2.5)                      | 0.81 (0.10)                               | 0.75 (0.09)                                 | 0.99  | 0.77                              |
| 8        | 2-4   | (9)  | 106.4 (1.8)                      | 0.75 (0.06)                               | 0.70 (0.05)                                 | 1.04  | 0.68                              |
| 8        | 3-1   | (10) | 128.5 (3.3)                      | 0.65 (0.10)                               | 0.50 (0.07)                                 | 0.76  | 0.66                              |
| 8        | 3-2   | (9)  | 132.2 (3.5)                      | 1.10 (0.15)                               | 0.82 (0.11)                                 | 1.17  | 0.71                              |
| 8        | 3-3   | (10) | 130.5 (2.2)                      | 0.84 (0.12)                               | 0.65 (0.09)                                 | 0.90  | 0.72                              |
| 8        | 3-4   | (10) | 131.8 (3.5)                      | 0.94 (0.13)                               | 0.71 (0.09)                                 | 0.94  | 0.76                              |
| 8        | 4-1   | (7)  | 150.9 (2.8)                      | 0.69 (0.16)                               | 0.45 (0.10)                                 | 0.85  | 0.54                              |
| 8        | 4-2   | (7)  | 154.6 (3.0)                      | 1.11 (0.13)                               | 0.72 (0.08)                                 | 1.06  | 0.68                              |
| 8        | 4-3   | (7)  | 151.1 (3.3)                      | 0.74 (0.10)                               | 0.49 (0.06)                                 | 0.84  | 0.59                              |
| 8        | 4-4   | (7)  | 150.4 (2.9)                      | 0.53 (0.18)                               | 0.34 (0.11)                                 | 0.76  | 0.46                              |
| 8        | 5-1   | (6)  | 173.7 (3.7)                      | 0.89 (0.09)                               | 0.51 (0.05)                                 | 0.75  | 0.68                              |
| 8        | 5-2   | (6)  | 172.4 (5.3)                      | 0.71 (0.22)                               | 0.40 (0.12)                                 | 0.72  | 0.57                              |
| 8        | 5-3   | (6)  | 172.2 (4.4)                      | 0.62 (0.29)                               | 0.34 (0.15)                                 | 0.71  | 0.51                              |
| 8        | 5-4   | (6)  | 172.9 (3.9)                      | 0.67 (0.19)                               | 0.39 (0.11)                                 | 0.79  | 0.49                              |
| 8        | 6-1   | (10) | 224.9 (8.8)                      | 1.34 (0.19)                               | 0.59 (0.08)                                 | 0.93  | 0.65                              |
| 8        | 6-2   | (10) | 225.4 (6.0)                      | 1.36 (0.14)                               | 0.60 (0.05)                                 | 0.99  | 0.61                              |
| 8        | 7-1   | (5)  | 54.8 (4.1)                       | 0.17 (0.10)                               | 0.28 (0.18)                                 | 0.83  | 0.38                              |
| 8        | 7-2   | (5)  | 53.4 (1.3)                       | 0.00 (0.13)                               | -0.02 (0.24)                                | 0.57  | 0.00                              |

\* group id: size class-replicate (number of fish)

\*\* Numbers in parenthesis are standard errors.

Table C Continued.

## Experiment 9

| Exp. No. | Group Id.*<br>(Fish No.) | average mean<br>body weight<br>(Wm, g) | average absolute<br>growth rate (WGm,<br>g/day) | average instant.<br>growth rate (Gm,<br>% bw/day) | average food com-<br>sumption rate (RCm,<br>% bw/day) | average food co-<br>nversion rate<br>(Fm) |
|----------|--------------------------|--|---|---|---|---|
|          |                          | **                                     | **  | **  |   |   |
| 9a       | 1-1 (13)                 | 85.5 (1.8)                             | -0.39 (0.02)                                    | -0.46 (0.02)                                      | 0.00  | 0.00                                      |
| 9a       | 2-1 (8)                  | 106.1 (2.1)                            | -0.39 (0.03)                                    | -0.37 (0.03)                                      | 0.00  | 0.00                                      |
| 9a       | 3-1 (10)                 | 132.8 (2.5)                            | -0.46 (0.04)                                    | -0.35 (0.03)                                      | 0.00  | 0.00                                      |
| 9a       | 4-1 (7)                  | 148.1 (2.8)                            | -0.44 (0.04)                                    | -0.30 (0.03)                                      | 0.00  | 0.00                                      |
| 9a       | 5-1 (6)                  | 176.1 (3.0)                            | -0.58 (0.04)                                    | -0.33 (0.02)                                      | 0.00  | 0.00                                      |
| 9a       | 6-1 (4)                  | 231.7 (12.2)                           | -0.79 (0.09)                                    | -0.34 (0.03)                                      | 0.00  | 0.00                                      |
| 9a       | 7-1 (10)                 | 52.8 (3.7)                             | -0.28 (0.02)                                    | -0.55 (0.03)                                      | 0.00  | 0.00                                      |
| 9a       | 8-1 (8)                  | 17.5 (1.3)                             | -0.13 (0.01)                                    | -0.73 (0.04)                                      | 0.00  | 0.00                                      |
|          |                          |  |   |   |   |   |
| 9b       | 1-1 (8)                  | 97.8 (3.0)                             | 0.81 (0.10)                                     | 0.82 (0.08)                                       | 3.08  | 0.27                                      |
| 9b       | 2-1 (8)                  | 115.1 (2.5)                            | 0.82 (0.14)                                     | 0.70 (0.11)                                       | 2.51  | 0.28                                      |
| 9b       | 3-1 (10)                 | 138.3 (1.8)                            | 1.00 (0.07)                                     | 0.72 (0.06)                                       | 2.96  | 0.24                                      |
| 9b       | 4-1 (7)                  | 164.8 (2.3)                            | 1.06 (0.09)                                     | 0.64 (0.05)                                       | 2.82  | 0.23                                      |
| 9b       | 5-1 (6)                  | 187.5 (6.5)                            | 0.89 (0.11)                                     | 0.47 (0.04)                                       | 2.36  | 0.20                                      |
| 9b       | 6-1 (5)                  | 256.0 (6.0)                            | 0.89 (0.24)                                     | 0.35 (0.10)                                       | 2.03  | 0.17                                      |
| 9b       | 7-1 (9)                  | 54.6 (5.0)                             | 0.19 (0.03)                                     | 0.34 (0.04)                                       | 1.50  | 0.23                                      |
|          |                          |  |   |   |   |   |
| 9c       | 1-1 (8)                  | 108.5 (2.0)                            | 1.60 (0.10)                                     | 1.47 (0.07)                                       | 1.78  | 0.83                                      |
| 9c       | 2-1 (9)                  | 129.8 (1.4)                            | 1.74 (0.19)                                     | 1.33 (0.13)                                       | 1.73  | 0.77                                      |
| 9c       | 3-1 (10)                 | 149.6 (3.4)                            | 1.47 (0.13)                                     | 0.98 (0.08)                                       | 1.43  | 0.69                                      |
| 9c       | 4-1 (7)                  | 169.5 (1.9)                            | 1.75 (0.24)                                     | 1.03 (0.14)                                       | 1.39  | 0.75                                      |
| 9c       | 5-1 (7)                  | 196.3 (3.2)                            | 1.46 (0.21)                                     | 0.75 (0.11)                                       | 0.97  | 0.77                                      |
| 9c       | 6-1 (5)                  | 242.8 (12.0)                           | 1.71 (0.15)                                     | 0.71 (0.08)                                       | 1.08  | 0.65                                      |
| 9c       | 7-1 (9)                  | 55.3 (4.5)                             | 0.51 (0.09)                                     | 1.02 (0.22)                                       | 1.37  | 0.68                                      |
| 9c       | 8-1 (8)                  | 18.7 (1.3)                             | 0.34 (0.10)                                     | 1.99 (0.57)                                       | 1.89  | 0.98                                      |
| 9c       | 8-2 (7)                  | 18.1 (2.2)                             | 0.37 (0.04)                                     | 2.08 (0.17)                                       | 1.48  | 1.38                                      |
|          |                          |  |   |   |   |   |
| 9d       | 1-1 (10)                 | 90.5 (2.3)                             | 0.74 (0.14)                                     | 0.82 (0.15)                                       | 0.89  | 0.91                                      |
| 9d       | 2-1 (9)                  | 116.3 (2.4)                            | 0.95 (0.08)                                     | 0.82 (0.07)                                       | 0.94  | 0.87                                      |
| 9d       | 3-1 (11)                 | 139.2 (3.7)                            | 1.04 (0.10)                                     | 0.74 (0.07)                                       | 0.71  | 1.06                                      |
| 9d       | 4-1 (7)                  | 160.1 (2.2)                            | 1.12 (0.10)                                     | 0.70 (0.06)                                       | 0.74  | 0.94                                      |
| 9d       | 5-1 (7)                  | 180.3 (3.0)                            | 0.86 (0.13)                                     | 0.48 (0.07)                                       | 0.55  | 0.87                                      |
| 9d       | 6-1 (5)                  | 233.0 (15.5)                           | 1.27 (0.18)                                     | 0.54 (0.06)                                       | 0.59  | 0.93                                      |
| 9d       | 7-1 (9)                  | 54.4 (4.3)                             | 0.37 (0.14)                                     | 0.73 (0.31)                                       | 0.69  | 0.96                                      |
| 9d       | 8-1 (7)                  | 19.4 (2.0)                             | 0.23 (0.09)                                     | 1.22 (0.37)                                       | 1.37  | 0.84                                      |

\* group id: size class-replicate (number of fish)

\*\* Numbers in parenthesis are standard errors.

Table C Continued.

## Experiment 10

| Exp. No. | Group Id.*<br>(Fish No.) | average<br>mean<br>body<br>weight<br>(Wm, g) | average<br>absolute<br>growth<br>rate (WGm,<br>g/day) | average<br>instant.<br>growth<br>rate (Gm,<br>% bw/day) | average<br>food com-<br>sumption<br>rate (RCm,<br>% bw/day) | average<br>food co-<br>nversion<br>rate<br>(Fm) |
|----------|--------------------------|--|---|---|---|---|
|          |                          | **   | **  | **  |   |   |
| 10a      | 1-1 (8)                  | 109.2 (2.4)                                  | -0.42 (0.04)  | -0.38 (0.04)  | 0.00  | 0.00  |
| 10a      | 2-1 (12)                 | 131.1 (1.6)                                  | -0.47 (0.02)  | -0.36 (0.02)  | 0.00  | 0.00  |
| 10a      | 3-1 (5)                  | 151.3 (4.0)                                  | -0.46 (0.05)  | -0.30 (0.03)  | 0.00  | 0.00  |
| 10a      | 4-1 (3)                  | 172.8 (5.2)                                  | -0.49 (0.02)  | -0.28 (0.01)  | 0.00  | 0.00  |
| 10a      | 5-1 (8)                  | 250.6 (12.4)                                 | -0.79 (0.10)  | -0.31 (0.03)  | 0.00  | 0.00  |
| 10a      | 6-1 (12)                 | 85.4 (2.3)                                   | -0.36 (0.03)  | -0.42 (0.04)  | 0.00  | 0.00  |
| 10a      | 7-1 (12)                 | 54.9 (4.0)                                   | -0.30 (0.02)  | -0.56 (0.03)  | 0.00  | 0.00  |
| 10a      | 8-1 (10)                 | 19.7 (2.5)                                   | -0.15 (0.02)  | -0.79 (0.03)  | 0.00  | 0.00  |
|          |                          |  |   |   |   |   |
| 10b      | 1-1 (7)                  | 114.4 (1.4)                                  | 0.11 (0.15)   | 0.09 (0.13)   | 1.82  | 0.05  |
| 10b      | 2-1 (8)                  | 134.3 (2.1)                                  | 0.00 (0.10)   | 0.00 (0.07)   | 1.55  | 0.00  |
| 10b      | 3-1 (9)                  | 157.4 (3.0)                                  | 0.50 (0.10)   | 0.32 (0.07)   | 2.75  | 0.12  |
| 10b      | 4-1 (8)                  | 182.9 (1.8)                                  | 0.45 (0.06)   | 0.25 (0.03)   | 2.28  | 0.11  |
| 10b      | 5-1 (8)                  | 245.2 (6.6)                                  | 0.45 (0.16)   | 0.19 (0.07)   | 1.77  | 0.10  |
| 10b      | 6-1 (7)                  | 91.3 (3.1)                                   | 0.03 (0.14)   | 0.03 (0.16)   | 0.88  | 0.03  |
| 10b      | 7-1 (7)                  | 52.0 (3.2)                                   | 0.12 (0.06)   | 0.23 (0.11)   | 2.22  | 0.10  |
|          |                          |  |   |   |   |   |
| 10c      | 1-1 (6)                  | 112.9 (3.0)                                  | 0.04 (0.32)   | 0.05 (0.31)   | 0.74  | 0.04  |
| 10c      | 2-1 (8)                  | 134.8 (1.2)                                  | -0.13 (0.12)  | -0.10 (0.09)  | 0.78  | 0.00  |
| 10c      | 3-1 (10)                 | 154.1 (3.1)                                  | 0.11 (0.20)   | 0.06 (0.13)   | 0.77  | 0.09  |
| 10c      | 4-1 (8)                  | 176.2 (2.5)                                  | -0.13 (0.16)  | -0.08 (0.09)  | 0.61  | 0.00  |
| 10c      | 5-1 (8)                  | 210.6 (6.2)                                  | 0.31 (0.20)   | 0.14 (0.09)   | 0.82  | 0.18  |
| 10c      | 6-1 (7)                  | 93.3 (3.3)                                   | 0.36 (0.17)   | 0.39 (0.18)   | 0.95  | 0.41  |
| 10c      | 7-1 (7)                  | 53.8 (2.5)                                   | 0.24 (0.10)   | 0.44 (0.18)   | 1.59  | 0.27  |
| 10c      | 8-1 (7)                  | 22.0 (2.2)                                   | 0.22 (0.05)   | 0.99 (0.20)   | 1.17  | 0.84  |
| 10c      | 8-2 (7)                  | 21.1 (1.0)                                   | 0.18 (0.11)   | 0.85 (0.52)   | 1.70  | 0.50  |
| 10c      | 9-1 (12)                 | 11.6 (0.9)                                   | 0.29 (0.02)   | 2.59 (0.08)   | 1.95  | 1.26  |
|          |                          |  |   |   |   |   |
| 10d      | 1-1 (6)                  | 115.7 (1.2)                                  | -0.08 (0.21)  | -0.07 (0.19)  | 0.53  | 0.00  |
| 10d      | 2-1 (7)                  | 134.5 (1.4)                                  | -0.02 (0.12)  | -0.01 (0.09)  | 0.52  | 0.00  |
| 10d      | 3-1 (9)                  | 159.7 (1.5)                                  | 0.14 (0.10)   | 0.09 (0.07)   | 0.48  | 0.18  |
| 10d      | 4-1 (8)                  | 176.4 (2.6)                                  | 0.01 (0.11)   | 0.00 (0.06)   | 0.43  | 0.01  |
| 10d      | 5-1 (8)                  | 208.0 (5.2)                                  | -0.24 (0.23)  | -0.11 (0.11)  | 0.50  | 0.00  |
| 10d      | 6-1 (7)                  | 90.4 (2.6)                                   | -0.15 (0.15)  | -0.15 (0.17)  | 0.50  | 0.00  |
| 10d      | 7-1 (7)                  | 52.2 (3.2)                                   | 0.11 (0.14)   | 0.22 (0.26)   | 1.00  | 0.20  |
| 10d      | 8-1 (7)                  | 20.5 (1.5)                                   | 0.23 (0.02)   | 1.17 (0.12)   | 1.10  | 1.02  |

\* group id: size class-replicate (number of fish)

\*\* Numbers in parenthesis are standard errors.

Table C Continued.

Experiments 11 and 12

| Exp. No. | Group Id.* | (Fish No.) | average mean body weight (Wm, g) | average absolute growth rate (WGm, g/day) | average instant. growth rate (Gm, % bw/day) | average food consumption rate (RCm, % bw/day) | average food conversion rate (Fm) |
|----------|------------|------------|----------------------------------|---|---|---|-----------------------------------|
|          |            |            | **                               | **  | **  |   |                                   |
| 11       | 1-1        | (76)       | 154.1 (6.3)                      | -0.64 (0.02)                              | -0.44 (0.01)                                | 0.00  | 0.00                              |
| 12       | 1-1        | (7)        | 23.9 (3.1)                       | 0.24 (0.09)                               | 0.86 (0.41)                                 | 1.38  | 0.72                              |
| 12       | 2-1        | (6)        | 58.0 (1.6)                       | 0.36 (0.11)                               | 0.62 (0.21)                                 | 0.87  | 0.70                              |
| 12       | 3-1        | (7)        | 80.2 (2.5)                       | 0.17 (0.08)                               | 0.21 (0.10)                                 | 0.64  | 0.32                              |
| 12       | 4-1        | (9)        | 103.5 (2.4)                      | 0.56 (0.14)                               | 0.53 (0.13)                                 | 0.87  | 0.62                              |
| 12       | 5-1        | (9)        | 116.9 (2.4)                      | 0.47 (0.20)                               | 0.38 (0.17)                                 | 0.80  | 0.50                              |
| 12       | 6-1        | (8)        | 130.3 (3.1)                      | 0.25 (0.18)                               | 0.17 (0.13)                                 | 0.61  | 0.32                              |
| 12       | 7-1        | (5)        | 144.7 (0.6)                      | 0.37 (0.06)                               | 0.26 (0.04)                                 | 0.52  | 0.49                              |
| 12       | 8-1        | (3)        | 173.9 (4.1)                      | 0.48 (0.15)                               | 0.27 (0.08)                                 | 0.60  | 0.46                              |

\* group id: size class-replicate (number of fish)

\*\* Numbers in parenthesis are standard errors.