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Size dependent variation in optimum growth temperature of red abalone (*Haliotis rufescens*)

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Abstract

Six size groups of red abalone *Haliotis rufescens* (geometric mean shell lengths: 21, 25, 33, 66, 81 and 98 mm) were reared on a macroalgal diet for 4 months at seven different temperatures between 11 and 22 °C. The results demonstrate that red abalone exhibit size dependent variation in growth potential and temperature optimum for growth. The maximum growth rate was found to have a skewed, third degree polynomial relationship with shell length, reaching a maximum of 111 $\mu\text{m day}^{-1}$ at 38 mm shell length. The temperature optimum for growth was found to have a symmetrical, concave relationship with shell length from 16 mm to maturity, reaching a peak of 17.8 °C at 44 mm shell length. The minimum grow-out time from spat to market size on an optimum temperature regime was predicted less than 2 years. The results from the present study could contribute to an increase in the potential yield from landbased abalone farming.

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Keywords: Abalone; Growth; Temperature; Ontogenetic variation; *Haliotis rufescens*

1. Introduction

Most abalone farms are located on-land where rearing temperatures can in some cases be adjusted to optimise the growth rates of the abalone. The abalone farmer must therefore know the optimal temperature for growth and how it may vary with the size of the abalone. The extra energy costs ultimately associated with an optimum temperature regime will, however, always be weighed against the benefits associated with increased growth rates.

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The effect of temperature on growth and/or nutritional indices has been investigated for the juvenile stages of several abalone species, *Haliotis rufescens* (Leighton, 1974), *Haliotis rubra* and *Haliotis laevigata* (Gilroy and Edwards, 1998), *Haliotis midae* (Britz et al., 1997), *Haliotis kamtschatkana* (Paul and Paul, 1981; Hoshikawa et al., 1998), *Haliotis tuberculata* (Lopez et al., 1998) and *Haliotis discus hannai* (Uki et al., 1981; Hoshikawa et al., 1998). The optimal temperatures for growth ($T_{\text{opt.G}}$) have been determined for some of these species but size dependent variation in $T_{\text{opt.G}}$ has never been reported. No laboratory studies have been performed on the effect of temperature on the growth of maturing abalone.

Ontogenetic changes in rearing temperatures have been demonstrated for the commercial scallop *Pecten fumatus* (Reeve) (Heasman et al., 1996). Further, size dependent variation in temperature optimum and growth potential has been reported for juvenile and adult stages of several marine fish species. The optimal temperatures for growth and/or growth efficiency have been shown to decrease with fish size for Atlantic cod *Gadus morhua* L. (Björnsson et al., 2001), Atlantic halibut *Hippoglossus hippoglossus* L. (Björnsson and Tryggvadóttir, 1996; Jonassen et al., 1999), turbot *Scophthalmus maximus* L. (Burel et al., 1996; Imsland et al., 1996), common wolffish *Anarhichas lupus* L. (McCarthy et al., 1998) and plaice *Pleuronectes platessa* L. (Fonds et al., 1992). The opposite ontogenetic trend has, however, been observed for larval cod, where optimal temperatures and maximum growth rates have been seen to increase with size and peak during the early juvenile stage (Steinarsson and Björnsson, 1999; Otterlei, 2000).

The aim of the present study was to investigate the effects of temperature and size on growth rates of red abalone, with special emphasis on detecting size dependent variation in temperature optimum and growth potential.

2. Materials and methods

2.1. Abalone stock and rearing conditions

The studies were carried out at the commercial abalone farm Sæbýli in southwest Iceland. The abalone used in the studies were offspring from the first and only lot of red abalone imported to Iceland from Morro Bay California in 1988.

The abalones were reared in square, white polyethylene containers with a rearing volume of 12 l. Seawater with a salinity of 36.0‰ (± 0.2) and temperature of 10.8 °C (± 0.1) was pumped from 70 m depth and heated geothermally through a heat exchanger so that all groups were reared at 15 °C (± 0.1) during whole juvenile cycle. This temperature regime was applied in all groups used in the experiment so that all animals had the same thermal history prior to start of the experiment. Water flow into each tank was 0.6 l min⁻¹ (± 0.2) and all tanks were continuously aerated. The abalones were reared in constant darkness with light only being turned on during feeding, surveillance and measurements. Water temperature was measured and adjusted every morning. The abalones were fed a 9:1 mixture of locally harvested brown kelp (*Laminaria digitata*) and red seaweed (*Palmaria palmata*). All groups were fed in excess and the leftover feed was regularly removed from the tanks.

2.2. Experimental design

Two separate experiments were carried out using abalones of different ages and initial mean shell lengths. Abalones of mixed parental origin from four different age-classes were removed from the farm's production line and transferred to the experiment chamber where individual abalones were selected randomly from each batch and measured for weight and shell length. Initial mean weight and shell length of the experimental groups in each age-class did not differ (two-way nested analysis of variance (ANOVA) Power $(1 - \beta) > 0.8$, Table 1). The abalones were transferred from the holding temperature of 15 °C with 2 days gradual adjustment to the five experimental temperatures. The first experiment started on 18–24 March 1997. Four age-classes of abalones, 8, 13, 28 and 54 months from hatch, were reared for 4 months at the five different temperatures 11, 12, 14, 16 and 18 °C. The initial number of abalones per group was 50, 40, 20 and 10, respectively, and the initial mean shell lengths were 18, 27, 61 and 94 mm, in the respective age-classes. These groups are called group: B, C, D and F, respectively. The latter experiment started on 31 January 1998. Two age-classes of abalones; 11 and 38 months from hatch, were reared for 4 months at the five different temperatures 14, 16, 18, 20 and 22 °C. The initial number of abalones per group was 50 and 10, respectively, and the initial mean shell lengths were 16 and 75 mm, in the respective age-classes.

Table 1

Mean temperature, initial and final number of abalone (n_1 , n_2), mortality (M), initial and final length of abalone (L_1 , L_2), in each part of the experiment (see Materials and methods for details on experimental groups A–F)

Group	A—21 mm					B—25 mm				
Temperature (°C)	14.1	16.1	18.1	20.1	22.0	11.1	11.9	13.7	15.6	17.7
L_1 (mm)	16.2	15.9	15.6	15.7	15.8	17	16.9	17.2	18.3	19
L_2 (mm)	27.2	29.5	29.1	24.2	20.7	24.4	25.5	27.7	31.5	31.7
n_1	150	150	150	150	150	150	150	150	150	150
n_2	139	131	115	71	34	125	133	142	133	143
M (%)	7.3	12.6	23.3	52.6	77.3	16.7	11.3	5.3	11.3	4.7
Group	C—33 mm					D—66 mm				
Temperature (°C)	11.1	11.9	13.7	15.6	17.7	11.1	11.9	13.7	15.6	17.7
L_1 (mm)	26.4	26.5	26.6	27.7	27.4	59.5	60.7	61.1	61.2	60.9
L_2 (mm)	35.6	36.7	39.1	40.6	41	66.1	68.7	71.1	72.4	72.2
n_1	120	120	120	120	120	60	60	60	60	60
n_2	111	117	112	118	120	60	57	60	60	59
M (%)	7.5	2.5	6.7	1.7	0	0	5.9	0	0	1.7
Group	E—81 mm					F—98 mm				
Temperature (°C)	14.1	16.1	18.1	20.1	22.0	11.1	11.9	13.7	15.6	17.7
L_1 (mm)	76.8	75.6	76.3	75.3	75.4	93.5	93.6	93.8	94.2	95.3
L_2 (mm)	86.2	85.2	83.6	75.2	76.5	100.1	100.1	99.8	102.4	101.4
n_1	30	30	30	30	30	30	30	30	30	30
n_2	30	27	20	10	5	29	29	30	29	28
M (%)	0	10.0	33.3	66.7	83.3	3.3	3.3	0	3.3	6.7

Size numbers for A–F refer to geometric mean shell length.

These groups are called groups A and E, respectively. All experimental groups in both experiments were reared in triplicate.

Originally, both shell length and total weight were measured for each individual. To facilitate the measurement of individual shell length and body weight, the abalones were anaesthetized with 1.5 ppm phenoxyethanol (ethylenglycolmonophenylether) for 10–15 min. The anaesthetization was found to cause duration-dependent weight loss in the abalone and therefore the weight measurements were not included in the results. Another reason to use shell growth, rather than weight increase, as an indicator of abalone growth rate, is the large seasonal variation in the foot/shell ratio of maturing abalone, associated with the storage of glycogen in the foot and the subsequent use of glycogen during gonadogenesis ([Hayashi, 1983](#)).

2.3. Data analysis and statistical methods

The shell length of the abalone was measured to the nearest 0.1 mm with digital calipers at the beginning and the end of the experimental period. The daily growth rate (G) of the abalone was measured in $\mu\text{m day}^{-1}$ according to the following formula:

$$G = (L_2 - L_1)/(t_2 - t_1)$$

where L_2 and L_1 are shell lengths (μm) at days t_2 and t_1 , respectively.

All statistical analyses were performed with Statistica™ 5.0. The relationship between growth and temperature was analysed by a second order polynomial fit to the data:

$$Y = a + bX + cX^2$$

where Y is daily growth rate (G), X is temperature ($^{\circ}\text{C}$) and a , b and c are constants determined by the regression. The optimal temperature for growth ($T_{\text{opt},G}$) was estimated as the zero solution [$X = -b/(2c)^{-1}$] to the first derivative of the polynomial equations. The daily growth rate at $T_{\text{opt},G}$ was defined as G_{max} . The relationship between size and optimal temperature was analysed by regressing $T_{\text{opt},G}$ against geometric mean shell length ($L = (L_1L_2)^{1/2}$), and the relationship between G_{max} and shell length was analysed by regressing G_{max} against L . Both these functions were analysed by a third order polynomial fit to the data:

$$Y = a + bX + cX^2 + dX^3$$

where Y is either $T_{\text{opt},G}$ or G_{max} , X is geometric mean shell length (mm) and a , b , c and d are constants determined by the regression. Data on mortality was analysed with Fisher exact test ([Zar, 1984](#)) and size specific mortality tested using one-way ANOVA ([Zar, 1984](#)). A significance level (α) of 0.05 was used.

3. Results

3.1. Mortality

A total of 413 abalones died during the experiments, which amounts to 15.3% overall mortality. Mortality was relatively low at intermediate temperatures but increased at 20–

22 °C (Table 1). Apart from 20 and 22 °C in experimental groups A and E there was no significant difference in mortality between the temperature groups (Fishers exact test, $P>0.2$). Due to the significant mortality, data from these two groups at 20 and 22 °C were excluded from further analyses in the study. Size specific mortality was found at 20 and 22 °C in the A experimental group (one-way ANOVA, $P<0.01$). Apart from this group, no size specific mortality was found within any temperature group (one-way ANOVA, $P>0.10$).

3.2. Growth: effect of temperature and size

The second order polynomial regressions of G against temperature were significant in all size classes (Fig. 1). $T_{\text{opt},G}$ increased from 16.7 °C for abalone with geometric mean shell length of 21 mm (Fig. 1a) to 17.2–17.3 °C for abalone in the size range 25–66 mm (Fig. 1b–d). For the larger abalone (81–98 mm, Fig. 1e–f) $T_{\text{opt},G}$ decreased steadily and

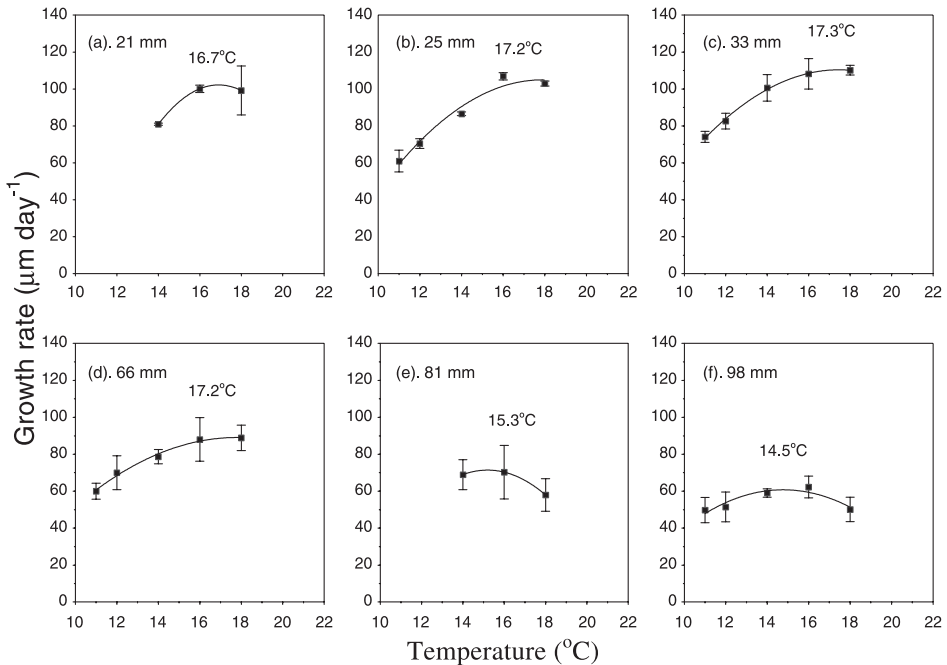


Fig. 1. Changes in daily growth rate with temperature for six different size classes of red abalone. The lines represent the least-squares second order polynomial fit to the data: $G = aT^2 + bT + c$ where G = Daily growth rate, T = temperature, and a , b and c are constants determined by the regression. Vertical lines indicate standard error of mean. Size numbers in legend refer to geometric mean shell length. (a) $G = -2.38T^2 + 79.69T - 566.67$, $r^2 = 0.96$. (b) $G = -1.19T^2 + 41.05T - 247.79$, $r^2 = 0.97$. (c) $G = -0.019T^2 + 0.495T - 1.929$, $r^2 = 0.98$. (d) $G = -0.74T^2 + 25.44T - 129.60$, $r^2 = 0.98$. (e) $G = -1.71T^2 + 52.27T - 328.32$, $r^2 = 0.98$. (f) $G = -1.08T^2 + 31.54T - 168.58$, $r^2 = 0.89$. The optimal temperatures for growth ($T_{\text{opt},G}$) indicated in each figure were calculated from the first order derivative of the parabolic regressions (i.e. when $dG/dT = 0$). r^2 represents the probability of fit of the least-squares second order polynomial to the data.

was calculated to be 14.5 °C for the largest size group (Fig. 1f). The maximum growth rates (G_{\max}) were similar for the 21, 25, 33 and 66 mm size groups and were calculated as 99, 105, 109 and 89 $\mu\text{m day}^{-1}$, respectively. G_{\max} decreased in the 81 and 98 mm groups and was calculated as 71 and 61 $\mu\text{m day}^{-1}$, respectively.

Both the optimal temperature for growth ($T_{\text{opt},G}$) and the maximum growth rate (G_{\max}) of the abalone were affected by the size of the abalone and both were described by a third order polynomial fit (Fig. 2). A significant concave relationship was found between $T_{\text{opt},G}$ and shell length, with a peak of 17.8 °C at 44.2 mm shell length (Fig. 2a). A similar

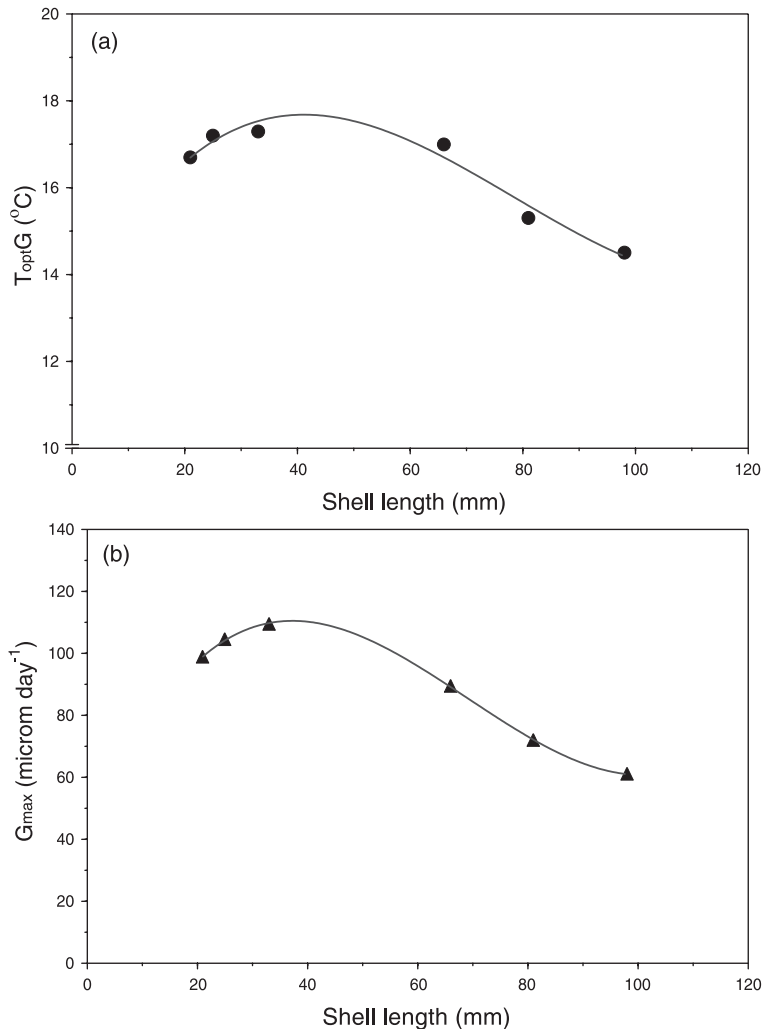


Fig. 2. Optimal temperature for growth ($T_{\text{opt},G}$) and maximum growth (G_{\max}) plotted against geometric mean shell length (mm) of red abalone. The lines represent third order polynomial regression to the data: (a) $T_{\text{opt},G} = 12.91 + 0.26L - 0.01L^2 + 0.0001L^3$, $r^2 = 0.96$; (b) $G_{\max} = 38.74 + 4.39L - 0.08L^2 + 0.0004L^3$, $r^2 = 0.98$.

relationship was found between G_{\max} and shell length, with a peak of $111 \mu\text{m day}^{-1}$ at 37.6 mm shell length (Fig. 2b).

4. Discussion

The growth rates in the present study compare favourably to those reported for red abalone in other laboratory or planting studies, i.e. $27\text{--}96 \mu\text{m day}^{-1}$ for juvenile abalone of various sizes (McBeth, 1972; Owen et al., 1984; Tegner and Butler, 1985; Greenier and Takekawa, 1992; Corazani and Illanes, 1998; Trevelyan et al., 1998). Growth rates of more than $100 \mu\text{m day}^{-1}$ have been reported for early juveniles (4–5 mm shell length) of other temperate latitude abalone species, like *H. tuberculata* (Lopez et al., 1998) and *H. discus hannai* (Hoshikawa et al., 1998), feeding on artificial feed and diatoms, respectively. Furthermore, even higher growth rates have been reported for 10–40 mm juveniles of several species, like *H. tuberculata* (Lopez et al., 1998), *Haliotis asinina* (Capinpin and Corre, 1996; Fermin, 2001), *H. laevigata* (Gilroy and Edwards, 1998) and *Haliotis iris* (Clarke and Creese, 1998), feeding on artificial feed. The growth rates reported for red abalone in field studies are generally much higher than growth rates normally achieved under culture conditions (Hines and Pierce, 1982; Haaker et al., 1998). Red abalone in southern California routinely reach shell lengths of 70–80 mm in only 2 years from hatch (Haaker et al., 1998), thus averaging ca. $100 \mu\text{m day}^{-1}$ from hatch to cultivation market size. A greater growth potential therefore appears to be associated with natural environment conditions and the more varied natural diet of red abalone in the field.

The results of the present study indicate that the temperature optimum for growth of red abalone has a symmetrical, concave relationship with shell length, from 16 mm to maturity (Fig. 2). The $T_{\text{opt.G}}$ thus rises from an initial level of approximately 15°C at hatch (Leighton, 1974), to a peak close to 18°C for 44 mm abalone, whereafter it falls to again reach the initial level of approximately 15°C at maturity. In the field, maturity ensues at a shell length of 80–90 mm (Ault, 1985), indicating that $T_{\text{opt.G}}$ peaks midway between hatch and maturity. The inflection of the curve at maturity may lead to the assumption that there is no further decrease in $T_{\text{opt.G}}$ with size. A peak in $T_{\text{opt.G}}$ at 18°C is only slightly lower than the preferred temperature of 18.8°C determined for red abalone in the size range 47–60 mm shell length (Díaz et al., 2000). Gilroy and Edwards (1998) calculated a $T_{\text{opt.G}}$ of 17.0°C for *H. rubra* and 18.3°C for *H. laevigata*. Early juvenile *H. tuberculata* have been shown to grow optimally when fed artificial feed at $18\text{--}22^\circ\text{C}$ (Lopez et al., 1998). Size dependent variation in temperature optimum was, however, not discussed in the above studies.

Britz et al. (1997) studied the effect of temperature on growth, feed consumption and nutritional indices of *H. midae*. Growth rates were only reported for one size group of juveniles and it was concluded that this species has a size-independent $T_{\text{opt.G}}$ of 20°C . Inspection of their feed consumption data provides some evidence for size dependent variation in temperature optimum, much like the one reported for red abalone in the present study. A similar relationship has been suggested for various teleost fish species (Fonds et al., 1992; Imsland et al., 1996; McCarthy et al., 1998;

Jonassen et al., 1999; Steinarsson and Björnsson, 1999; Björnsson et al., 2001). The present results therefore support the contention that an ontogenetic variation in temperature optimum and growth potential may be a physiological trait common to many marine fish and shellfish species.

Potential maximum growth rates are subject to the interaction of many biological, environmental and nutritional factors. It has been demonstrated that the inherent growth potential of the red abalone is strongly dependent upon the age of the abalone (Greenier and Takekawa, 1992). Haaker et al. (1998) have demonstrated that abalones that grow slowly initially will never recover and fail to reach their potential maximum size. It is therefore possible that the growth potential of the abalones in the present study may have been diminished by their sub-optimal growth record of $60\text{--}80\ \mu\text{m day}^{-1}$ and that G_{max} , and perhaps also $T_{\text{opt},G}$, may have been underestimated. Nevertheless, since the abalones all had similar growth histories, it can be argued that the results correctly demonstrate how temperature optimum and growth potential are related to the shell length of the abalone.

The results from the present study may help optimise production in intensive abalone husbandry. Assuming an initial shell length of 0.3 mm at settlement, an extrapolation of the maximum growth relationship suggests a potential size of 29 and 67 mm at 1 and 2 years, respectively, with only five more months remaining towards a market size of 80 mm. A farmed red abalone will typically require 3 years to grow from a shell length of 20–80 mm, whereas it could potentially do the same in just 20 months, on an optimal temperature and feeding regime. The farmer would reap the benefits from doubling the biomass turnover to 0.47% per day or 170% per year. The potential yield from a standing stock of 30 tons could thus be doubled from 25 to 50 tons per year. Optimal rearing conditions and diets are required for the abalone to live up to its maximum growth potential but field data suggest that red abalone are indeed capable of such growth rates (Haaker et al., 1998).

Optimal temperature control is especially important during the first 18 months, as the early growth performance of the abalone appears decisive for its subsequent growth potential (Greenier and Takekawa, 1992). During the later, more water demanding stages, the rearing temperatures can safely be lowered below the optimum without seriously affecting the growth rates of the abalone. Thus, a $5\ ^\circ\text{C}$ deviation from the optimum will only lead to a 20% decrease in the growth rate of a 66-mm red abalone (Fig. 1d). Although only directly applicable for red abalone, it stands to reason that the results could be adopted for other abalone species, by adjusting for differences in natural temperature ranges.

In conclusion, the present study found that red abalone exhibit size dependent variation in growth potential and temperature optimum for growth. An optimum temperature regime may increase the potential yield from land-based abalone farming.

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References

- Ault, J.S., 1985. Some quantitative aspects of reproduction and growth of the red abalone, *Haliotis rufescens*, Swainson. J. World Maricult. Soc. 16, 398–425.
- Björnsson, B., Tryggvadóttir, S.V., 1996. Effects of size on optimal temperature for growth and growth efficiency of immature Atlantic halibut (*Hippoglossus hippoglossus* L.). Aquaculture 142, 33–42.
- Björnsson, B., Steinarsson, A., Oddgeirsson, M., 2001. The optimal temperature for growth and feed consumption of cod (*Gadus morhua*). ICES J. Mar. Sci. 58, 29–38.
- Britz, P.J., Hecht, T., Mangold, S., 1997. Effect of temperature on growth, feed consumption and nutritional indices of *Haliotis midae* fed a formulated diet. Aquaculture 152, 191–203.
- Burel, C., Person-Le Ruyet, J., Gaumet, F., Le Roux, A., Sévère, A., Boeuf, G., 1996. Effects of temperature on growth and metabolism in juvenile turbot. J. Fish Biol. 49, 678–692.
- Capinpin Jr., E.C., Corre, K.G., 1996. Growth of juvenile abalone, *Haliotis discus hannai* Ino 1953 and fed an artificial diet and macroalgae. Aquaculture 144, 81–89.
- Clarke, C.B., Creese, R.G., 1998. On-growing cultured abalone (*Haliotis iris*) in northern New Zealand. J. Shellfish Res. 17, 607–613.
- Corazani, D., Illanes, J.E., 1998. Growth rate of Philippine abalone, *Haliotis asinina* and *Haliotis rufescens* Swainson 1822, fed with different diets. J. Shellfish Res. 17, 663–666.
- Díaz, F., del Río Portilla, M.A., Aguilar, M., Sierra, E., Re Araujo, A.D., 2000. Preferred temperature and critical thermal maxima of red abalone *Haliotis rufescens*. J. Therm. Biol. 25, 257–261.
- Fermin, A.C., 2001. Effects of alternative starvation and refeeding cycles on food consumption and compensatory growth of abalone, *Haliotis asinina* (Linnaeus). Aquacult. Res. 33, 197–202.
- Fonds, M., Cronie, R., Vethaak, A.D., van der Puyl, P., 1992. Metabolism, food consumption and growth of plaice (*Pleuronectes platessa*) and flounder (*Platichthys flesus*) in relation to fish size and temperature. Neth. J. Fish Res. 29, 127–143.
- Gilroy, A., Edwards, S.J., 1998. Optimum temperature for growth of Australian abalone: preferred temperature and critical thermal maximum for blacklip abalone, *Haliotis rubra* (Leach), and greenlip abalone, *Haliotis laevigata* (Leach). Aquacult. Res. 29, 481–485.
- Greenier, J.L., Takekawa, J.Y., 1992. Growth models and food conversion of juvenile red abalone, *Haliotis rufescens*. In: Shepherd, S.A., Tegner, M.J., Guzman del Proo, S.A. (Eds.), Abalone of the World. Fishing News Books, Cambridge, MA, pp. 527–537.
- Haaker, P.L., Parker, D.O., Barsky, K.C., Chun, C.S.Y., 1998. Growth of red abalone, *Haliotis rufescens* (Swainson), at Johnsons Lee, Santa Rosa Island, California. J. Shellfish Res. 17, 747–753.
- Hayashi, I., 1983. Seasonal changes in condition factors and in the C:N ratio of the foot of the ormer, *Haliotis tuberculata*. J. Mar. Biol. Assoc. 63, 85–95.
- Heasman, M.P., O'Connor, W.A., Frazer, A.W.J., 1996. Ontogenetic changes in optimal rearing temperatures for the commercial scallop, *Pecten fumatus* Reeve. J. Shellfish Res. 15, 627–634.
- Hines, A.H., Pierce, J.S., 1982. Abalones, shells and sea otters: dynamics of prey populations in central California. Ecology 63, 1547–1560.
- Hoshikawa, H., Sakai, Y., Kijima, A., 1998. Growth characteristics of the hybrid between pinto abalone, *Haliotis kamtschatkana* Jonas, and ezo abalone, *H. discus hannai* Ino, under high and low temperature. J. Shellfish Res. 17, 673–677.
- Imsland, A.K., Sunde, L.M., Folkvord, A., Stefansson, S.O., 1996. The interaction of temperature and size on growth of juvenile turbot. J. Fish Biol. 49, 926–940.
- Jonassen, T.M., Imsland, A.K., Stefansson, S.O., 1999. The interaction of temperature and size on growth of juvenile halibut. J. Fish Biol. 54, 556–572.
- Leighton, D.L., 1974. The influence of temperature on larval and juvenile growth in three species of southern California abalones. Fish. Bull. 72, 1137–1145.
- Lopez, L.M., Tyler, P.A., Viana, M.T., 1998. The effect of temperature and artificial diets on growth rates of juvenile *Haliotis tuberculata* (Linnaeus, 1758). J. Shellfish Res. 17, 657–662.

- McBeth, J.W., 1972. The growth and survival of the California red abalone in Japan. *Venus* 31, 122–125.
- McCarthy, I., Moksness, E., Pavlov, D.A., 1998. The effects of temperature on growth rate and growth efficiency of juvenile common wolffish. *Aquac. Int.* 6, 207–218.
- Otterlei, E., 2000. Temperature and size-dependent growth of larval and early juvenile Atlantic cod (*Gadus morhua* L.). PhD thesis, University of Bergen, Norway. 114 pp.
- Owen, B.L., Di Salvo, H., Ebert, E.E., Fonck, E., 1984. Culture of the red abalone *Haliotis rufescens* (Swainson 1822) in Chile. *Veliger* 27, 101–105.
- Paul, A.J., Paul, J.M., 1981. Temperature and growth of maturing *Haliotis kamtschatkana* Jonas. *Veliger* 23, 321–324.
- Steinarsson, A., Björnsson, B., 1999. The effects of temperature and size on growth and mortality of cod larvae. *J. Fish Biol.* 55 (Suppl. A), 100–109.
- Tegner, M.J., Butler, R.A., 1985. The survival and mortality of seeded and native red abalone, *Haliotis rufescens*, on the Palos Verdes Peninsula. *Calif. Fish Game* 71, 150–163.
- Trevelyan, G.A., Mendoza, J.L., Buckley, B., 1998. Increasing the yield of red abalone with the alga, *Microcladia coulteri*. *J. Shellfish Res.* 17, 631–633.
- Uki, N., Grant, J.F., Kikuchi, S., 1981. Juvenile growth of the abalone, *Haliotis discus hannai*, fed certain benthic micro algae related to temperature. *Bull. Tohoku Reg. Fish. Res. Lab.* 40, 47–52.
- Zar, J.H., 1984. *Biostatistical Analysis*, 2nd ed. Prentice-Hall, Englewood Cliffs. 718 pp.