

THE COMBINED EFFECTS OF TEMPERATURE, SALINITY, AND DECLINING OXYGEN TENSION ON OXYGEN CONSUMPTION IN THE MARINE PULMONATE *AMPHIBOLA CRENATA* (Gmelin, 1791)

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Abstract: Oxygen consumption of *Amphibola crenata* (Gmelin) was measured in various salinity–temperature combinations (< 0.1‰ to 41‰ salinity and 5 to 30 °C) in air, and following exposure to declining oxygen tensions. In all experimental conditions, respiration varied with the 0.44 power of the body weight ($SD = 0.14$). The aquatic rate was consistently higher than the aerial rate of oxygen consumption, although at 30 °C the two rates were similar. Oxygen consumption increased with temperature up to 25 °C in all salinities; the lowest values were recorded at temperatures below 10 °C and at 30 °C in the most dilute medium. At all exposure temperatures, the oxygen consumption of *Amphibola* decreased regularly with salinity down to 0.1‰, and following exposure to concentrated sea water (41‰). Salinity had the least effect at 15 °C which was the acclimation temperature. In general, all of the temperature coefficients (Q_{10} values) were low, < 1.65. However, Q_{10} values above 2.8 were recorded at a salinity of 17.8‰ between 10 and 15 °C. Oxygen consumption of all size classes of *Amphibola* was more temperature dependent in air than in water and small individuals show a greater difference between their aerial and aquatic rates than larger snails. The rates of oxygen consumption in declining oxygen tensions were expressed as fractions of the rates in air saturated sea water at each experimental salinity–temperature combination. The quadratic coefficient B_2 becomes increasingly more negative with both decreasing salinity and temperatures up to 20 °C. At higher temperatures (25 and 30 °C) the response is reversed such that O_2 uptake in snails becomes increasingly independent of declining oxygen tensions at higher salinities. On exposure to a salinity of 41‰, *Amphibola* showed no systematic response to declining oxygen tension with respect to temperature. The ability of *Amphibola* to maintain its rate of oxygen consumption in a wide range of environmental conditions is discussed in relation to its potential for invading terrestrial habitats and its widespread distribution on New Zealand's intertidal mudflats.

INTRODUCTION

Gastropod molluscs occupying the high intertidal zone are subjected to greater environmental stress than their low shore counterparts and many times distribution is determined by the species' ability to maintain basic metabolic requirements. While there are a multitude of factors which can affect an animal's respiration rate, three of the most

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prevalent environmental factors are salinity, temperature and ambient oxygen concentration. The effect of each of these individual factors on oxygen consumption rate has been well documented (see Kinne, 1971; Newell & Branch, 1980 for review on salinity and temperature effects; Mangum & Van Winkle, 1973; McMahon, 1973; McMahon & Russell-Hunter, 1978 for discussions on declining oxygen tension).

Animals living in the intertidal zone of estuaries, in general, are exposed simultaneously to combinations of fluctuations in salinity, temperature, and oxygen concentration. In particular, these factors vary most widely for animals in the high intertidal habitat. In spite of this fact, there are few studies dealing with the combined effects of salinity, temperature, and oxygen tension on oxygen consumption. Newell *et al.* (1977) and Hawkins & Ultsch (1979) studied the effects of temperature and declining oxygen tension in gastropods while only Bayne (1971) and Shumway (1981) have looked at the combined effects of salinity and low oxygen tension on oxygen consumption. To date, there are no studies in which the combined effects of temperature, salinity and declining oxygen tension have been studied simultaneously with respect to their effect on oxygen consumption.

A species particularly well suited to this type of investigation is the marine pulmonate gastropod *Amphibola crenata* (Gmelin, 1791). The snails are endemic to New Zealand and occupy a transitional habitat between marine and terrestrial conditions. They occur on sand and mudflats which are generally exposed to large daily as well as seasonal fluctuations in temperature, salinity, and dissolved oxygen (see below). Morton (1955) believes that *A. crenata* is evolving from the estuaries to land and fresh water and the present study is an attempt to determine the extent *Amphibola* is physiologically able to withstand the harsh conditions imposed by the extreme high intertidal zone.

MATERIALS AND METHODS

Amphibola crenata in the size range 0.004 to 1.0 g dry tissue wt (\approx 0.75 to 3.5 cm shell height) were collected from Hoopers Inlet, Portobello and the Avon-Heathcote Estuary, Christchurch, New Zealand. The snails were maintained, unfed in tanks arranged such that the snails were able to crawl on substratum brought from the collection site or in 100% sea water at 15 °C for 1 wk prior to use in experiments. Animals were always used within 3 wk of collection. No differences were found between populations with respect to oxygen consumption and the results reported here represent pooled data from the two populations. The results reported concern normally active snails since no differences in oxygen consumption were determined between moving and resting snails. All data were used to compute uptake rates.

Dry tissue weights were determined from the following equation (Shumway, 1981): $Y = 0.022X + 3.01$, where Y is dry tissue weight (g), X is shell height (cm).

Aquatic oxygen consumption rates were measured at all combinations of 0, 25, 50, 75, 100, 125% sea water (100% = 33.5‰) and 5, 10, 15, 20, 25, and 30 °C while

exposed to declining oxygen tension. Individual snails were placed in the respirometer chamber and allowed to deplete completely the available oxygen. The method has been described previously (Shumway, 1981). A Gilson differential respirometer was used to measure aerial oxygen consumption at various experimental temperatures. Again, measurements were made on individual snails. Animals were placed in damp respirometer vessels to ensure water vapour saturation of the atmosphere. Otago Harbour sea water was diluted with rain water or evaporated to give the desired salinities.

In all experiments, animals were placed directly into the appropriate experimental salinity-temperature combination and given 1 h to equilibrate. Animals placed in 0% sea water withdrew into their shells and did not emerge for 2 h; therefore, these animals were left in the experimental media for 3 h before readings began. It is the acute response to salinity-temperature reported here. Experiments on animals exposed to declining oxygen tension were carried out with a narrow size range of animals (≈ 0.3 g dry wt) and variations in the data due to weight differences minimized by relating V_{O_2} measurements to $W^{0.45}$ where W is dry weight (g) and 0.45 is the value of the exponent relating V_{O_2} to body size ($V_{O_2} = aW^{0.45}$) (Bayne & Livingstone, 1977; Shumway, 1981).

HABITAT AND DISTRIBUTION

Watters (1964) described the environment in the area of Hoopers Inlet inhabited by *A. crenata* in great detail, and physical conditions with respect to salinity and temperature do not seem to have altered since then (pers. obs.). Air temperatures of 19.5 °C in February and 9.9 °C in July were recorded with a water temperature range between 20.5 and 6 °C. Snails are sometimes exposed to the air for several weeks and surface substratum temperatures follow the air temperature closely. Large fluctuations in temperature have been recorded and on a sunny winter's day varied between 5 and 26 °C. The habitat of *A. crenata* is also characterized by salinity extremes and in Hoopers Inlet, following strong southerly winds, the area can be submerged for several days. A further investigation of *Amphibola* habitats was made during the autumn of the present study at the Tautuku River Estuary. It was found here that *Amphibola* were exposed to large salinity (0.5 to 34‰), temperature (10 to 20 °C), and dissolved oxygen (2 to 8.2 ml $O_2 \cdot l^{-1}$) fluctuations during each tidal cycle.

In previous studies (Watters, 1964; Briggs, 1972; Morton, 1975), it has been reported that *Amphibola* possesses a well-defined pattern of activity and inactivity in which the animal burrows beneath the mud on the flowing tide, but emerges to feed during the ebb tide. While *Amphibola* is found to be most active during periods of low tide when they feed and egest almost continuously, no strict tidal rhythm was seen in the present study. Although snails were buried during high tide, many animals were found actively crawling at all stages of the tidal cycle in Hoopers Inlet and in both the Tautuku and Avon-Heathcote Estuaries (pers. obs.; Butler & Tutty, unpubl.). *Amphibola* failed to emerge from their burrows when substratum temperatures approached zero and also during periods of heavy rain.

Studies on the distribution of *Amphibola* suggest that this species is not uniformly distributed with respect to size. While the smaller specimens are commonly aggregated at mid-shore level associated with finer sediments, adults including sexually mature specimens have wider distribution (Briggs, 1972; Bennington, 1979; pers. obs.) and may extend down to low water of spring tides and inhabit coarse sandy substrata up to the supralittoral zone.

RESULTS

Fig. 1A shows the regression lines describing the data for oxygen consumption as a function of tissue dry weight for *Amphibola* in 100% sea water at various experimental temperatures. The regression equations are given in Table I along with those for all other salinity-temperature combinations tested. Aerial rates are shown in Fig. 1B. The snail's response to temperature was similar to that in 100% sea water in all experimental salinities. At a given salinity, \dot{V}_{O_2} increased, as expected, with increased experimental temperatures although the increase was slight. There were no significant differences between slopes for any experimental treatment, although differences in slopes due to temperature have been shown for other gastropod species (Newell, 1969; Branch, 1979). A four-level contour map showing the combined effect of salinity and temperature on the oxygen consumption of *Amphibola* is shown in Fig. 2. The multiple regression equation relating \dot{V}_{O_2} to acclimation temperature (T) and salinity (S) for a standard 0.3 g animal is:

$$\dot{V}_{O_2} = 0.0521 + 0.0000918S + 0.00132T \quad (F_{2,33} = 28; P < 0.001)$$

This equation explains 52.2% of the observed variation, indicating that some other factor(s) are influencing \dot{V}_{O_2} , e.g. time of acclimation, starvation, submergence time. For a number of temperature-salinity combinations between 10 and 30 °C and 25% to 100% sea water \dot{V}_{O_2} did not vary significantly. Depressed oxygen consumption was recorded mainly below 10 °C, but also at 30 °C in the most dilute salinity. The highest oxygen consumption was recorded between 50 and 100% sea water on exposure to temperatures of 25 and 30 °C. At all exposure temperatures the oxygen consumption of *Amphibola* decreased regularly with salinity down to 0.1‰ and also declined above 34‰. However, at 15 °C the salinity effects on respiration were minimal.

\dot{V}_{O_2} in water and air are remarkably similar, the aquatic rate being slightly but consistently higher than the aerial rate, with the exception of large (0.3 g) snails at 30 °C where the rates are equal. In addition, the respiratory sensitivity to temperature in air is more prominent in smaller animals (see Table II for Q_{10} values) between 10 and 20 °C. It is also shown that all size classes are marginally more temperature dependent in air than in water. While some differences in \dot{V}_{O_2} between experimental temperatures and salinities can be shown, it should be pointed out that all Q_{10} values are very low (with the exception of snails in 50% sea water between 10 and 15 °C; see Table II), indicating excellent thermocompensatory capabilities.

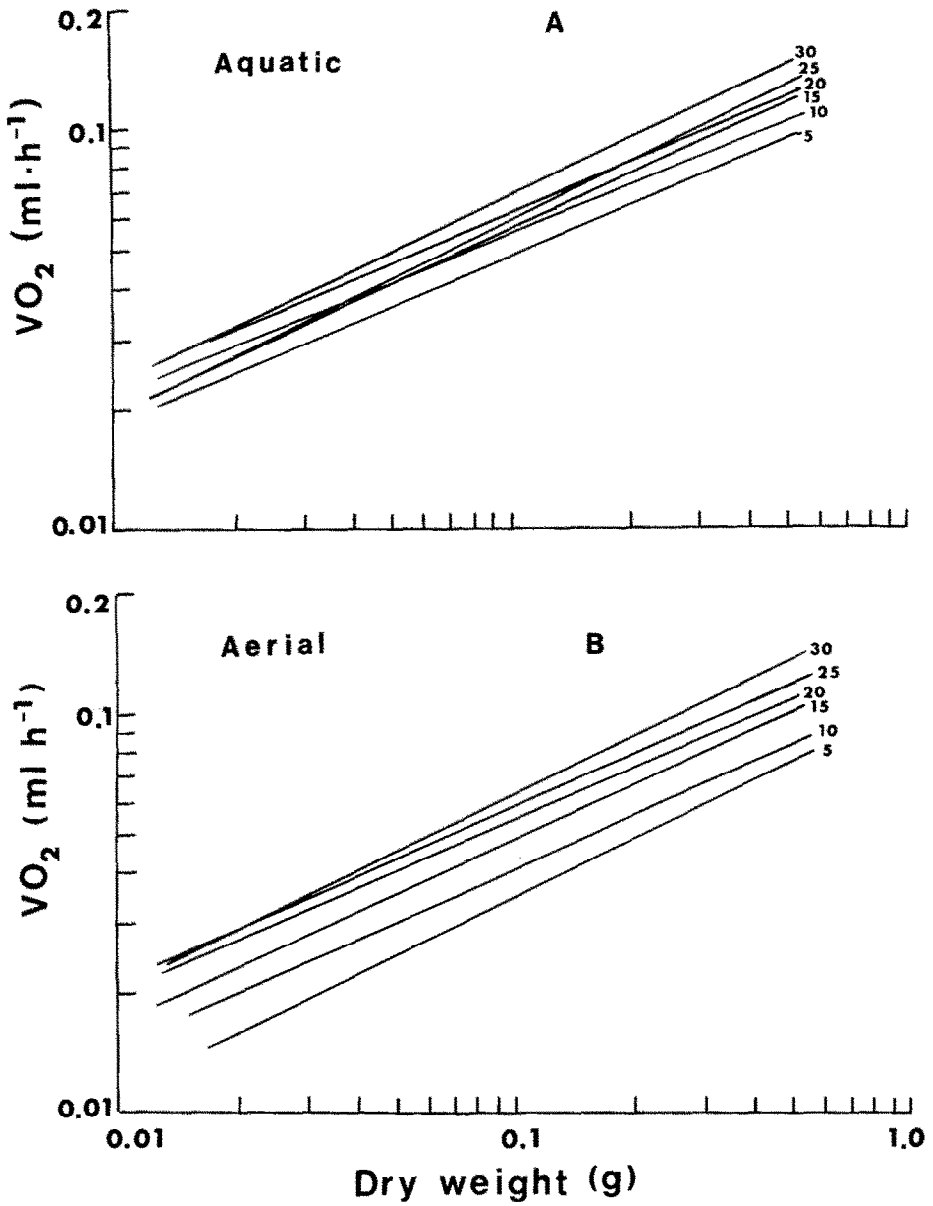


Fig. 1. Regression lines describing the relationship between oxygen consumption and dry tissue weight in *Amphibola crenata* in 100% sea water and in air: experimental temperatures (°C) are given next to each regression line; regression data are given in Table I.

TABLE I
 Linear regression equations relating tissue dry weight (W , g) to oxygen uptake (V_{O_2} ; ml · h⁻¹) in air and in varying concentrations of sea water.

Temp. (°C)	Sea-water concentration (%)																				
	0			25			50			75			100			125			Aerial		
	V_{O_2}	n	r	V_{O_2}	n	r	V_{O_2}	n	r	V_{O_2}	n	r	V_{O_2}	n	r	V_{O_2}	n	r	V_{O_2}	n	r
5	0.091 $W^{0.40}$	11	0.91	0.107 $W^{0.44}$	14	0.86	0.124 $W^{0.43}$	14	0.91	0.122 $W^{0.45}$	16	0.87	0.127 $W^{0.42}$	15	0.91	0.104 $W^{0.42}$	10	0.94	0.109 $W^{0.46}$	20	0.93
10	0.101 $W^{0.42}$	13	0.88	0.091 $W^{0.42}$	18	0.90	0.080 $W^{0.45}$	12	0.98	0.140 $W^{0.44}$	17	0.90	0.149 $W^{0.43}$	17	0.87	0.109 $W^{0.44}$	11	0.89	0.127 $W^{0.49}$	18	0.90
15	0.131 $W^{0.43}$	25	0.86	0.128 $W^{0.46}$	35	0.88	0.134 $W^{0.45}$	30	0.60	0.139 $W^{0.44}$	30	0.88	0.158 $W^{0.45}$	70	0.89	0.108 $W^{0.43}$	30	0.84	0.138 $W^{0.46}$	20	0.87
20	0.136 $W^{0.44}$	19	0.83	0.140 $W^{0.44}$	17	0.74	0.153 $W^{0.42}$	14	0.87	0.159 $W^{0.41}$	12	0.84	0.161 $W^{0.43}$	20	0.93	0.126 $W^{0.44}$	15	0.87	0.149 $W^{0.43}$	42	0.56
25	0.131 $W^{0.43}$	10	0.81	0.151 $W^{0.42}$	12	0.78	0.173 $W^{0.45}$	18	0.89	0.177 $W^{0.44}$	14	0.92	0.176 $W^{0.45}$	22	0.90	0.129 $W^{0.44}$	18	0.89	0.161 $W^{0.44}$	15	0.82
30	0.104 $W^{0.42}$	12	0.86	0.158 $W^{0.45}$	9	0.77	0.173 $W^{0.44}$	11	0.90	0.190 $W^{0.43}$	9	0.93	0.199 $W^{0.47}$	19	0.95	0.154 $W^{0.42}$	14	0.82	0.194 $W^{0.49}$	19	0.96

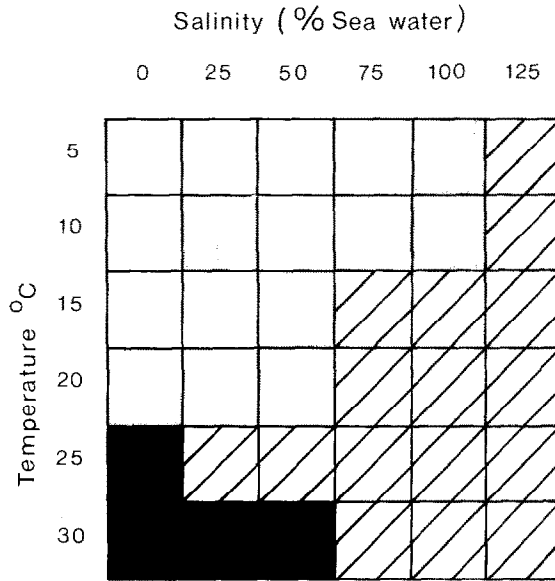


Fig. 2. A four-level contour map relating oxygen consumption to acclimation temperature and salinity; white spaces indicate values < 0.064; stippled areas values < 0.081; slashed areas values < 0.098; solid areas values > 0.098; see text for multiple regression equation.

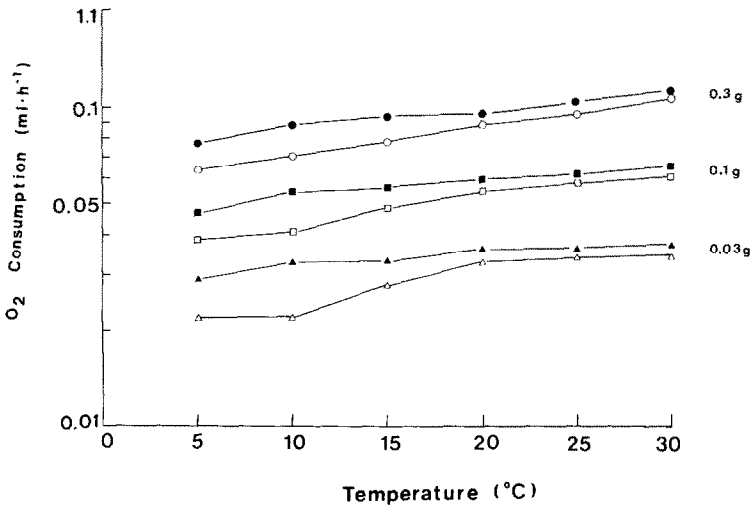


Fig. 3. Respiratory rate-temperature curves for *Amphibola crenata* for standard 0.03, 0.1, and 0.3 g animals in air (open symbols) and in 100% sea water (closed symbols); Q_{10} values are given in Table II.

TABLE II

Temperature coefficients (Q_{10}) for oxygen consumption: data are given in terms of standard individuals of 0.03, 0.1, and 0.3 g dry tissue wt.

Sea water concentration (%)	Salinity (‰)	Temperature interval (°C)	Weight of individuals (g)		
			0.03	0.10	0.30
125	41.9	5-10	0.92	1.00	1.05
		10-15	1.08	1.03	1.00
		15-20	1.26	1.31	1.33
		20-25	1.04	1.05	1.05
		25-30	1.59	1.56	1.50
		mean			
100	33.5	5-10	1.16	1.17	1.17
		10-15	1.29	1.31	1.28
		15-20	0.98	1.02	1.07
		20-25	1.19	1.14	1.09
		25-30	1.04	1.09	1.14
		mean	1.11	1.17	1.22
75	25.1	5-10	1.12	1.14	1.16
		10-15	1.41	1.38	1.35
		15-20	0.99	0.99	0.99
		20-25	1.62	1.50	1.41
		25-30	1.00	1.08	1.15
		mean	1.24	1.21	1.18
50	16.8	5-10	1.23	1.22	1.21
		10-15	0.36	0.38	0.40
		15-20	2.81	2.80	2.81
		20-25	1.60	1.50	1.40
		25-30	1.03	1.11	1.19
		mean	1.07	1.05	1.03
25	8.4	5-10	1.13	1.13	1.14
		10-15	0.83	0.81	0.76
		15-20	1.49	1.65	1.80
		20-25	1.38	1.31	1.25
		25-30	1.33	1.28	1.22
		mean	0.89	0.95	1.02
0	< 1	5-10	1.15	1.16	1.16
		10-15	1.07	1.12	1.17
		15-20	1.56	1.61	1.64
		20-25	1.00	1.03	1.05
		25-30	1.00	0.97	0.95
		mean	0.68	0.66	0.64
Aerial	Aerial	5-10	1.02	1.03	1.04
		10-15	1.10	1.18	1.26
		15-20	1.45	1.35	1.27
		20-25	1.44	1.34	1.25
		25-30	1.09	1.11	1.14
		mean	1.02	1.15	1.29
		5-30	1.21	1.22	1.24

The relationship between mean Q_{10} and salinity is shown in Fig. 4 where it can be seen that the greatest change with respect to temperature takes place between 0 and 25‰ sea water. Maximum Q_{10} is seen in animals exposed to 75‰ sea water. There were no significant differences between sizes.

According to the procedure described by Mangum & Van Winkle (1973), rates of oxygen consumption in declining oxygen tensions (P_{O_2} , mm Hg) were expressed as fractions of the rates in air saturated sea water (at each experimental salinity-temperature combination) and fitted to a quadratic equation. The resulting quadratic coefficient, B_2 can then be used as an indicator of the degree of regulation of oxygen consumption

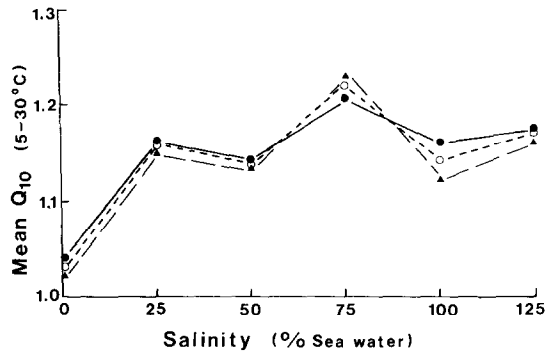


Fig. 4. The relationship between mean respiratory temperature coefficients (Q_{10} between 5 and 30 °C) and salinity in *Amphibola crenata* of 0.03 (▲), 0.1 (○), and 0.3 (●) g dry weight.

TABLE III

Quadratic coefficients ($B_2 \times 10^3$) for *Amphibola crenata* exposed to declining oxygen tensions at various salinity-temperature combinations: arrows indicate direction of increasing regulation.

Temp. (°C)	Sea-water concentration (%)					
	0	25	50	75	100	125
5	-0.0732	-0.0685	-0.0691	-0.0681	-0.0582	-0.0481
10	-0.0707	-0.0646	-0.0683	-0.0647	-0.0564	-0.0501
15 ^a	-0.0681	-0.0662	-0.0590	-0.0522	-0.0513	-0.0497
20	-0.0639	-0.0588	-0.0572	-0.0481	-0.0493	-0.0400
25	-0.0304	-0.0416	-0.0408	-0.0481	-0.0493	-0.0400
30	-0.0221	-0.0209	-0.0340	-0.0390	-0.0422	-0.0515

^a From Shumway (1981).

in that $B_2 (\times 10^3)$ becomes increasingly more negative as the degree of oxygen independence increases. The $B_2 (\times 10^3)$ values for all salinity–temperature combinations are given in Table III. The multiple regression equation relating the B_2 value to acclimation temperature (T) and salinity (S) is:

$$B_2 (\times 10^3) = -0.0772 + 0.0001S + 0.0012T \quad (F_{2,33} = 38.52; P < 0.001)$$

and explains 63.3% of the experimental variation. It can be seen that, at salinities between 0 and 100% sea water, B_2 becomes increasingly more negative with decreasing temperature, i.e., animals at low temperatures are more independent of declining oxygen tensions than animals at high temperatures. Animals in 125% sea water showed no systematic response to declining oxygen tension with respect to temperature.

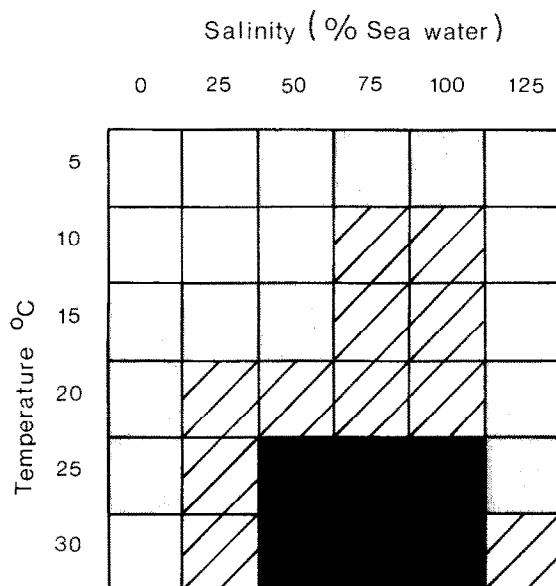


Fig. 5. A four-level contour map relating B_2 to acclimation temperature and salinity: white spaces indicate values < -0.0660 ; stippled areas values < -0.0523 ; slashed areas values < -0.03870 ; and solid areas values > -0.03870 ; see text for multiple regression equations.

Fig. 5 shows a four-level contour map relating B_2 to temperature and salinity and indicates that between 5 and 20 °C oxygen independence increases with decreasing salinity. Thus between 5 and 20 °C the highest degree of oxygen independence is seen in cold, fresh water. At higher temperatures (25 and 30 °C), however, the response is reversed in that the degree of oxygen independence decreases with decreasing salinity.

DISCUSSION

Several authors (Sandison, 1966; Micallef, 1967; Bannister, 1974; McMahon & Russell-Hunter, 1977; Branch, 1979; Houlihan, 1979) have compared gastropod respiratory rates in air with those in water. These studies indicate that respiratory rates in air and water vary according to the length of time the animals are normally exposed or submerged, higher shore species supposedly respiring faster in air than in water when compared with their low shore counterparts. As pointed out by Branch (1979) the generalization that upper shore species respire faster in air may not always be valid. In some species, food availability during periods of aerial exposure has also been shown to affect the relative rates of oxygen consumption in air and water in that species experiencing a food shortage during periods of high temperatures and aerial exposure have been shown to conserve energy during these periods by maintaining lower than expected rates of oxygen consumption. It has already been shown (Shumway, 1981) that the rate of oxygen consumption in *Amphibola* is similar to that of intertidal prosobranchs. Many intertidal invertebrates avoid the full impact of large temperature variation by occupying sheltered crevices, rock pools, etc. during low tide. *A. crenata*, however, is most active during these periods.

In discussing the methods of energy conservation during aerial exposure in intertidal prosobranchs, Newell (1979) gives the principal pattern of adaptation in upper shore species as involving: (a) the maintenance of aerobic respiration during the period of exposure to air; (b) a reduction in the rate of oxygen consumption in both air and water; (c) a reduction in the temperature coefficient of metabolism.

The need to conform to the above criteria is based on the assumption that high shore normally means low food availability. The high shore limpet *Patella granularis* is faced with the problems of aerial respiration in an environment of reduced food availability and high temperature variation and copes with the situation as follows: the absolute level of the respiratory rate-temperature curve is suppressed compared with that of similar sized individuals of other limpets, Q_{10} values are low and the species shows differences in aerial and aquatic consumption rates such that \dot{V}_{O_2} is minimal under normally encountered conditions (Branch & Newell, 1978). *P. granularis* is a prosobranch whose respiratory structures are designed primarily for aquatic respiration. In *Amphibola*, however, submersion represents a period during which the respiration rate may or may not be reduced and feeding may or may not be suspended, depending on whether the animals burrow beneath the surface. *Amphibola* exhibits very low Q_{10} values in both air and water and has aerial rates similar to aquatic rates allowing maximum energetic gain (minimum energetic loss) during adverse conditions when they may be exposed to aerial conditions for several weeks and subjected to wide-ranging temperatures. A low Q_{10} value will help the animals to conserve energy when not feeding or exposed to substrata of low food availability. The low Q_{10} value does not necessarily mean suppressed respiration at high temperatures, but as shown for the limpet *Patella granatina* (Branch, 1979) may be a mechanism for maintaining a constant

metabolic rate regardless of low temperatures often encountered in the environment. This may have special significance for *Amphibola* as well since this species, at least in the south of New Zealand, is normally exposed to rather low temperatures and the range may be as much as 15 °C within a few hours. Thus, in *Amphibola*, the consistently low Q_{10} values allow maintenance of a constant rate of metabolism in an environment where temperature may change radically with tidal and diurnal cycles and may also benefit the animal during exposure to variations in air and sea temperatures on rising and falling tides.

While both small and large animals show effectively the same respiratory response to temperature, it is interesting to note that small snails show a greater difference between the aerial and the aquatic rates of oxygen consumption at low temperatures (5 to 15 °C) than do larger specimens. The temperature range most likely to be experienced by small, mid-tide level animals is \approx 5 to 20 °C and it appears that the capabilities for maintaining the same metabolic rate in air and water at higher temperatures develops with increased size (age). Temperature is not the sole determining factor in the species' size distribution and since the larger specimens, located in the high-intertidal/supra-littoral zone show the same respiratory response to temperature in air and in water, temperature is clearly not a factor which would inhibit their further penetration toward land.

There have been few studies in which factors affecting oxygen consumption during declining oxygen tension have been investigated. Newell *et al.* (1977) studied the effect of temperature on V_{O_2} during declining oxygen tension in *Crepidula fornicata* and found that oxygen independence increased with decreasing temperature. A similar response was reported for two species of freshwater snails, *Goniobasis cahawbensis* and *G. cochliaris* (Hawkins & Ultsch, 1979). The present findings are in partial agreement with previous studies in that *Amphibola* shows increasing oxygen independence with decreasing temperature between 5 and 30 °C at all salinities between 0 and 100% sea water. At temperatures between 5 and 20 °C, the degree of oxygen independence increases with decreasing salinity. At high temperatures, however, this response is reversed. These results are not as startling as first imagined. McMahon & Russell-Hunter (1974, 1977) have shown that interspecific differences in response to low oxygen tension are less related to vertical zonation than to microhabitat and more to the physiological ecology of the individual species. *Amphibola* are rarely exposed to temperatures above 25 °C when submerged. Normally these high temperatures are encountered while the animals are exposed on the mudflats and are respiring aerially, thus there is little need to have developed the capability for remaining oxygen independent at high temperatures. Specimens of *A. crenata* which are found in water at high temperatures are usually in at least 75% sea water, often above 125% (due to evaporation of small tidal pools) and under these conditions have similar quadratic coefficients to animals at lower temperatures in more dilute media (see Table III). In addition, for an animal to remain oxygen independence during declining oxygen tension would require increased metabolic expenditure and place an extra burden on an already strained system.

Daniels & Armitage (1968) studied temperature acclimation and oxygen consumption in *Physa hawnii*, a freshwater pulmonate which occurs commonly in drainage ditches, and they found that at 62% oxygen saturation and 30 °C, oxygen consumption was reduced and the species showed 46.6% mortality. In addition, the Q_{10} values reported for *Physa* were very high when compared with those obtained in the present study for *Amphibola*. Thus here is a pulmonate with lower temperature and oxygen tolerances than *Amphibola*, but which has successfully invaded the terrestrial freshwater habitat.

It has been shown that all size classes of *Amphibola crenata* are tolerant of combinations of temperature, salinity, and oxygen concentrations greater than those normally encountered in the field. While the distribution of *Amphibola* in intertidal areas cannot be fully explained by adaptations in the respiratory physiology, they explain the success of large individuals in high intertidal habitats. The inability of smaller *Amphibola* to maintain low rates of respiration when submerged, may prevent the seaward distribution of this group. Preference for finer sediments with high organic and microorganism levels probably explains the high densities of juvenile *Amphibola* found at the mid-tide level. Active or passive migration of larger individuals from this level onto adjoining mudflat areas prior to breeding and egg laying may be the main factor regulating the wider distribution of this snail (Briggs, 1972). In a recent study, Bennington (1979) showed that hatching of *Amphibola* eggs was reduced at salinities below 10‰ sea water (3.4‰). Large adults found at the high water mark are rarely exposed to salinities below 8.3‰ (Voller, 1973) and this feature may explain the preference of larger individuals for high intertidal levels. In *Amphibola* the veliger larva is less sensitive to reduced salinities than either the juvenile or the adult (Bennington, 1979) and this stage must therefore be responsible for the effective and wide distribution of this species throughout New Zealand estuaries.

Amphibola is able to withstand the harsh conditions of high intertidal environment at least in part by possession of a highly adaptive respiratory physiology which allows utilization of available oxygen over a wide range of environmental conditions. It is more likely that the possession of a veliger larva is restricting *Amphibola* to the intertidal habitat than a physiological restriction.

ACKNOWLEDGEMENTS

This work was carried out during tenure of a University of Otago post-doctoral fellowship and was partially supported by University of Otago Research Grant No. 37-842 and University of Canterbury Research Grant No. C76178. The authors wish to thank Professor G. H. Satchell and Dr. P. A. Sullivan for the loan of essential equipment, Professor R. F. H. Freeman and M. Saks for helpful discussions and Dr. J. B. Jillett for providing facilities at the Portobello Marine Laboratory. M. Butler, C. Tutty and R. Murdoch kindly furnished unpublished data.

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