

# Desiccation, Higher Temperatures and Upper Intertidal Limits of Three Species of Sea Mussels (Mollusca: Bivalvia) in New Zealand

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## Abstract

Distribution, abundance, and resistance adaptations to higher temperature and desiccation of three species of intertidal mussels (*Mytilus edulis aoteanus*, *Perna canaliculus* and *Aulacomya maoriana*) were studied in New Zealand. *M. edulis aoteanus* generally was more abundant upshore, with *P. canaliculus* dominating downshore. *M. edulis aoteanus* was more common than *P. canaliculus* on the outside of mixed-species clumps. Abundance of *A. maoriana* was variable, with individuals favouring damp habitats such as inside mussel clumps. In moving air at 75% relative humidity and at 20°C or 30°C, median lethal levels of water loss were similar for *P. canaliculus* and *M. edulis aoteanus* but lower for *A. maoriana*. Rates of desiccation varied inversely with size and were higher for *P. canaliculus*, due mainly to valve gaping with resultant loss of water from the mantle cavity. *M. edulis aoteanus* was more tolerant of higher water temperatures than were the other species. Success in colonizing upshore or more aerially exposed habitats seems to be related to ability of small mussels to tolerate desiccation, especially during hot, windy weather.

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## Introduction

In the eulittoral zone of some New Zealand rocky shores, three common species of the bivalve family Mytilidae overlap in their distributions. These species are the blue mussel *Mytilus edulis aoteanus* (Powell, 1958), the green mussel *Perna canaliculus* (Gmelin, 1791), and the ribbed mussel *Aulacomya maoriana* (Iredale, 1915). As part of a study on competitive interactions among these species, I attempted to estimate their tolerances of desiccation and higher temperatures. Such tolerances appear to be important in determining upper limits to distribution of intertidal organisms (Newell, 1970; Connell, 1972). This paper reports on differing resistance adaptations of these three species of mussels to increased desiccation and higher temperatures, and relates the findings to differences in intertidal distribution of the species.

## Materials and Methods

### Field Studies

#### Intertidal Distributions

Three locations were chosen for detailed study on the Canterbury coast, South Is-

land, New Zealand (Fig. 1, Table 1). Five transects were made at Tumbledown Bay, a relatively isolated and undisturbed bay 80 km from Christchurch. Two transects were made near Christchurch at Taylor's Mistake, a popular recreational area in summer. An additional transect was made on an isolated, undisturbed rocky platform near Kaikoura. Transects at Tumbledown Bay and Taylor's Mistake were on near-vertical surfaces, perhaps the predominant topographic gradient in the lower eulittoral zone on these rocky shores. The Kaikoura transect was on a gently sloping rock platform because vertical surfaces were limited in extent.

Where sufficient numbers of these three species occur, they form a prominent band in the lower eulittoral zone (Morton and Miller, 1973). At Taylor's Mistake, the upper limit of this band occurs between extreme high-water neap and mean tidal level (Knox, 1953; Fearon, 1962), and it is presumed that this generalization holds at the other two locations studied. Transects ranged from the top of this band down to either low-tide level (Kaikoura) or the sand beach at the base of the rock faces being examined. A 0.1 m<sup>2</sup> quadrat was used to take samples (contiguous, except at Kaikoura),

Table 1. Description of transects made in mussel zone at Tumbledown Bay, Taylor's Mistake, and Kaikoura, New Zealand. Transects were on vertical or nearly vertical surfaces, except at Kaikoura

Location and transect	Description
Tumbledown Bay (43°51'S; 172°46'E)	Part of Akaroa volcano; shores of andesitic basalt. Faces south-west, exposed to swells.
Transect 1 (1.3 m long)	Isolated rock, east shore, between low and mean-tide level, facing bay mouth. Sampled 20 July, 1973.
Transect 2 (1.3 m)	Isolated rock, east shore, low-tide level, facing bay mouth. 31 July, 1973.
Transect 3 (1.3 m)	Isolated rock, west shore, same level as Transect 1, facing east shore at approximate right-angles to bay mouth. 31 July, 1973.
Transect 4 (1.0 m)	Reverse face of Transect 1 rock, more sheltered. 28 August, 1973.
Transect 5 (1.3 m)	Reverse face of Transect 2 rock, more sheltered. 28 August, 1973.
Taylor's Mistake (43°35'S; 172°47'E)	Described by Knox (1953). Part of Lyttleton volcano; basalt shores. Faces north-east, exposed to swells.
Transect 1 (1.6 m)	East shore between low and mean-tide level, at approximate right-angles to bay mouth. 2 August, 1973.
Transect 2 (2 m)	20 m from Transect 1 at low-tide level, at approximate right-angles to bay mouth. 17 September, 1973.
Kaikoura (42°17'S; 173°46'E)	Rocky outcrop about 15 km north of town, with mussels on greywacke boulders and shallow platforms. One transect of 4 non-contiguous 0.1 m <sup>2</sup> quadrats. 21 January, 1974.

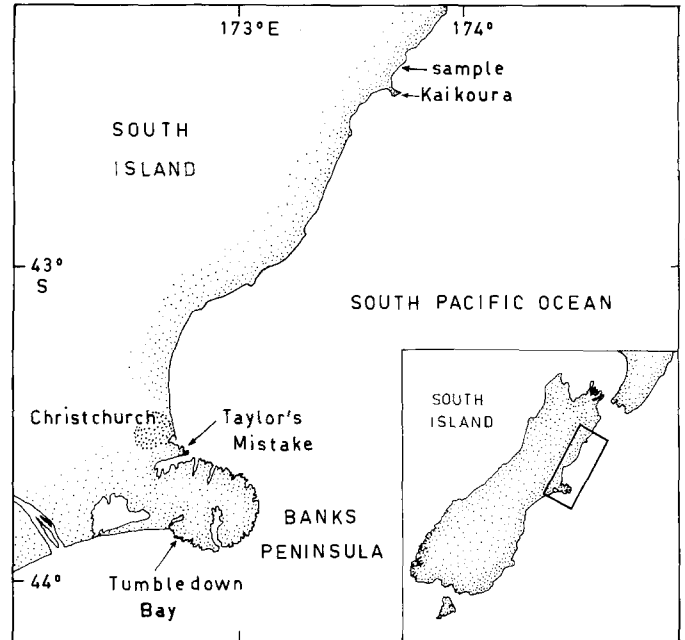


Fig. 1. Locations of three sampling stations for sea mussels on Canterbury coast, South Island, New Zealand

with all animals removed from the area enclosed by the quadrat. Mussels were sorted to species and were counted. Extensive qualitative observations of distribution patterns were made elsewhere on these three shores, and at additional locations along the east coast of the South Island.

#### "Within-Clumps" Distributions

Clumps of mussels were examined at Taylor's Mistake for "micro-distribution" patterns. White paint was brushed on the outer surface of clumps exposed by low tide. When the paint dried, the mussels were collected. Those with paint on the shell were considered to be from the outer surface of the clump, and those with no paint from the inside (Harger, 1968). Lengths (maximum anterior-posterior axis; Seed, 1968) were measured to the nearest millimetre.

#### Temperature Measurements

Temperatures were measured at Kaikoura during low spring tides in January and March, 1974 using a Zeatron remote sensing unit and thermistors painted matte black. Rock and mussel-shell temperatures at the upper level of the mussel zone were determined using thermistors with flat sensing surfaces. Body tempera-

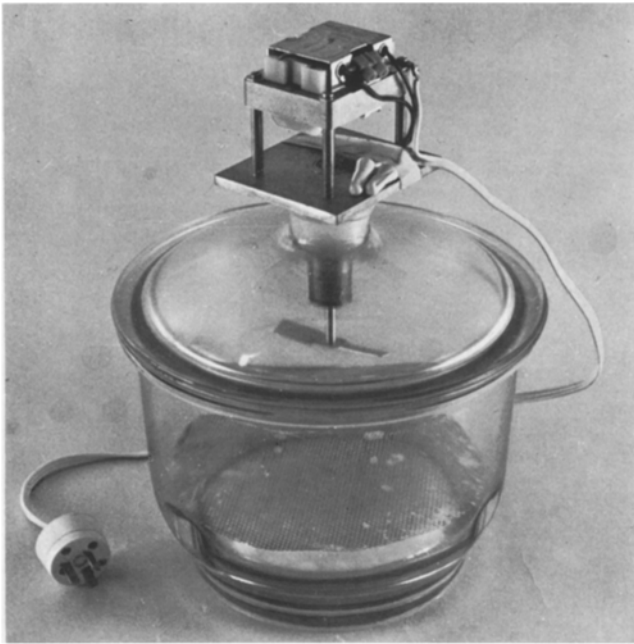


Fig. 2. Desiccator modified by addition of fan powered by phonograph turntable-motor

tures were estimated by opening mussels *in situ* and inserting a tubular thermistor into the flesh. The same thermistor was used for air temperatures.

#### Laboratory Studies

Mussels from the middle of the mussel band at Taylor's Mistake were maintained in aerated sea water (collected regularly from Taylor's Mistake) in a controlled-temperature room with a 16 h light:8 h dark photoperiod. Salinities of collection, holding and experimentation were 32.6 to 33.7‰.

#### Higher Temperatures

Specimens were collected 2 to 5 days before use and held at 12°C (September - October, 1973) or 20°C (January, 1974). Temperatures of collection ranged from 9° to 13°C (water) and 10° to 15°C (air) in late winter, and from 16° to 19°C (water) and 17° to 23°C (air) in summer. After the holding period, the mussels were placed in baths of well-aerated sea water at constant high temperatures for 6 h and then removed to cool sea water for 24 h to check survival. Criteria of survival included ability to react to stimulation of mantle and foot by exhibiting shell or foot movement, or to hold valves closed when pressed shut.

#### Desiccation

Four glass desiccators were each modified by incorporation of a fan powered by a small phonograph turntable-motor (Fig. 2). This allowed reduction of the normal boundary layer of evaporating water surrounding individuals being desiccated (Ramsay, 1935; Kensler, 1967). Tests with an Alnor Thermoanemometer indicated that, at the position of experimental mussels in the desiccators, wind speed varied from about 0.5 to 1.5 km h<sup>-1</sup> (0.3 to 0.8 knots).

Experimental mussels had their shells cleaned, were blotted dry externally, weighed, and measured as to length. Large specimens (3 to 6 cm) were placed (10/desiccator) in wire baskets so that their ventral-posterior end pointed upward. Small mussels (5 to 14 mm) were placed (30/desiccator) in the same position on plastic netting in Petri dishes. Periodically, mussels were removed and re-weighed. Those not returned to the desiccators after weighing were placed in aerated sea water for a 24-h recovery period. Survival criteria included foot movements, byssal attachment, or ability to close valves upon stimulation of mantle or foot. Preliminary experiments used CaCl<sub>2</sub> to provide 0% relative humidity (RH), but later studies employed a supersaturated solution of NaCl to achieve 75% RH within the desiccators (Winston and Bates, 1960). Preliminary experiments were at 12°C, but later experiments were at 20° and 30°C using mussels held at 20°C. Control experiments were made on specimens held in still air.

#### Results

##### Field Studies

##### Intertidal Distributions

For the three geographic localities, average numbers of each species at each quadrat level on the shore were determined (Fig. 3). *Mytilus edulis aoteanus* consistently increased in numbers from the top quadrat to the next, decreasing thereafter. Numbers of *Perna canaliculus* were low upshore, increasing downshore and then decreasing at Taylor's Mistake and Kaikoura. The pattern for *Aulacomya maoriana* was erratic, with higher numbers downshore at Tumbledown Bay, lower numbers downshore at Taylor's Mistake, and very high numbers upshore with few downshore at Kaikoura.

Comparison of relative abundances (Fig. 4) revealed *Mytilus edulis aoteanus* as the most abundant mussel upshore, ex-

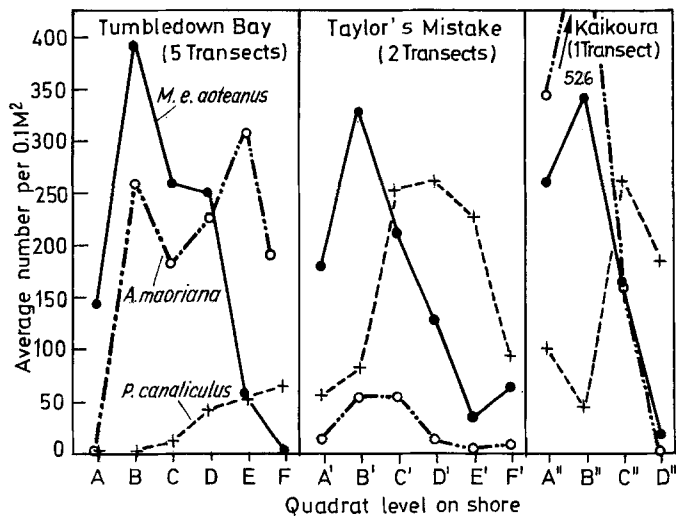


Fig. 3. *Mytilus edulis aoteanus*, *Perna canaliculus* and *Aulacomya maoriana*. Average numbers per 0.1 m<sup>2</sup> quadrat at three coastal locations in Canterbury. Numbers of transects on each shore are indicated; Quadrat A is always the top quadrat upshore. Exposure levels of quadrats may or may not be comparable among shores as indicated by use of prime marks (' , ")

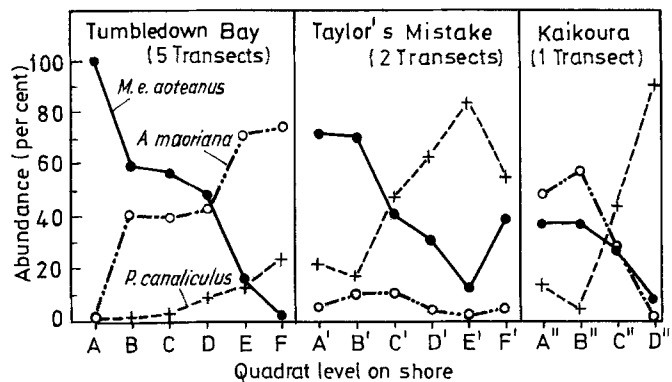


Fig. 4. *Mytilus edulis aoteanus*, *Perna canaliculus* and *Aulacomya maoriana*. Percentage abundances per 0.1 m<sup>2</sup> quadrat. For further details see legend to Fig. 3

cept at Kaikoura, with decreasing abundance downshore. *Perna canaliculus* increased in relative abundance downshore, dominating in this region at Taylor's Mistake and Kaikoura. *Aulacomya maoriana* varied in relative abundance from shore to shore.

#### "Within-Clumps" Distributions

Relative abundances of these species within three clumps of different size in the upper two-thirds of the mussel band at Taylor's Mistake were calculated (Fig. 5). The clumps were about 0.5 m apart in a vertical line. Mussels on the outside of the clumps were predominantly *Mytilus edulis aoteanus*, with abundance declining downshore, where *Perna canaliculus* became more common. No *Aulacomya maoriana* was found on the outside of these clumps. Inside, abundance of *M. edulis aoteanus* was similar from clump to clump, *P. canaliculus* was more common downshore, and *A. maoriana* declined in abundance downshore. *M. edulis aoteanus* was relatively more abundant on the outside of clumps than inside; *P. canaliculus* was the reverse. Similar patterns were noted for other clumps surveyed quantitatively at Taylor's Mistake and qualitatively elsewhere.

Size differences in these "micro-distributions" were surveyed by separating mussels arbitrarily into those larger or smaller than 2 cm (Fig. 6).

*Mytilus edulis aoteanus* specimens were larger both on the outside of the clumps than inside, and downshore compared with upshore. The same pattern held for *Perna canaliculus* except in the upper clump, where very few *P. canaliculus* were collected. Larger *Aulacomya maoriana* became more predominant downshore.

#### Temperature Measurements

Unfortunately, cloudy, relatively cool weather during spring tides hindered observations of extreme temperatures at the upper edge of the mussel band near Kaikoura. The highest temperatures were measured on January 21, 1974, with rock-surface temperatures up to 33.5°C and air temperatures reaching 32°C. Highest temperatures of shells of mussels on these rocks were 31.5°C for *Perna canaliculus* and *Aulacomya maoriana* and 32.0°C for *Mytilus edulis aoteanus*, with body temperatures 2 to 3°C lower.

#### Laboratory Studies

##### Higher Temperatures

No size differences in temperature tolerances were noted for the lengths used (1 to 6 cm). Both in late winter and mid-summer, *Mytilus edulis aoteanus* was more temperature-tolerant than *Perna canaliculus*

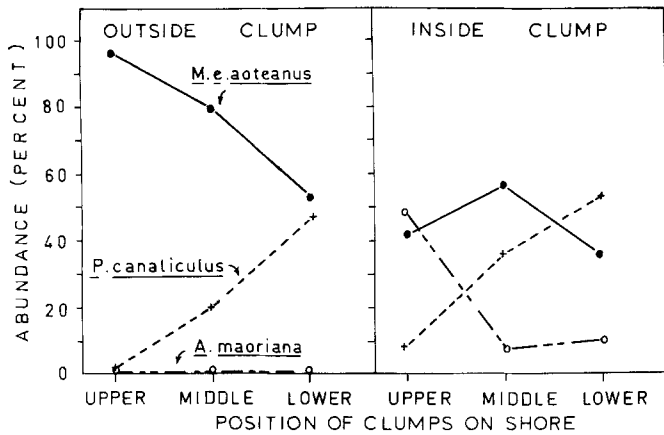


Fig. 5. *Mytilus edulis aoteanus*, *Perna canaliculus* and *Aulacomya maoriana*. Percentage abundances on outside and inside of 3 mussel clumps aligned vertically at Taylor's Mistake

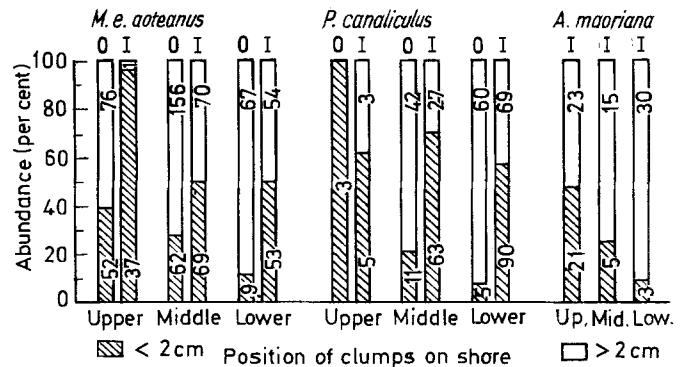


Fig. 6. *Mytilus edulis aoteanus*, *Perna canaliculus* and *Aulacomya maoriana*. Percentage abundances of 2 size-classes on outside (O) and inside (I) of 3 mussel clumps aligned vertically at Taylor's Mistake. Numbers in each size class are indicated in the columns

Table 2. Median lethal levels (LC<sub>50</sub>) of tolerance to higher temperature after 6 h for 3 species of sea mussels after acclimation in late winter (12°C) and mid-summer (20°C)

Acclimation temperature	Species	6-h LC <sub>50</sub> (°C)
12°C	<i>Mytilus edulis aoteanus</i>	35-36
	<i>Perna canaliculus</i>	32-33
	<i>Aulacomya maoriana</i>	about 32
20°C	<i>Mytilus edulis aoteanus</i>	36-37
	<i>Perna canaliculus</i>	33-34
	<i>Aulacomya maoriana</i>	32-33

and *Aulacomya maoriana*, with *P. canaliculus* slightly more tolerant than *A. maoriana* (Table 2).

Desiccation

Large mussels (3 to 6 cm) survived 0% RH in moving air at 12°C for many hours (up to 200 h for *Mytilus edulis aoteanus*, 133 h for *Aulacomya maoriana*, and 130 h for *Perna canaliculus*). Consequently, my attention shifted to small individuals (<15 mm) at 75% RH and at higher temperatures (20°C and 30°C). Percentage body-weight loss was calculated for each mussel after each weighing. These estimates of weight loss over time were collected for each specimen which survived its period of

exposure. For each species, weight losses after 6 and 12 h at 20°C and 30°C were plotted against body length (Fig. 7), and regression lines were fitted using the least-squares technique. Regression equations are presented in Table 3, along with correlation coefficients and their level of significance.

For each species, analysis of covariance (Snedecor and Cochran, 1967) was made on all regressions significantly different from zero (Table 4). At 20°C and 6 h, the regressions for *Mytilus edulis aoteanus* and *Aulacomya maoriana* were judged to have similar slopes but not elevations, whereas at 12 h both slopes and elevations were similar. When the data for the two time periods were combined, the null hypothesis was accepted for slopes but not for elevations. A pooled slope was determined for these two species at the two time periods and recalculated equations were developed using this common regression coefficient (Table 5). At 30°C and 6 h, the null hypothesis was accepted for slopes but not elevations for *Perna canaliculus* and *A. maoriana* data (Table 4), and a common regression coefficient was calculated for these data (Table 5). When the analysis was extended to compare the 5 new regressions at 20°C and 30°C (Table 5), the variances were judged not to be homogeneous (Table 4) so the data for the two temperatures were kept distinct.

Table 3. Regression equations of percentage body-weight loss (Y) on length (X), correlation coefficients (r), level of significance of r, and numbers (n) for 3 species of sea mussels at 2 temperatures and 75% relative humidity in moving air over two time periods. ns: not significant

Experimental temperature	Species	Time (h)	Equation	r	Level of significance	n
20°C	<i>Mytilus edulis aoteanus</i>	6	$Y = 14.75 - 0.64X$	-0.345	<0.01	58
		12	$Y = 25.21 - 1.11X$	-0.444	<0.01	109
	<i>Perna canaliculus</i>	6	$Y = 22.15 - 0.62X$	-0.366	ns	18
		12	$Y = 33.92 - 1.01X$	-0.323	ns	37
	<i>Aulacomya maoriana</i>	6	$Y = 26.53 - 1.49X$	-0.752	<0.01	17
		12	$Y = 29.02 - 1.37X$	-0.676	<0.05	13
30°C	<i>Mytilus edulis aoteanus</i>	6	$Y = 18.04 - 0.38X$	-0.173	ns	43
		12	$Y = 29.20 - 0.89X$	-0.206	ns	66
	<i>Perna canaliculus</i>	6	$Y = 37.22 - 1.47X$	-0.438	<0.05	31
		12	$Y = 40.44 - 1.27X$	-0.372	ns	19
	<i>Aulacomya maoriana</i>	6	$Y = 23.83 - 1.15X$	-0.534	<0.05	14
		12	$Y = 17.96 - 0.32X$	-0.142	ns	6

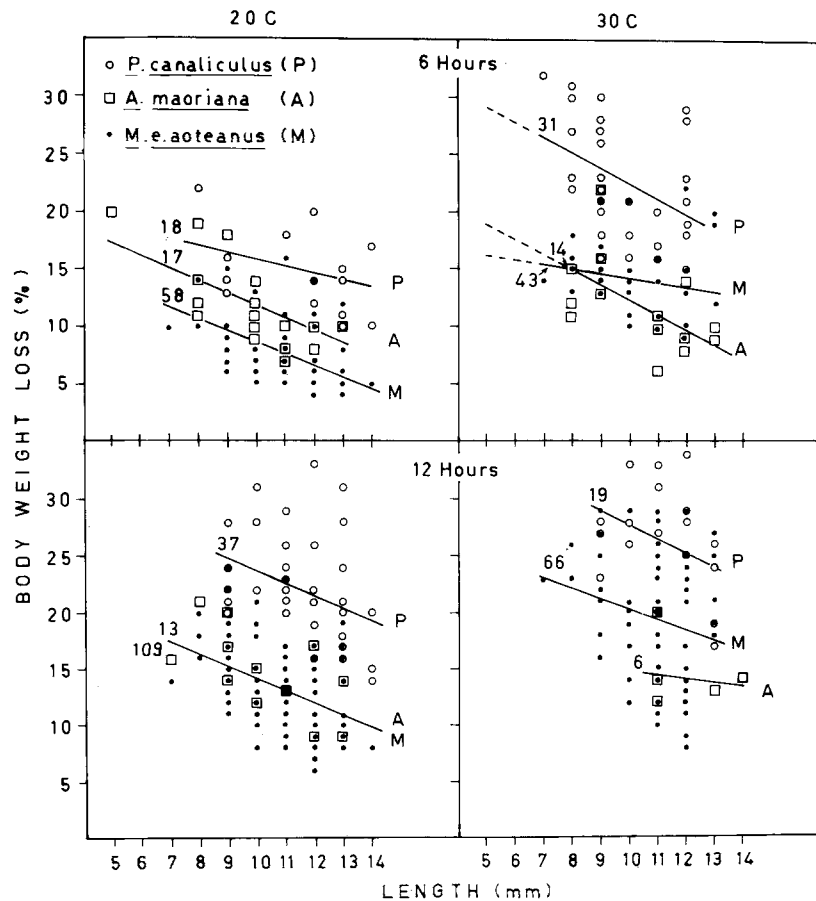


Fig. 7. *Mytilus edulis aoteanus*, *Perna canaliculus* and *Aulacomya maoriana*. Relation of percentage body-weight loss to size over two time periods for three species of sea mussels at 75% relative humidity and 20° and 30°C. Numbers are sample size for each species. Data are for mussels surviving these treatments. At 30°C and 6 h, regression lines have been extrapolated to estimate desiccation of a 5-mm individual

Table 4. Summary of results of analyses of covariance on regressions of percentage body-weight loss on length, for *Mytilus edulis aoteanus* (*M*), *Perna canaliculus* (*P*), and *Aulacomya maoriana* (*A*) at 20°C and 30°C (75% relative humidity; moving air). ns: not significant at  $P = 0.05$ ; \*\*\*:  $P = 0.001$

Comparisons of regressions	Statistic	Calculated values for <i>F</i> (degrees of freedom)
20°C		
(i) 6 h M and A	Variances	$F = 1.00$ (15,56) ns
	Slopes	$F = 3.48$ (1,71) ns
	Elevations	$F = 15.63$ (1,72) ***
(ii) 12 h M and A	Variances	$F = 1.15$ (107,11) ns
	Slopes	$F = 0.23$ (1,118) ns
	Elevations	$F = 1.31$ (1,119) ns
(iii) Combinations M and A combined for 6 and 12 h	Variances	$F = 1.23$ (120,73) ns
	Slopes	$F = 0.06$ (1,193) ns
	Elevations	$F = 105.78$ (1,194) ***
30°C		
6 h A and P	Variances	$F = 1.76$ (29,12) ns
	Slopes	$F = 0.14$ (1,41) ns
	Elevations	$F = 50.28$ (1,42) ***
20°C and 30°C compared		
A and M combined for 6 and 12 h (20°C) and A and P combined for 6 h (30°C)	Variances	$F = 2.62$ (43,195) ***
	Slopes	$F = 3.15$ (1,238) ns
	Elevations	$F = 83.07$ (1,239) ***

Table 5. Regression equations of percentage body-weight loss (*Y*) on length (*X*) for 3 species of sea mussels, recalculated to common regression coefficients

Temperature and time (h)	Species	Recalculated equation
20°C		
6 h	<i>Mytilus edulis aoteanus</i>	$Y = 20.4 - 1.16X$
	<i>Aulacomya maoriana</i>	$Y = 23.4 - 1.16X$
12 h	<i>Mytilus edulis aoteanus</i> and <i>Aulacomya maoriana</i> combined	$Y = 25.8 - 1.16X$
30°C		
6 h	<i>Perna canaliculus</i>	$Y = 36.0 - 1.35X$
	<i>Aulacomya maoriana</i>	$Y = 25.9 - 1.35X$

Table 6. Percentage mortality for 3 species of sea mussels at different levels of body-weight loss for 75% relative humidity and 2 temperatures. Values are combined data for mussels weighing up to 0.30 g and measuring 5 to 14 mm in length. Numbers in parentheses are numbers used for determinations of mortality

Body weight loss (%)	<i>Mytilus edulis aoteanus</i>		<i>Perna canaliculus</i>		<i>Aulacomya maoriana</i>	
	20°C	30°C	20°C	30°C	20°C	30°C
9-11.9	-	-	-	-	-	0 (2)
12-14.9	0 (1)	-	-	-	0 (3)	18 (11)
15-17.9	0 (10)	17 (6)	0 (15)	0 (1)	25 (8)	43 (14)
18-20.9	0 (9)	31 (13)	0 (18)	0 (1)	9 (23)	78 (9)
21-23.9	0 (14)	17 (12)	7 (15)	0 (1)	36 (22)	86 (7)
24-26.9	33 (15)	41 (32)	22 (9)	33 (9)	88 (16)	100 (3)
27-29.9	52 (23)	60 (48)	21 (33)	19 (36)	100 (1)	
30-32.9	43 (21)	72 (25)	46 (22)	69 (39)		
33-35.9	89 (9)	81 (16)	71 (7)	80 (30)		
36-38.9	100 (4)	75 (12)	-	92 (13)		
39-41.9	100 (1)	100 (1)	100 (1)	100 (8)		
Total number	(107)	(165)	(120)	(138)	(73)	(46)

Table 7. Estimated median lethal level of total water loss (including mantle-cavity water) for 3 species of sea mussels at 2 temperatures. Size of mussels = 5 to 14 mm, or up to 0.30 g

Species	Temperature (°C)	Median lethal water loss (%)
<i>Mytilus edulis aoteanus</i>	20	72
	30	59
<i>Perna canaliculus</i>	20	67
	30	61
<i>Aulacomya maoriana</i>	20	59
	30	44

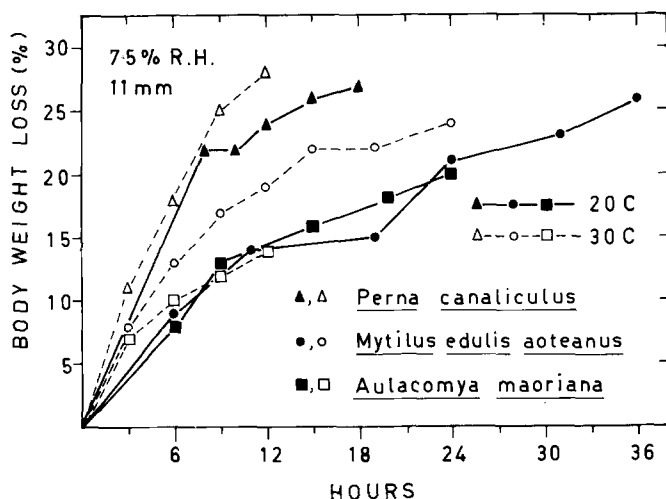


Fig. 8. *Mytilus edulis aoteanus*, *Perna canaliculus* and *Aulacomya maoriana*. Average rates of desiccation of 11-mm individuals at two temperatures, based on data for mussels surviving desiccation for times indicated. RH: relative humidity

Regression lines were plotted (Fig. 7) using the recalculated equations (Table 5) and the equations for those regressions whose slopes were not significantly different from zero (Table 3). Percentage body-weight loss for *Perna canaliculus* was generally greater than for the other species under similar conditions of length, temperature and time. *Mytilus edulis aoteanus* and *Aulacomya maoriana* appeared to be similar to one another except after 6 h at 20°C. Percentage body-weight loss for all species was greater at 30°C than 20°C for comparable time periods.

To estimate rates of desiccation, percentage body-weight loss was plotted against time. A typical example was developed using data for 11-mm individuals at 20°C and 30°C (Fig. 8). Many data were available for all three species at this size, facilitating comparisons (patterns for mussels larger or smaller than 11 mm were comparable). *Perna canaliculus* lost weight faster than the other two species, with the rate at 30°C outstripping that at 20°C. *Mytilus edulis aoteanus* also lost weight faster at 30°C than 20°C. At 20°C, the pattern for *Aulacomya maoriana* closely approximated that for *Mytilus edulis aoteanus*. At 30°C, *A. maoriana* lost weight rapidly over 3 h, then the rate slowed and resembled that at 20°C.

Percentage mortality at different levels of body-weight loss was estimated by noting numbers alive and dead after reaching these levels. These survival data were collected for mussels measuring between 5 and 14 mm in length and weighing up to 0.30 g (Table 6). The median lethal level of weight loss var-



ied with species and temperature. For *Perna canaliculus* it was estimated to occur between 33 and 36% body-weight loss at 20°C and between 30 and 33% at 30°C. For *Mytilus edulis aoteanus* the median lethal level was estimated to be between 33 and 36% at 20°C and between 27 and 30% at 30°C. *Aulacomya maoriana* tolerated much less weight loss, with the median lethal level occurring between 24 and 27% at 20°C and between 18 and 21% at 30°C.

To allow estimates of desiccation in terms of water loss, a large number of individuals of the three species was measured for length, blotted free of external water, weighed, dried to constant weight at 80°C for 24 h, and reweighed. Regressions of dry weight on wet weight and on length, and of wet weight on length were calculated and used to determine that mussels weighing up to 0.30 g or measuring 5 to 14 mm long contained water (including mantle cavity water) in the following average proportions: *Perna canaliculus*, 49%; *Mytilus edulis aoteanus*, 46%; *Aulacomya maoriana*, 41%. From this, the median lethal level of loss of total water (Table 7) was estimated for each species by dividing the lower value of the range containing the median lethal level of body-weight loss (Table 6) by the proportion of the body weight that was water. *M. edulis aoteanus* and *P. canaliculus* tolerated greater water loss than *A. maoriana* at both temperatures used. At 20°C, *M. edulis aoteanus* tolerated slightly more water loss than *P. canaliculus*, both species dropping in tolerance at 30°C and becoming similar.

#### Discussion and Conclusions

Upper limits to distribution of intertidal organisms seem to be governed by physical factors (Connell, 1972). For the three species of New Zealand sea mussels studied, differences in their upper limits to distribution in the eulittoral zone appear to be related to differences in tolerances of higher temperatures and (especially) of water loss.

*Mytilus edulis aoteanus* may be less limited by higher temperatures than are *Perna canaliculus* or *Aulacomya maoriana* (Table 2). However, water temperatures around South Island never approach 30°C (Knox, 1963), with 20°C the highest sea temperature recorded at Taylor's Mistake by Knox (1953). Air temperature during emersion may be more of a limiting factor. At Taylor's Mistake, Knox (1953) recorded a rock-surface temperature of 29°C when the air temperature nearby was 24°C. Fearon (1962) reported rock temperatures up to 44°C at Taylor's Mistake. My measured values were not as high be-

cause of relatively cool weather during the spring tides in the southern summer of 1973-1974. Nevertheless, it would appear that during prolonged emersion in hot weather, body temperatures of mussels might attain those levels judged lethal for mussels in water (Table 2). What lethal levels are in air has not been determined. Temperature tolerances of limpets measured in air under simulated natural conditions were about 5°C higher than tolerances measured during immersion (Wolcott, 1973). Perhaps balancing this to some extent, thermal tolerances of desiccated *Acmaea digitalis* Eschscholtz (20 to 60% of total body water lost) were reduced by about 3°C compared with non-desiccated limpets (Wolcott, 1973). I have no information on the responses of mussels under such conditions.

Undoubtedly of more importance than single factors, synergistic interactions of several factors are involved in governing intertidal distribution patterns. Desiccation results from the compound influences of wind, temperature and relative humidity during emersion. In the laboratory, small *Perna canaliculus* consistently lost weight faster than *Mytilus edulis aoteanus* or *Aulacomya maoriana* of similar size (Figs. 7, 8). Contributing to this, many small *P. canaliculus* opened and shut their shells sporadically while in the desiccators; in contrast, few *A. maoriana* or *M. edulis aoteanus* gaped noticeably. Coleman (1973) noted similar behavioural differences between two European mussel species, with *Modiolus modiolus* (L.) gaping periodically and losing water from the mantle cavity, resulting in increased evaporative loss from body tissues, while *Mytilus edulis* L. did not behave in this manner. In my experiments, individual *P. canaliculus* of a size similar to Coleman's specimens of *Modiolus modiolus* (above 3 cm) did not gape noticeably during desiccation experiments. Apparently *P. canaliculus* loses this activity pattern as it grows.

Limited observations at Taylor's Mistake indicated that small *Mytilus edulis aoteanus*, *Perna canaliculus* and *Aulacomya maoriana* (up to 2 cm) would open in the field, with *P. canaliculus* apparently gaping more widely than the others on occasion. Further, a film of water usually bridged the gap between parted valves of *M. edulis aoteanus* and *A. maoriana* while *P. canaliculus* often seemed to lack this film. This water may help retard desiccation of tissues. These observations are neither extensive nor conclusive, but provide evidence that the laboratory observations were not just experimental artifacts.

Shells of small *Perna canaliculus* appeared to be thinner and more fragile than those of *Mytilus edulis aoteanus* or *Aulacomya maoriana*, but I have no quantitative information. Such thin valves may also influence the resistance of *P. canaliculus* to water loss.

*Mytilus edulis aoteanus* and *Aulacomya maoriana* were very similar to each other in patterns of desiccation except for rates of weight loss at 30°C (Fig. 8). The coincidence of the rates of desiccation of *A. maoriana* beyond the first 6 h at 20°C and 30°C may have been due to a behavioural characteristic, that of remaining shut under stress conditions. Specimens of *A. maoriana* judged to be dead at the end of 24 h in a recovery bath after desiccation often remained closed, the only sign of death being a fuzzy growth, presumably bacterial, around the valve edge. Dead *M. edulis aoteanus* and *Perna canaliculus* generally gaped to some extent under these conditions. Similarly, while *M. edulis aoteanus* and *P. canaliculus* would usually gape at lethal temperatures in experiments on temperature tolerance in water, *A. maoriana* would often be closed or just slightly agape. If increased environmental stress were to stimulate *A. maoriana* to remain closed, desiccation might be retarded for this species.

In summary, smaller individuals (5 to 14 mm) of the three species lost weight more rapidly and died more quickly during desiccation experiments than did larger individuals (3 to 6 cm). While *Perna canaliculus* was similar to *Mytilus edulis aoteanus* in its tolerances of body-water loss under similar experimental conditions, its rate of desiccation was faster, and it reached lethal levels more quickly. The rate of desiccation for *Aulacomya maoriana* was relatively low, but the species was less tolerant of loss of body water. *M. edulis aoteanus* combined relatively high tolerances of body-water loss with relatively low rates of desiccation.

The present observations concern resistance to acute exposure to desiccation. Presumably the different tolerances noted for the three species reflect tolerances to chronic exposure as well. Such exposure may be more common in the lower eulittoral than acute exposure. To estimate the possibilities of tiny mussels reaching lethal levels of desiccation on shore during one tidal emersion, the regression lines relating percentage body-weight-loss to size after 6 h exposure at 30°C were extrapolated to a size of 5 mm (Fig. 7). Individuals this size and smaller can be found in clumps upshore near the upper

limit of the mussel band. The resulting level of weight loss was about 29% for 5-mm *Perna canaliculus* and about 19% for *Aulacomya maoriana*, both near lethal limits (Table 6). The level reached by *Mytilus edulis aoteanus* (about 16%) was below the median lethal level at 30°C (Table 6).

As noted, rock surfaces on Canterbury beaches exposed to sunshine during tidal emersion may exceed the temperature of 30°C used in my laboratory experiments. Seventy-five percent RH is not unusual on a rock shore, values of 60 to 75% having been measured near the sea surface on calm, hot days near Kaikoura (J. Ottaway, personal communication). Stronger winds than those employed in the experiments are often experienced on shore (Courtney, 1972; Wolcott, 1973). Thus, desiccation of small exposed mussels in nature might be even more extreme than it was under my experimental conditions.

From these data, it appears that differing desiccation tolerances may influence the upper intertidal limit of mussel distributions. Small mussels were more susceptible to drying conditions than were large mussels and predominated on the inside of clumps (Fig. 6) where conditions were cooler and wetter. *Perna canaliculus* may be less common upshore because of intolerance of desiccation by small individuals. *Mytilus edulis aoteanus* desiccated less rapidly than *P. canaliculus* and had a higher tolerance of water loss than *Aulacomya maoriana*; it was more common on the outside of clumps than the other species (Fig. 5), and tended to be more common upshore (Fig. 4). An exception was at Kaikoura, where *A. maoriana* was more abundant upshore. Here, individual *A. maoriana* were living almost totally covered by *M. edulis aoteanus* specimens on a slowly-draining rock platform, thus living in a moist, cool habitat. Where *A. maoriana* is found high in the mussel band, it is generally in tide pools, in shade, in cracks or crevices, or under *M. edulis aoteanus*.

Paine (1971) described the radial pattern of dispersal of groups of *Perna canaliculus* recolonising a cleared habitat in the North Island of New Zealand (see his Fig. 4). Larger individuals occurred at the periphery of invading clusters, with smaller mussels in the centre. The centre of such clusters should be less subject to drying than would the periphery, sustaining survival of the smaller individuals.

Ross and Goodman (1974) studied vertical intertidal distribution of *Mytilus edulis* in British Columbia, Canada. Adult mussels, transplanted on July 2, 1970 (northern summer) to a flat rock surface

0.3 m above their normal level of occurrence and protected from predation, survived until December 30, 1970 with only 1 to 3% mortality. Ross and Goodman concluded that, since adult mussels could survive above the mussel zone, the upper limits of this zone must depend upon survival of young stages. Paine (1974) supposed that, since mussels in his study areas in Washington State, USA do not appear to be competitively limited by other species, their upper limit of distribution is probably set by resistance to desiccation. My results appear to support these suppositions.

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