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EFFECTS OF TEMPERATURE AND FEEDING LEVEL ON GROWTH OF THE AMERICAN LOBSTER, *HOMARUS AMERICANUS*[1]

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ABSTRACT

To optimize culture conditions for the American lobster, *Homarus americanus*, experiments evaluating the effects of temperature and feeding level on growth rate and conversion efficiency were conducted at the San Diego State University Aquaculture Laboratory. Juvenile lobsters were maintained in recirculating seawater systems at temperatures of 10, 15, 20 and 25°C. At each constant temperature groups of 25 lobsters were fed rations of 0, 1, 2 and 4% of their wet body weight per day; 25 lobsters were also fed to excess at each temperature.

For the starvation groups, time to 50% mortality (LT 50) varied inversely with temperature. At 10°C the LT 50 was 114 days, while at 25°C it was only 47 days. Survival exceeded 90% in all cases except for those groups fed to excess, indicating toxic effects from the decomposition of unconsumed food. Instantaneous growth rate ranged from a low of 0.43% increase wet body weight per day at 10°C and a 1% feeding level, to 1.38% at 25°C and a 4% feeding level. Gross conversion efficiency (increase in wet body weight divided by total dry weight of food fed) ranged from 33.1% at 10°C and a 4% feeding level to 91.4% at 15°C and a 1% feeding level. The optimum combination of temperature and feeding level appears to occur near 20°C and a 2% feeding level.

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RÈSUMÈ

Pour donner à la culture du homard Américain, Homarus americanus, ses conditions optimales, le laboratorie d'Aquaculture de l'San Diego State University à fait des expériences pour évaluer les effets qu'ait la température et le niveau d'alimentation sur le degré de croissance et sur l'efficacité de conversion. De jeunes homards furent maintenus daus des systèmes qui recirculent l'eau de mer á des températures de 10, 15, 20 et 25°C. A chaque constance de température, on donna à des groupes de 25 homards des rations de 0, 1, 2 et 4% de leur poid lorsque mouillé. Assi, 25 homards furent nourri à excès à chaque temperature.

Pour les groupes d'ininitim, le temps pour 50% de mortalité (LT 50) varia inversement à la température. A 10°C le LT 50 était de 114 jours tandis qu' à 25°C il était seulement de 47 jours. Dous tores les cas, la survie exéda 90% souf pour les groupes qui furent trop nourri, ceci indique qu la décomposition de nourriture non consommée à un effet toxique. Les degrés de croissance instantané se distribuèrent à partir de 0.43% d'accroissement par jour de poid morillé à 10°C et à un niveau d'alimentation de 1%. Jusqua 1.38% à 25°C et a un niveau d'alimentation de 4%. L'efficacite de transformation brute (accroissement du poid mouillé divisé par le total du poid sec d'aliments) se distribua entre 33.1% à 10°C et a un niveau d'alimentation de 4% le niveau d'alimentation et 91.4% a 15°C et à un niveau d'alimentation de 1%. La combinaison optimale de température et niveau d'alimentation semble se trocever à 20°C et à un niveau d'aumentation de 2%.

Introduction

The growth rate of the American Lobster, Homarus americanus, is accelerated at elevated temperatures within the tolerance limits for this species (McLeese, 1956; Hughes et al., 1972). Lobsters grow to a weight of 454 g in 4-10 years in areas where ambient temperatures range from 8-15°C (Cooper, 1977). When reared at elevated temperatures (22°C) they can attain this size in as little as 18-24 months (Hughes et al., 1972). This acceleration in rate of growth has stimulated interest in developing methods for the commercial culture of this species. However, elevated temperatures also increases metabolic demands (Winget, 1969; Blecha, 1972; Johnson, 1977) and results in increased food requirements (Carlberg, 1975; Johnson, 1977). Increased consumption of food and the associated increased feed costs may partially negate gains from the accelerated rate of growth achieved by lobsters reared at higher temperatures.

Gross conversion efficiency (K) describes the increase in wet weight of an organism as a function of the dry weight of feed consumed. The range of reported K values for aquatic consumers is large and can be greatly affected by type of diet (Adron et al., 1976; Clifford and Brick, 1978; Capuzzo and Lancaster, 1979; Sedgwick, 1979), age and body size (Brett et al., 1969; Elliot, 1975), salinity (Kinne, 1962), and feeding level and temperature (Richman, 1958; Mason, 1963; Brett et al., 1969; Kerr, 1971; Blecha, 1972; Williams and Caldwell, 1978). At low feeding levels just above maintenance levels, poikilothermic organisms normally convert food to tissue more efficiently but growth rates are often reduced. At higher feeding levels increased growth rates are obtained, but often at the expense of a lower conversion efficiency (Paloheimo and Dickie, 1966). To reduce production costs in aquaculture the culturist is interested in determining the feeding level which maximizes both growth rate and conversion efficiency. This ration should be intermediate to the feeding level yielding the most efficient use of food (maximum conversion efficiency) and the feeding level yielding the maximum growth rate (Brett et al., 1969).

This paper describes the results of laboratory experiments concerning the combined effects of temperature and feeding level on growth, survival and conversion efficiency of H. americanus. The hypothesis was that the highest conversion efficiencies would be found at low feeding levels and low culture temperatures, since at lower temperatures the energy required for basal metabolism of poikilothermic organisms is less. Reduced metabolic requirements allow a larger portion of the energy from the available food to be used for growth processes. Low feeding levels at elevated temperatures would not fulfill the increased metabolic needs associated with higher temperatures and therefore, more of the energy derived from the consumed food would be expended on metabolism. Although laboratory studies of this kind may have limited application in the management of natural populations (Kerr, 1971), they are useful in developing cost-effective techniques to be used in the culture of lobsters and other species.

Materials and Methods

The research was conducted at the San Diego State University (SDSU) Aquaculture Laboratory located at the Scripps Institution of Oceanography (SIO), La Jolla, California. Berried female lobsters were obtained from Mr. John T. Hughes, director of the Massachusetts State Lobster Hatchery, Vineyard Haven, Massachusetts. Upon hatching, larvae were cultured in plankton kriesels (Hughes *et al.*, 1974) at 20°C, until the last larval stage (IV) was reached. Post-larval lobsters were placed in individual plastic rearing compartments measuring 10.5 by 15.5 cm. The compartments had perforated bottoms and were positioned in fiberglass culture trays equipped with a partially recirculating seawater system. Seawater was supplied by pumps located at the distal end of the SIO pier and filtered by high-rate sand filters. Experimental temperatures were maintained with electric quartz sleve immersion heaters and refrigeration units fitted with non-corrosive plastic cooling coils. Styrofoam covers were fitted on all trays for added insulation to reduce temperature fluctuations and to provide reduced levels of light. Kwok (1979) found increased growth rates for American lobsters cultured under 24 hours of darkness.

Seawater temperature in each tray was measured daily. Occasional power failures caused some temporary fluctuations in temperature, however abrupt temperature changes have been shown to have little effect on growth or survival of *H. americanus* (Felix, 1978).

A 4 by 5 matrix experimental design was used to examine the combined effects of feeding level and temperature. Several groups of 25 lobsters were held at the 4 test temperatures of 10, 15, 20 and 25°C and fed rations of 0, 1, 2, and 4 percent of their live body weight daily. Other groups of 25 lobsters were fed *ad libitum* amounts once daily.

The food ration tested was adult brine shrimp, *Artemia salina*. Frozen adult brine shrimp were thawed, drained for 10 minutes, and mixed in a 0.6% sodium alginate solution. Measured amounts of this slurry were extruded into a calcium chloride bath and refrigerated for 1 hour to form a calcium alginate bound brine shrimp pellet. Animals were fed daily 6 days a week. All uneaten food from the previous day's feeding was removed prior to each feeding.

Survival of juvenile lobsters from all treatment groups was recorded daily. Growth was monitored by monthly measurements of the lobster's carapace length (C.L.) to the nearest 0.1 mm by use of vernier calipers. Weight determinations were calculated from the length to weight conversion formula: wet weight = $.0002\ (\text{C.L.})^{3.39}$ (Bartley, 1979). After each monthly survey the amount of feed was adjusted to maintain constant feeding levels on a percent body weight basis.

Results

Survival

Survival was high for groups of lobsters at all temperatures and feeding levels except those groups receiving no food or those receiving the excess feeding levels. Reduced survival in the latter group probably was due to the toxic effects caused by the decomposition of large quantities of uneaten food and fecal material (Table 1). Chi-square analysis indicated significant differences in survival ($p < .05$) between the excess feeding groups and all other treatment groups except the one receiving a 4% feeding level at 20°C, which also had substantial mortality. Similarly, there were no significant differences in survival for any of the restricted feeding levels except the 4% level at 20°C. The cause of the poor survival of this group is unknown.

The time to 50% mortality (LT 50) for each starvation group is shown in Table 2. As expected, LT 50 times were inversely proportional to temperature.

Growth

Little growth was shown by the juvenile lobsters in the starvation groups. Length to wet lobster weight transformations were performed on the monthly survey data (Bartley, 1979). Comparisons of the growth slopes were made using the Newman-Kuels Multiple Range Test (Zar, 1974). At all feeding levels, culture temperature had a significant effect on lobster growth ($p < .05$). Also, at any given temperature there were significant differences in the growth of lobsters receiving the four different feeding levels ($p < .05$).

Specific growth rates or instantaneous growth rates, which are defined as the natural log of the final wet weight minus the natural log of the initial wet weight divided by time, were plotted against temperature (Figure 1) and feeding level (Figure 2). As feeding level decreases, the temperature promoting maximum growth also decreases. At the 4% feeding level most rapid growth was observed at 25°C while at the 1% level 20°C yielded maximum growth.

Conversion Efficiency

The log of gross conversion efficiency ($\log_{10} K$) plotted against feeding level (Figure 3) revealed that conversion efficiency decreased with increasing feeding levels at all temperatures except 20°C. For the 20°C treatment the maximum conversion efficiency occurred at the 2% feeding level. As the feeding level is reduced the temperature promoting greatest conversion efficiency decreases. At the 4% feeding level, 25°C was the optimum temperature. At the 2% feeding level the maximum occurred at 20°C and at the 1% feeding level 15°C promoted greatest conversion efficiency.

Generally, conversion efficiency decreases with body size and age (Brett et al., 1969). Using the 1% feeding level at 20°C as an example, analysis of variance revealed significant differences among the conversion efficiency values at different survey dates ($p < .05$). A T-test comparison of the conversion efficiency values at 54 days and 188 days revealed that the conversion efficiencies of the older group was significantly lower ($p < .05$). Therefore, lobster conversion efficiency will decrease with age when temperature and feeding level are held constant.

Optimization of Temperature and Feeding Level

The optimum temperature and feeding level was determined by maximizing the specific growth conversion index (SGCI), which is defined as the specific growth rate multiplied by the gross conversion efficiency (Farmanfarmaian and Lauterio, 1979). Over the range of temperatures and feeding levels tested the best growth rate for the least amount of food provided occurred at a 2% feeding level and a temperature of 20°C. Figure 4 indicates the specific growth conversion index obtained at the various feeding levels and culture temperatures. More data points are necessary for a complete understanding of this relationship in juvenile lobsters. However, as feeding level increased the temperature promoting optimum growth also increased. Also, it is apparent that the optimum temperature-feeding level combination for 10 and 25°C cannot be determined from these results. Evaluation of feeding levels in excess of 4% and below 1% body weight per day appear necessary to determine the optimum feeding level for the 25 and 10°C temperature treatments respectively.

Discussion

Survival

McLeese (1956) and Felix (1978) established the upper and lower incipient lethal temperature for Homarus americanus to be near 32° and -1.7°C respectively. Since all of the culture temperatures maintained in this study were within this range, temperature alone should not have caused the observed mortality.

Survival of the lobsters receiving large amounts of food apparently were influenced by the decomposition of uneaten food which fouled the water in the individual rearing compartments. Many crustaceans do not eat immediately prior to ecdysis (Lasker, 1966; Johnson, 1977) and therefore a large ration presented just prior to molting would not be consumed and would begin to decay and adversely affect water quality. Bacterial growth on unconsumed food is enhanced at high temperatures, further stressing the lobsters. Similar negative effects of high feeding levels on survival were observed by Shleser and Gallagher (1974) in their work on the evaluation of artificial diets for juvenile H. americanus. In their study a starvation group had higher survival than a group fed a natural diet representing 5% body weight per day.

Survival of the starvation groups was inversely related to culture temperature in this study. Reductions in gastric fluid protein level, hemocyanin level, and hepatopancreas weight have been found in starved H. americanus (Stewart et al., 1967) and starved Western rock lobster, Panulirus longipes (Dall, 1975). These reductions were dependent on both duration of starvation and water temperature (Dall, 1975). Reduced hemocyanin levels interfere with oxygen transport within lobsters (Stewart et al., 1967). Blecha (1972) showed peak O_2 demands prior to ecdysis and immediately thereafter in the California Spiny lobster, Panulirus interruptus. This increased demand coupled with reduced O_2 transport may also influence mortality of starved American lobsters.

Growth

Lobster growth has typically been expressed as an increase in carapace length per day. Growth rates presented in Table 1 when expressed as an increase in length over time agree with previously reported values. Van Olst and Carlberg (1979) report values of .049-.059 mm/day for juvenile *H. americanus*, *H. gammarus*, and their hybrid cross grown at 22°C on a diet of live adult brine shrimp. Johnson (1977) reports growth rates slightly higher (.066 mm/day) for younger juveniles reared on the same diet at 24°C. The younger lobsters would be expected to show higher growth rates (Brett *et al.*, 1969; Royce, 1972). Felix (1978) reports growth rates near .035 mm/day for control and experimental lobsters subjected to abrupt temperature shocks.

In this study higher growth rates were correlated with increasing feeding levels (Table 1). However, *ad libitum* amounts of food did not promote the highest rates of growth. This phenomenon of diminishing returns may be related to fouling of the system and also to the manner in which the excess ration was presented. Providing a large amount of food once per day may be less satisfactory than feeding to satiation several times daily; a technique which has been used effectively in the culture of fishes (Kinne, 1962). High feeding levels depressed growth rates in channel catfish even though no deterioration in water quality was observed (Andrews, 1979). The carp, *Cyprinus carpio*, also showed reduced growth rates at high feeding levels (Huisman, 1976).

Conversion Efficiency

The gross conversion efficiencies found in this study and others (Hughes *et al.*, 1972) appear favorable for the aquaculturist. Poikilothermic animals may be more efficient converters of food to animal tissue than homeotherms. Thermal conformers require less energy to maintain homeostasis, i.e. maintenance of body composition and temperature (Calow, 1977). Capuzzo and Lancaster (1979) found gross conversion efficiencies from 30-35% for post larval lobsters fed 5% (dry/wet) of their body weight at 20°C. This is in agreement with the findings of this study (K = 43% at a 4% feeding level.) Blecha (1972), measuring gross conversion efficiency in energy units for California spiny lobsters, reports values near 10%. When these results are converted to wet weight of lobster per dry weight food fed the efficiency values are near 36%. Capuzzo and Lancaster (1978) maintained lobsters on a slightly higher feeding level than in this study, while Blecha (1972) fed lobster a diet of mussel which is considered to be a less suitable diet than adult brine shirmp (Van Olst *et al.*, 1976). Both factors would lead to decreased efficiency values.

At a constant temperature, K values decrease with increasing feeding level after the maximum K value has been reached. Metabolic energy needs associated with increased spontaneous activity caused by high feeding levels increase at a greater rate than the energy derived from the increased amount of food available. Therefore, a larger fraction of the energy is dissipated as metabolism (Kerr, 1971). A smaller ration requires relatively less post-absorptive processing, at a lower metabolic cost or lower Specific Dynamic Action as described by Calow (1977).

The hypothesis that highest conversion efficiency would be found at low feeding levels and culture temperatures was supported. The lower metabolic demands of lobsters at reduced temperatures allow for a larger proportion of the ration to be allocated for growth. This phenomenon is only possible when the action of digestive enzymes and internal growth processes are not unduly inhibited by low temperatures. Apparently the effective temperature range of these processes is sufficiently large or alternate enzymes begin to function at low temperatures to sustain K values (Brett et al., 1969). A lower temperture limit probably exists for the action of these enzymes, since Aiken and Waddy (1975) found no growth for lobsters at 5°C.

If the conversion efficiency values determined in this study for lobsters fed a diet of brine shrimp are applicable for other, less expensive diets, lobster culture may prove to be economically feasible when suitable culture techniques are developed. Sedgwick (1979) indicate that a conversion efficiency of approximately 50% ($\log_{10} K = 1.7$) is necessary before penaeid shrimp can be cultured economically. The efficiencies found in this study show that H. americanus can meet and perhaps exceed this criterion.

Optimization of Temperature and Feeding Level

Aquaculturists seek to provide culture conditions which maximize profits rather than growth rate or conversion of efficiency alone. The feeding level that produces the greatest conversion efficiency is not always with the ration which produces the fastest growth for the least amount of food. Huisman (1976) states that Brett et al. (1969) equate these two feeding levels, but the data of Brett et al. indicates that the optimum ration will be intermediate to the feeding level providing for maximum conversion efficiency and the feeding level producing maximum growth rate. In that study, the feeding level providing optimum growth rate was determined to be 3.25% body weight per day at 10°C while the feeding level producing maximum conversion efficiency at the same temperature is near 1.25% body weight per day for young sockeye salmon.

In this study it was determined that a 2% feeding level at 20°C is an optimum combination for the culture of juvenile lobsters. It should be stressed that this only optimizes growth in relation to feeding level. A complete aquaculture facility is complex and involves optimization of numerous variables in addition to temperature and amount of food, such as space, labor, feed ingredients, water circulation, and waste treatment (Rauche et al., 1975).

Table 1. Percent survival and specific growth rate (G)* for groups of 25 juvenile lobsters at four feeding levels and four temperatures.

Temperature (°C)	Feeding Level (% body wt. fed/day)	Survival (%)	Specific Growth Rate (G)
10	1	96	0.43
10	2	96	0.57
10	4	96	0.75
15	1	92	0.62
15	2	100	0.98
15	4	88	1.21
15	Excess	52	1.00
20	1	96	0.68
20	2	96	1.05
20	4	52	1.25
20	Excess	52	1.03
25	1	88	0.55
25	2	96	0.95
25	4	96	1.38
25	Excess	56	0.86

*G = [(ln final wet weight - ln initial wet weight)/time] and represents % increase in wet weight per day.

Table 2. Time to 50% mortality (LT 50) for starved juvenile lobsters at four constant temperatures.

Temperature (°C)	LT 50 (days)
10	114
15	79
20	46
25	47

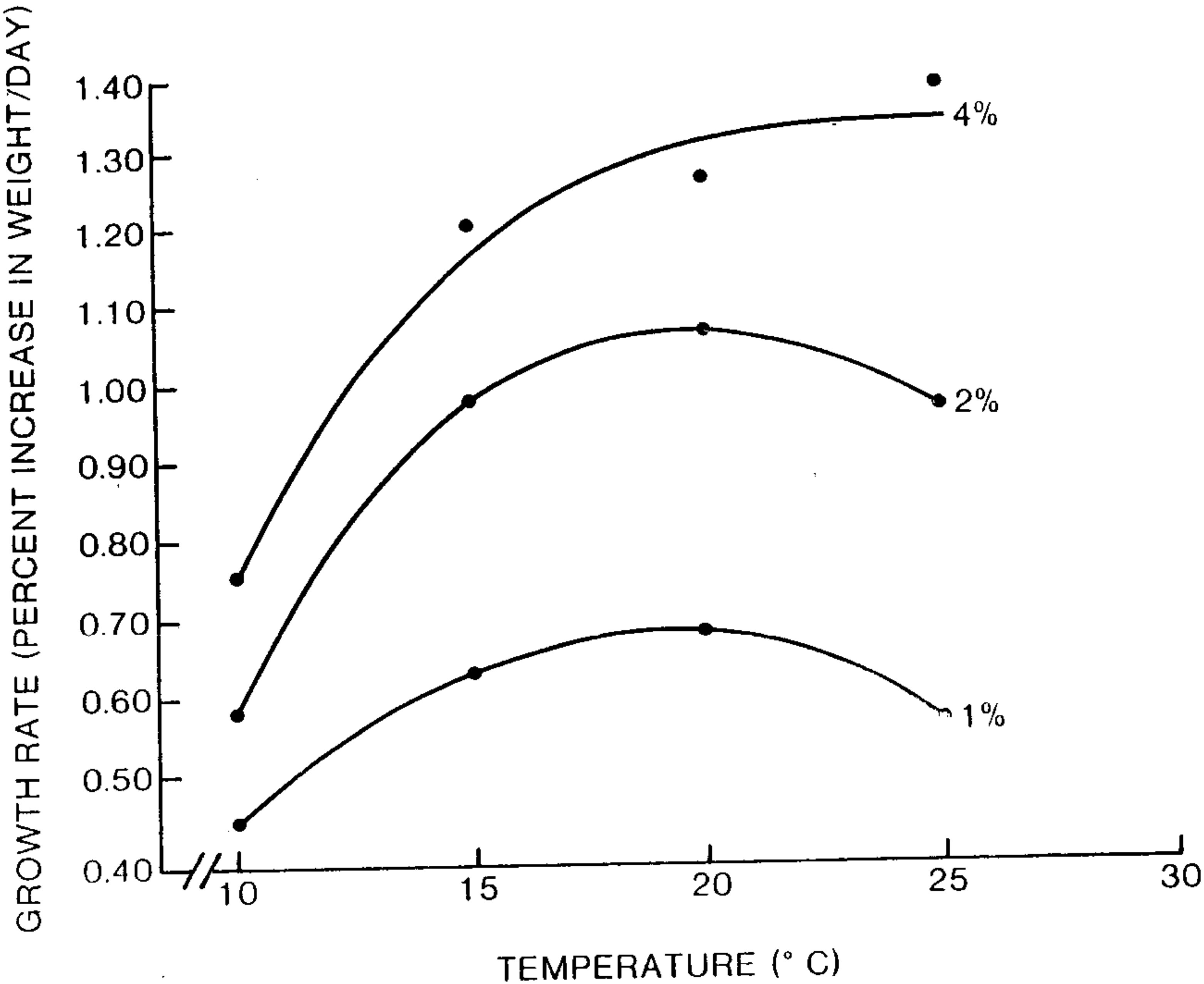

Figure 1. Growth rate of H. americanus at four different culture temperatures when fed brine shrimp at three levels of feeding (1, 2 and 4% body weight per day).

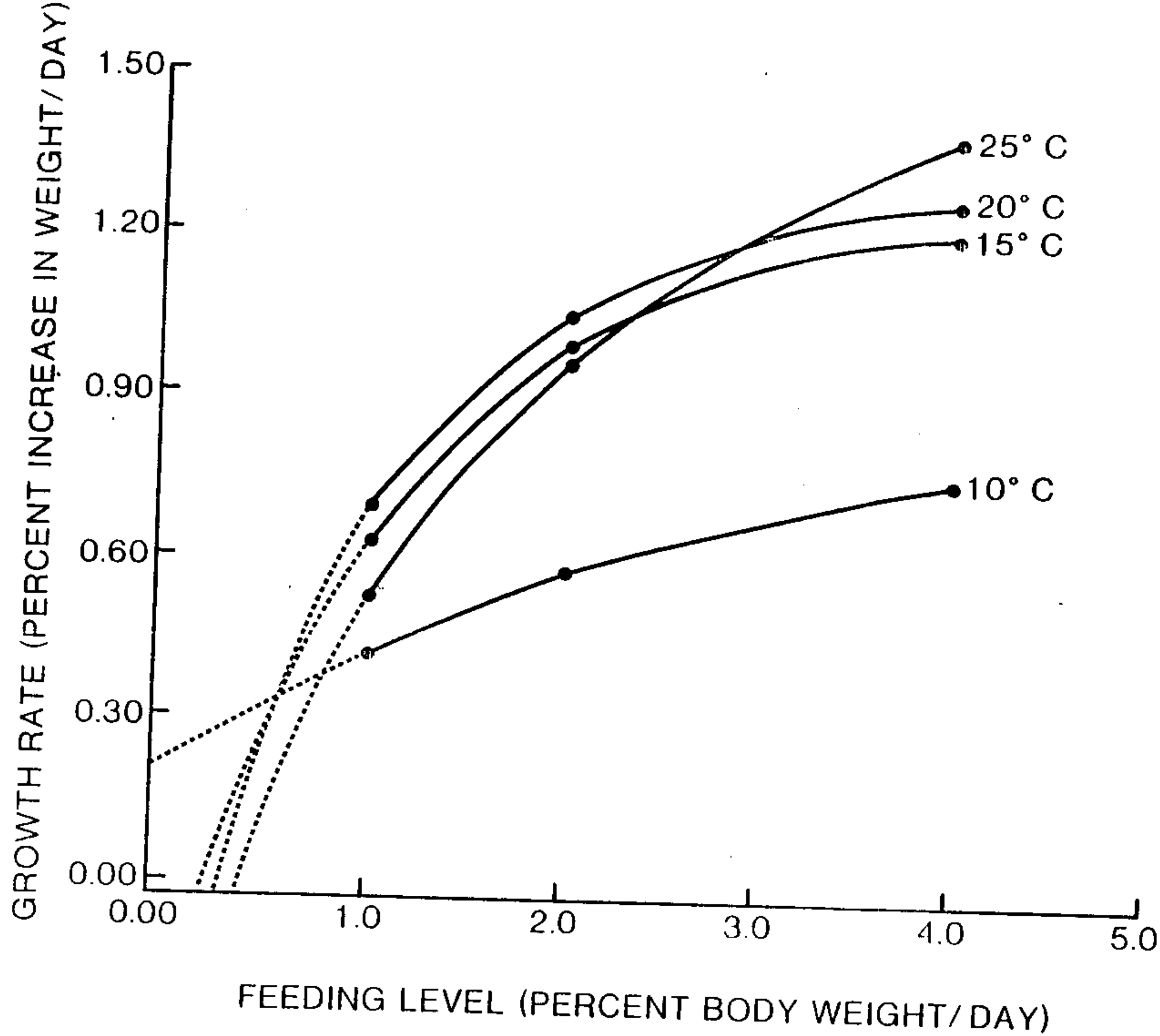

Figure 2. Growth rate of H. americanus at three different feeding levels when held at four different culture temperatures (10, 15, 20 and 25°C).

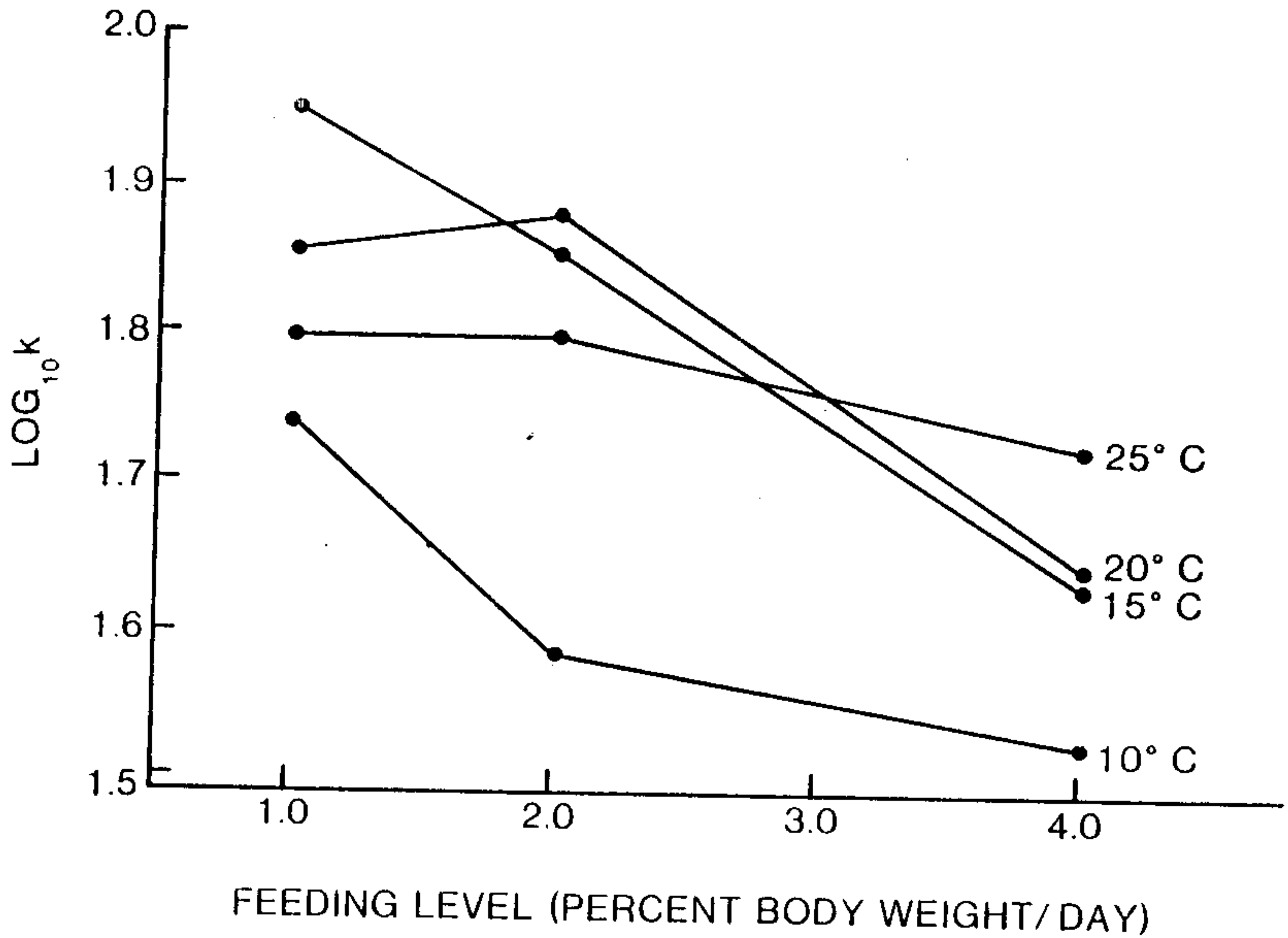

Figure 3. The log of food conversion efficiency in H. americanus is shown as a function of feeding level. The four lines represent the four culture temperature indicated.

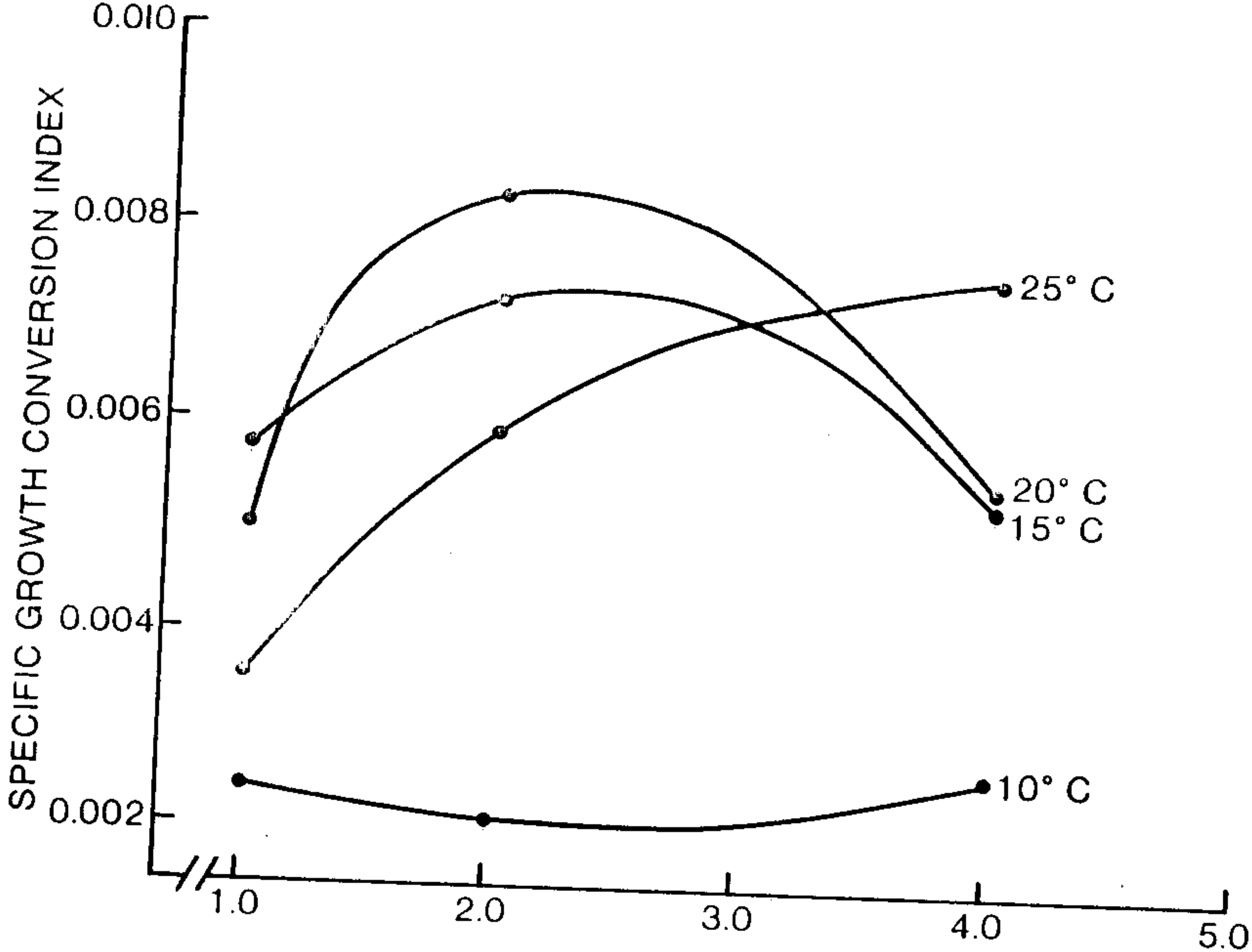

Figure 4. The Specific Growth Conversion Index for H. americanus is shown as a function of feeding level. The four lines represent the four culture temperatures indicated.

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