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THE ROLE OF DESICCATION PRESSURES AND SURFACE AREA/VOLUME RELATIONSHIPS ON SEASONAL ZONATION AND SIZE DISTRIBUTION OF FOUR INTERTIDAL DECAPOD CRUSTACEA FROM NEW ZEALAND: IMPLICATIONS FOR ADAPTATION TO LAND

BY

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INTRODUCTION

Compared with subtidal levels, the intertidal zone is characterized by environmental variability. Organisms living in this region are subjected to cyclic fluctuations in temperature, moisture, salinity, and other physical parameters. Resistance to desiccation during low tides becomes a major adaptive problem, especially during the summer months, when water loss is accelerated by higher temperatures.

Arthropods inhabiting exposed rocky beaches exhibit various capacities for survival away from water. From the low tide level to the high tide mark they can be viewed as models for the transition from water to land. Although insects and arachnids have extended their range even into the deserts of our world, the Crustacea have lagged far behind in their colonization of the land. The brachyuran and anomuran decapods (crabs and hermit crabs) in particular do not generally stray far from water. Their advance inland would seem to be limited significantly by a relatively poor ability to prevent water loss by evaporation (Edney, 1960). Apparently, the difference arises from a waxy layer in the cuticle, which is present in insects and arachnids, but absent in Crustacea. Hence, the Crustacea are restricted in their landward movement by a water permeable exoskeleton.

On the intertidal zone, *Cyclograpsus lavauxi* H. Milne Edwards, 1853, are concentrated primarily between 0.7 and 1.6 m above the low tide level. *Hemigrapsus edwardsi* (Hilgendorf, 1882) is found generally within the 0.2 to 1.1 m level; *Heterozius rotundifrons* H. Milne Edwards, 1867, between 0.0 and 1.0 m; and *Petrolisthes elongatus* (H. Milne Edwards, 1837), an anomuran species, between 0.0 and 0.9 m. A study of four species that are concentrated, during any given month, at different levels within the intertidal zone provides insight into certain design modifications—especially surface area/volume relationships—that might be brought to bear against the desiccation problem.

At the Wellington Marine Laboratory (Victoria University, Island Bay, North Island, New Zealand), surveys indicated a lower size limit, which rose proportionally with increasing elevation from the low tide level and extended across sex, species, genus, and family lines (fig. 1). Individuals with carapace

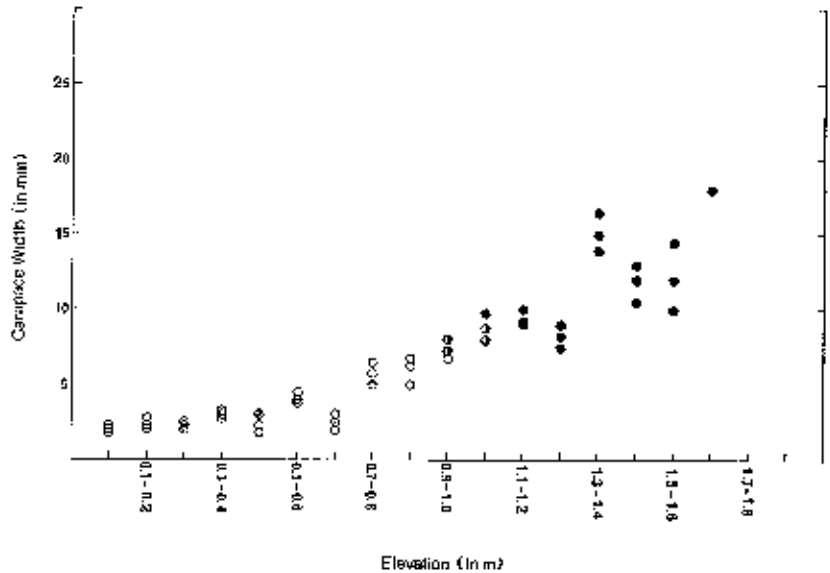


Fig. 1. 3 smallest representatives of *Petrolisthes elongatus* (○), *Heterozius rotundifrons* (upper circle of fifth vertical row, at 0.4-0.5 m), *Hemigrapsus edwardsi* (half filled circles), and *Cyclograpsus lavauxi* (●) from each 0.1 m horizon above the sublittoral fringe. (Compiled from 2 survey transects over a 6 month period. Sample size per species: *Petrolisthes elongatus* = 508; *Heterozius rotundifrons* = 439; *Hemigrapsus edwardsi* = 232; *Cyclograpsus lavauxi* = 156. Total area sampled = 70 m²). Both sexes are represented in the sample.

diameters ≤ 5.0 mm — mostly *Petrolisthes elongatus* — were restricted to the 0.0-0.7 m level. Penetration higher on the shore, into the 0.7-1.2 m zone seems to require, for all species, a higher carapace width (5.0-7.5 mm). Above the 1.3 m level, a region dominated by *Cyclograpsus lavauxi*, carapace widths did not range below 10.0 mm (with but a single exception: an 8.5 mm individual found at 1.42 m in August 1981). In essence, the smallest individuals were restricted to the lower shore, while larger crabs could range more freely and, particularly in the case of the two grapsid species (*Hemigrapsus edwardsi* and *Cyclograpsus lavauxi*), were the only ones able to advance higher than 1.1 m above the low tide level. Herreid (1969a) and Warner (1969, 1977) have suggested that rates of water loss change in a regular way as body size increases. Different rates of desiccation appear to be rooted in geometry (Pellegrino & Stoff, 1983): as objects of the same shape become larger, volumes increase faster than surface areas; hence, juvenile crabs, with their high ratio of surface to volume, quickly evaporate water and cannot venture as far ashore at their larger conspecifics.

The Cook Strait region is climatically temperate but equable, with summer extremes of air temperature rarely exceeding 20°C and freezing conditions absent during winter. Equable climate probably accounts for the year-round persistence of the four species above the sublittoral fringe, a region exposed only during low spring tides and northerly offshore squalls. By contrast, rocky beaches at the same latitude on the New York side of Long Island Sound are subject to winter freezing, and intertidal crabs shelter in sublittoral waters during this time.

This paper examines the role of exponential relationships between surface area and volume on each species' tolerance to desiccating conditions. An apparent relationship between surface area/volume ratios and resistance to desiccation as a cause for seasonal changes in population density and size distribution (at given horizons above the low tide level) of four different littoral species is discussed.

METHODS

From April 1980 through June 1981, *Petrolisthes elongatus*, *Heterozius rotundifrons*, *Hemigrapsus edwardsi* and *Cyclograpsus lavauxi* were sampled monthly from one of two well defined transects at Island Bay. The transects were chosen for their relatively gradual inclination and an abundant supply of loose rocks with diameters between 50 and 250 mm. The substrate is pebbly, becoming fine-grained (silt) between 30 and 80 mm below the surface. True burrowing species are absent. The chief behavioural mechanism demonstrated by all four species to combat desiccation is to shelter under rocks during the low tide, and not to move from their shelter, at least during daylight hours, until it is again submerged. The crabs display an apparent preference for rocks less than 300 mm across that do not penetrate more than 50 mm into the substrate. The lateral separation between transects is ≈ 200 m. The transects were sampled alternately (starting with transect A in April 1980, transect B in May, transect A in June, etc.) to maximize the interval between samples at each site, during which time a transect could be re-occupied by crabs from adjacent areas. Also, the use of two transects permitted an interpretation of whether the results were representative of what might be found on similar beaches elsewhere, or whether they were merely an artifact of each transect. For each transect, a line of metre squares was sampled from the low tide level (ELWN or ELWS for the day of sample) to the maritime zone, which begins about 2.0 m above the sublittoral fringe. This region is under the strong influence of salt spray, but is reached by the tides only during southerly gales. The elevation of each metre square, from the seaward to the landward side, was measured with two sticks, each 1 m long. The first was placed vertically on the seaward side, and the second horizontally (using a spirit level) with one end raised on the landward side and the other brought level against the first metre stick. A mean area of 14 m^2,

yielding an average total of 85 *Petrolisthes elongatus*, 65 *Heterozius rotundifrons*, 31 *Hemigrapsus edwardsi*, and 29 *Cyclograpsus lavauxi*, was sampled each month. Specimens sampled from each metre square were preserved immediately in 70% ethanol.

Size distribution was derived from the carapace widths of all collected individuals, measured in the laboratory to the nearest 0.25 mm using hand calipers (for individuals with carapace widths >10.0 mm) or a micrometer eyepiece in a stereo microscope calibrated to the hand calipers.

For the desiccation portion of the study, crabs representing the range of carapace widths observed for each species were collected from both transects and maintained in a laboratory aquarium overnight. Water loss was measured as percent weight loss (over a 10 hour period) from the fraction of water content in the tissues of each species: *Petrolisthes elongatus* ($67.6 \pm 0.5\%$), *Heterozius rotundifrons* ($46.3 + 1.0\%$), *Hemigrapsus edwardsi* ($59.0 \pm 1.0\%$), and *Cyclograpsus lavauxi* ($60.0 \pm 1.0\%$). Percent water content was derived from the difference between initial weights and dry weights of 10 individuals of each species (obtained after 12 hours under vacuum at 10^{-5} tor). Percent water loss data were preferred over percent weight loss to limit bias resulting from interspecies differences in the concentration of skeletal material (Young, 1978). For example, if more of the initial weight is water (as in the case of *Petrolisthes elongatus*, which appears to display a relatively reduced skeletal mass), then loss of this water will be recorded as a relatively higher percentage loss of initial weight.

Crabs were blotted with tissue paper for 30 seconds to absorb excess water on the integument, then placed in individual open-top plastic containers. Each container was housed in a separate silica gel desiccator throughout the 10 hours experiment (except for hourly weighings, each occupying <30 seconds). The temperature remained at $14 \pm 1°C$ and the room humidity at $75 \pm 2\%$. The humidity in the desiccators remained at 70% throughout the experiment (temperature and humidity were statistically determined from continuous monitoring throughout the experiment). The desiccators remained unsealed until commencement of the experiment, and were used only to maintain constant humidity during a 10 hour period. 70% humidiy is consistent with humidity in the field, and the results obtained depict water loss in the absence of shelter.

Surface areas were measured by applying a thin, even coat of aluminium over crabs. Line-of-sight application (i.e., radiating from the aluminium source) was made using an Edwards 306 S.E.M. Planetary Workholder (rotation of central disc was 110 rpm; with orbiting discs, on which the crabs were mounted, making four rotations per orbit). 20 mg of aluminium was evaporated onto the ventral, and then onto the dorsal surfaces of the crabs. The coating time was 1 minute 15 seconds for each surface at a vacuum of 10^{-5} tor. Crabs were killed by desiccation (which induces members of all four species to strike a characteristic pose with chelae and legs outspread), dried for

one week over silica gel, then stored overnight under vacuum prior to coating. Under a microscope, all crabs appeared evenly coated on all body surfaces, except for minor shadowing at the leg joints, particularly points of attachment to the cephalothorax. This source of error is, however, relatively standard among all individuals, regardless of size or species. As a calibration, against which surface areas could be plotted, sheet polythene was cut into squares of known surface area and coated alongside the crabs. The amount of aluminium coated onto the crabs and the controls was then measured by atomic absorption spectrometry. The aluminium was dissolved from the crabs' bodies with 15% hydrochloric acid, and distilled water added until the total weight of the solution was brought up to 4.0 g, occupying a volume of 4.0 ml (after coating under vacuum, the crabs, through a range of sizes up to 15.0 mm, varied between 0.015 and 0.340 g; a 17.0 mm *Cyclograpsus lavauxi* weighed 0.530 g)[1]). The mixture was allowed to sit for 24 hours prior to atomic absorption analysis to ensure a homogenous concentration of aluminium throughout the solution and also in the crab residues. From this homogenous and mildly acidic solution, a sample (< 0.5 ml) was extracted, filtered and passed through an atomic absorption spectrometer. The concentrations thus obtained ranged within 1 and 100 parts per million and the a.a. spectrometer was scaled accordingly (Price, 1972). Uncoated crabs were shown to contain negligible amounts of aluminium already in their bodies.

Volume was measured by displacement of vegetable oil, which was preferred over water because it took 15 to 25 sec longer to enter the space of the branchial chambers; hence, volumetric measurement of a dried crab more accurately represents actual displacement by the crab body, rather than seepage into the body.

RESULTS

The surface area/volume data presented in fig. 2, against which desiccation rates are plotted in fig. 3, were derived from 10 representatives of each species (carapace widths are included primarily as points of reference for future application of the method). The surface area data represent three separate experiments (the first two conducted on four members of each species, the third on two), which verified the repeatability of the method, as data from the second and third experiments fell squarely within the surface area/volume curves

[1]) In the case of the 17.0 mm *Cyclograpsus lavauxi*, the total weight of the solution was brought up to 8.0 g (8.0 ml). The result obtained was thus half of what it would be at 4.0 g (except for a reduced crab dry weight error), and could be scaled to the polythene controls accordingly. The methods used in this study can be applied to a broad range of irregularly-shaped objects, including such things as crystal clusters. A source of error, of course, is displacement volume of the object to be studied. Surface area resolution can be improved by adding a thicker coat of aluminium, which permits the use of a greater volume of HCl and water. If organic material is being studied, some gains may be achieved by ashing residues in an oven prior to dissolving the aluminium in solution.

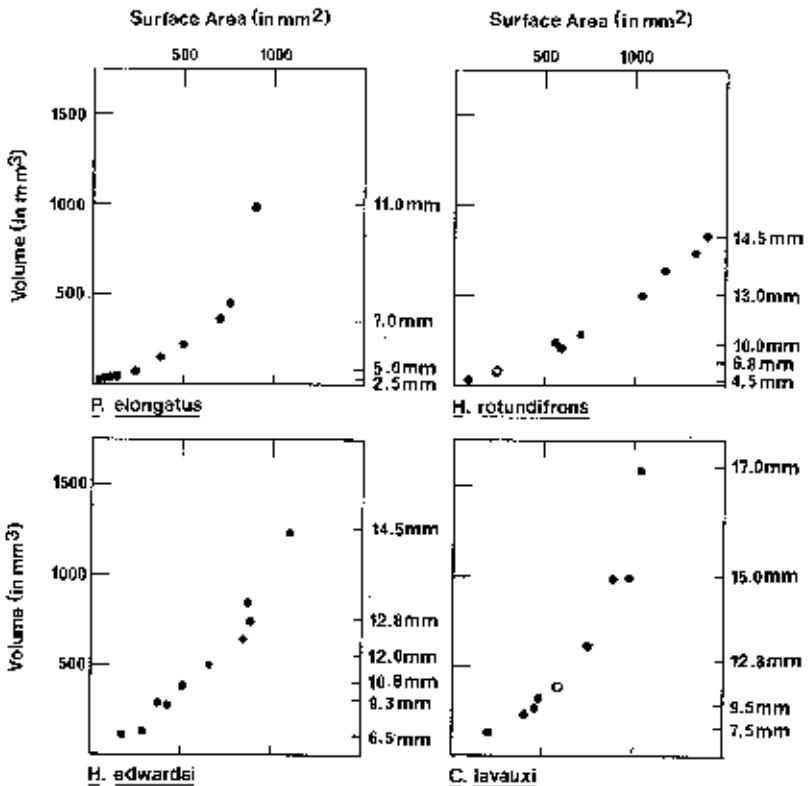


Fig. 2. Surface area/volume curves for each species. Corresponding carapace widths are indicated (in mm) in the column at the right of each chart. o indicates 2 individuals (match from 2 different series).

established by the first. Above carapace widths of 11 mm, the males of all species except *Petrolisthes elongatus* exhibited a slightly higher ratio of volume to surface. The male chelipeds in these species begin to grow faster in proportion to the body (generally above carapace widths of 11.0 mm). Both sexes were found in approximately equal numbers at all levels.

The smallest members of each species died before the 10 hours desiccation experiment was concluded, after which their weight continued to decline at the same rate for several hours (this by itself is evidence that metabolic activities such as respiration are only a minor route of water loss). The water loss at death was as follows: *Petrolisthes elongatus* (34-40%), *Heterozius rotundifrons* (62-66%), *Hemigrapsus edwardsi* ($\simeq$ 40%), and *Cyclograpsus lavauxi* ($\simeq$ 50%).

A monthly record of the three smallest individuals of each species at each 0.10 m horizon above the low tide level (ELWN or ELWS for day of sample) is presented in fig. 4. This approximates the lower size limit for desiccation tolerance.

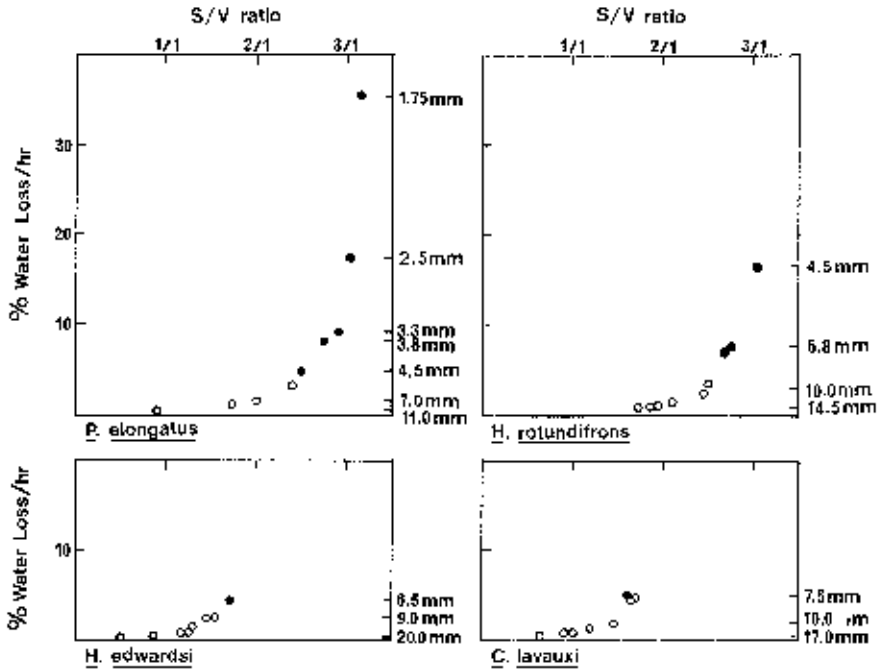
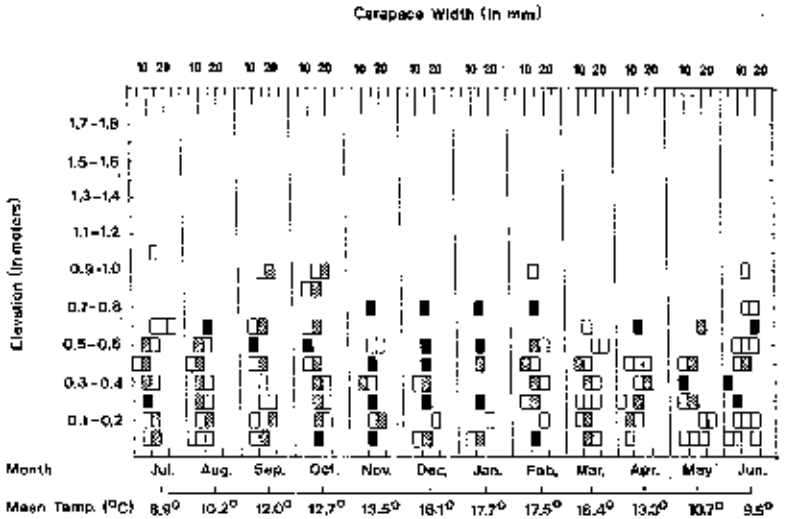


Fig. 3. Desiccation rates for each species (at 14 ± 1°C and humidity 70%) plotted against surface area/volume ratios. Corresponding carapace widths are indicated in the column at the right of each chart. ● indicate lethal water loss within 10 hours.

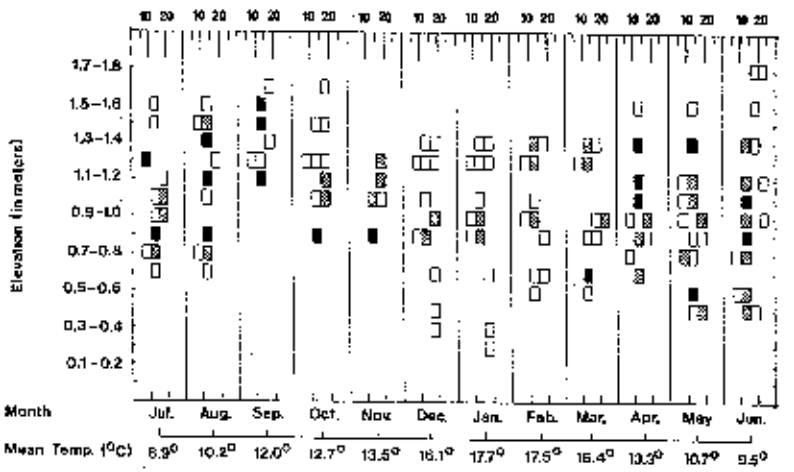
During the summer months, *Petrolisthes elongatus* and *Cyclograpsus lavauxi* experienced vertical range restrictions (fig. 4); and agreement between both transects, sampled during alternate months, is strong evidence that the results are not unique to either sample site.

Fig. 5 presents monthly frequency histograms for each species at given elevations above the low tide level. For example, in July, at elevations between 0.0-0.5 m, *Petrolisthes elongatus* represented 57% of the sample, *Heterozius rotundifrons* = 33%, *Hemigrapsus edwardsi* = 10%, and *Cyclograpsus lavauxi* = 0%. Fig. 5, which, unlike fig. 4, includes all individuals sampled, embodies the zonation of the four species. *Petrolisthes elongatus*, *Hemigrapsus edwardsi* and *Cyclograpsus lavauxi* all experience a decline in numbers during the summer, while *Heterozius rotundifrons* increases in frequency, possibly replacing *Petrolisthes elongatus* at the 0.5-1.0 m levels.

Cyclograpsus lavauxi, which resides highest on the intertidal zone, retreated from the 1.4-2.0 m region from November through March and penetrated downward as far as 0.2 m (fig. 4). Seasonal variation of the lower size limit (horizontal axis, fig. 4) was not so apparent as with *Petrolisthes elongatus* and *Heterozius rotundifrons*. This is because few *Cyclograpsus lavauxi* with carapace



H. rotundifrons



C. lavauxi

1 individual
2 individuals
3 individuals

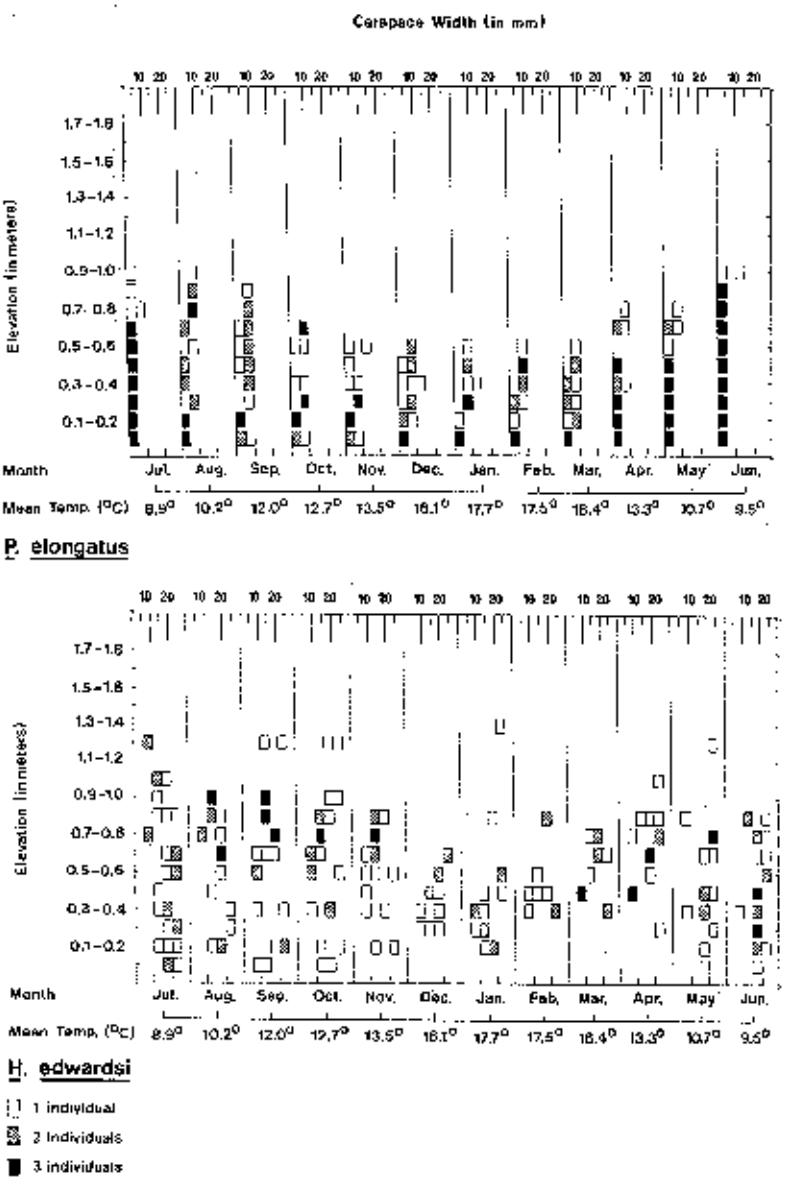
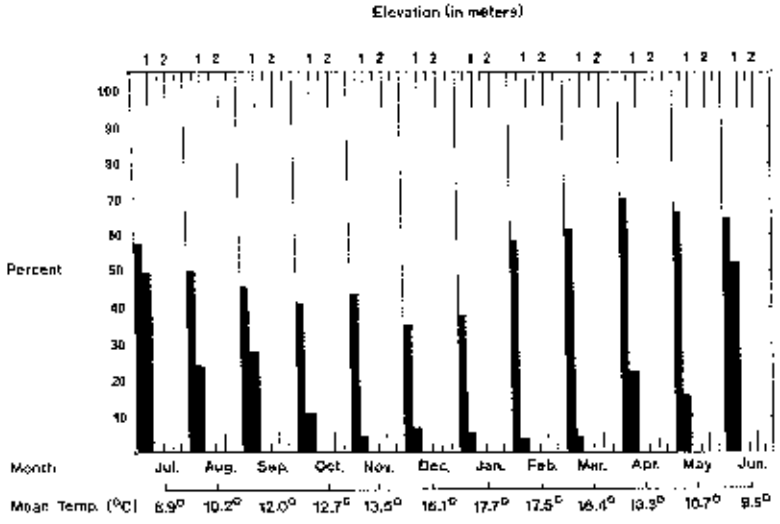
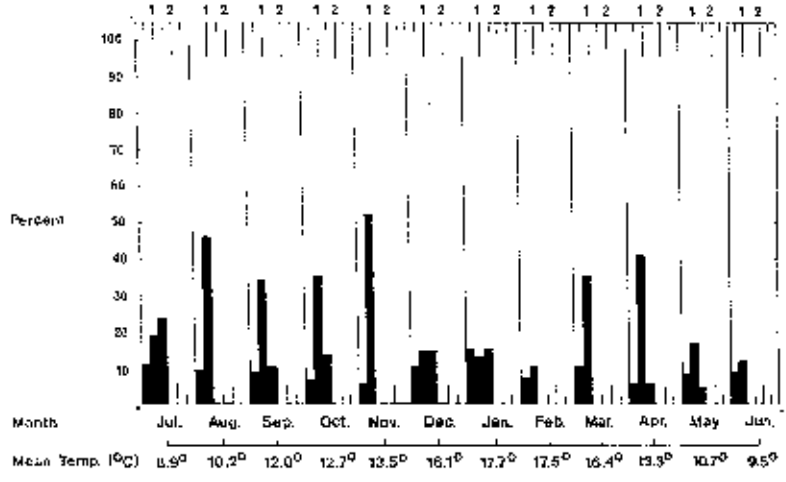


Fig. 4. Monthly variation in minimum carapace width at different elevations between low and high tide levels. The 3 smallest individuals representing each 0.1 m horizon are shown. At horizons represented by only 1 or 2 individuals, these include the entire sample at that level. Total area sampled = 146 m². The smallest individuals, shown here, represent the following total sample numbers: *Petrolisthes elongatus* = 1010, *Heterozius rotundifrons* = 757, *Hemigrapsus edwardsi* = 341, *Cyclograpsus lavauxi* = 357. Seasonal air temperatures are indicated.



P. elongatus



H. edwardsi

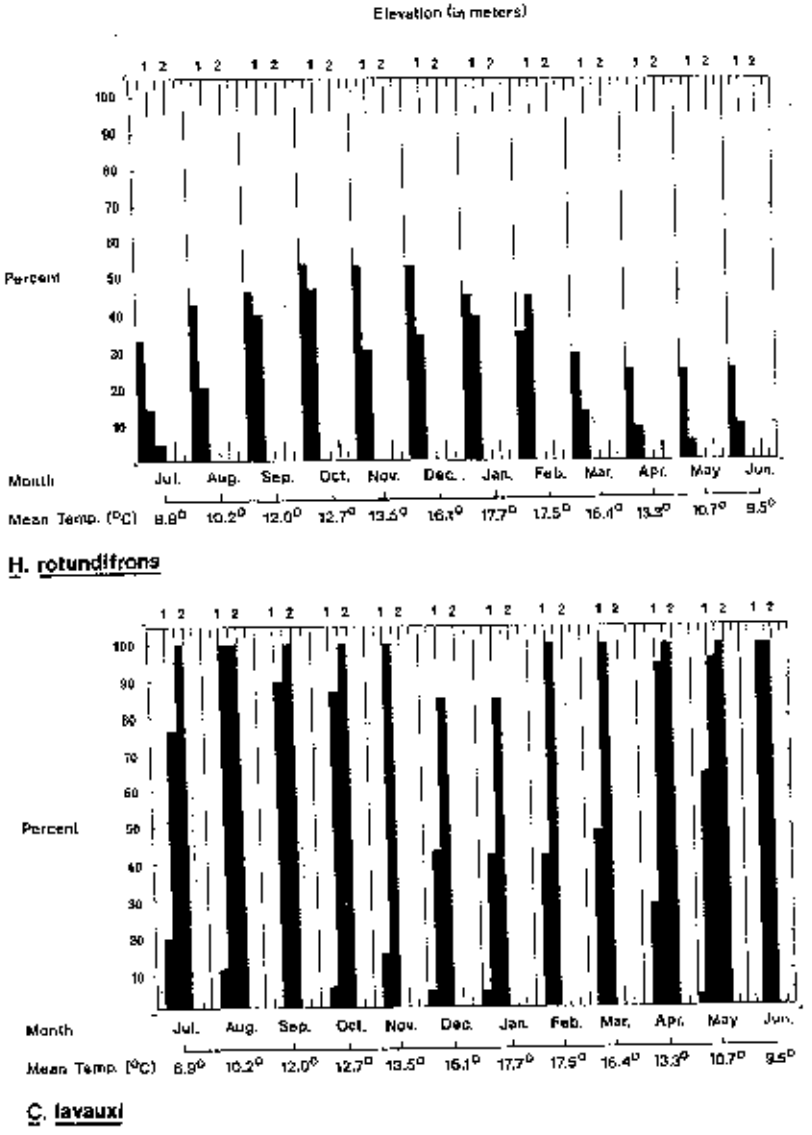


Fig. 5. Monthly frequency histograms for *Petrolisthes elongatus*, *Heterozius rotundifrons*, *Hemigrapsus edwardsii*, and *Cyclograpsus lavauxi* showing percent of sample represented by each species at given elevations above the low tide level. For total sample number, see fig. 4.

widths <10.0 mm, and none <7.5 mm (corresponding to a volume of 125 mm^3) were present in the transect samples. Fig. 3 exemplifies the absence of small individuals among species residing progressively higher on the shore. All crabs described in fig. 3 were collected between the sublittoral fringe and the maritime zone. *Petrolisthes elongatus* with carapace widths as low as 1.75 mm (volume <25 mm^3) are represented in this sample. No *Heterozius rotundifrons* with carapace widths <4.50 mm (volume $\simeq$ 25 mm^3) were present. Residing higher on the shore, *Hemigrapsus edwardsi* occurred at a minimum carapace width of 6.50 mm (volume $\simeq$ 110 mm^3), and *Cyclograpsus lavauxi* >7.50 mm (volume $\simeq$ 125 mm^3). Thus, the carapace widths listed in fig. 3 suggest a progressive decrease in the availability of small individuals among species ranging higher on the shore: a lower size limit whose "value" is indicated by desiccation rates of the smallest members of each species at $14 \pm 1°C$ and 70% humidity. The smallest individuals of *Petrolisthes elongatus* and *Heterozius rotundifrons*, which were found predominantly in the sublittoral fringe and lower midlittoral zone, experienced $>50\%$ water loss during the first 3 hours of the desiccation experiment. The smaller members of the two grapsid species, which were concentrated higher in the midlittoral zone and ranged upward into the littoral fringe, took 10 to 12 hours to loose the same amount of water. A higher minimum size range for the two grapsid species is consistent with existence relatively higher in the intertidal zone, as their immediate surroundings are uncovered for longer periods during low tides (up to 12 hours near the littoral fringe). Juveniles of both species reside in subtidal waters until they can advance landward.

P. elongatus and *Heterozius rotundifrons* were observed climbing over and between submerged rocks in the sublittoral fringe during all seasons. No *Hemigrapsus edwardsi* or *Cyclograpsus lavauxi* were observed moving among submerged rocks in this zone, although both species are active in the upper midlittoral zone during high tides. At night, when desiccation pressures are reduced, adult grapsids are active on the shore during low tides.

Laboratory observations suggest that *Cyclograpsus lavauxi* is more active than *Hemigrapsus edwardsi* when submerged. By day and night, given $\simeq$ 25 members of each species, 5 to 15 *Cyclograpsus lavauxi* were seen climbing on crevieed rock or traversing the bottom at any particular time, compared with <5 *Hemigrapsus edwardsi*. Moreover, $\simeq$ 80% of the *Cyclograpsus lavauxi* contained in an uncovered laboratory aquarium escaped within two weeks, whereas $>80\%$ of the *Hemigrapsus edwardsi* population remained. Such differences are to be anticipated if, residing higher on the shore, *Cyclograpsus lavauxi* remains sheltered under rocks during low tides for longer periods than *Hemigrapsus edwardsi*.

During January and February, crabs collected at elevations >0.8 m were found under rocks >130 mm across, compared with 30 to 50 mm during the winter. From January through March, *Cyclograpsus lavauxi*, at elevations >1.0 m, dug approximately cylindrical burrows under sheltering rocks. These

were roughly as wide as the carapace and 20 to 40 mm deep. Upper midlittoral *C. lavauxi* were also found buried under 30 to 40 mm of gravel beneath sheltering rocks. Three or four individuals were occasionally found together. By April, as temperatures began to decline and landward penetration by *C. lavauxi* became more pronounced, burrowing behavior ceased.

DISCUSSION

Surface area/volume relationships. — It is evident in fig. 3 that gradations in desiccation rate, within each of the four species, show exponential relationships with the surface area/volume ratio at increasing or decreasing size.

Among the three brachyuran species studied here, the surface/volume curve for *Heterozius rotundifrons* is skewed farthest to the right (fig. 2). The specific details of body design responsible for this skewness are not yet well understood, but are apparently tied, at least in part, to the proportion of body mass distributed over the leg appendages and the degree of flattening or cylindricality of the walking legs, chelipeds,and cephalothorax. *Cyclograpsus lavauxi* individuals with volumes < 600 mm^3 have 54% of their body mass concentrated in the legs and chelae, while *Heterozius rotundifrons* (< 850 mm^3) and *Hemigrapsus edwardsi* (< 600 mm^3) both $\simeq$ 42% body mass in the leg appendages.

Heterozius rotundifrons differs from *Hemigrapsus edwardsi* in having more cylindrically constructed legs, chelae, and body. For analogy, if 1 mm of depth is added to a strip of cardboard 10 mm long, 5 mm wide, and 1 mm deep, its volume will be effectively doubled, while its surface area will increase only slightly. If the same is added to a 10 mm long by 5 mm wide cylinder, its volume will increase at a slower rate relative to surface area, which seems to conform to the relative rotundity of *Heterozius rotundifrons* and its correspondingly higher ratio of surface to volume. By contrast, *Petrolisthes elongatus*, throughout its entire size range, carries approximately 70% of its body mass in its walking legs and large, flattened chelipeds; and its volume relative to surface area begins to increase dramatically before it reaches a volume of 350 mm^3.

A rapid decrease of surface area over volume is understandably important to *Cyclograpsus lavauxi* which, residing highest on the shore, is exposed to desiccating conditions for the longest periods of time; and also to *Petrolisthes elongatus*, whose smallest members penetrate as high in the intertidal zone as larger representatives of *Heterozius rotundifrons* and *Hemigrapsus edwardsi*. Notably, *Heterozius rotundifrons* has the highest concentration of skeletal material (nearly 53%) and a correspondingly thicker integument through which water may be evaporated. A rapid decrease of surface area over volume is therefore relatively unimportant to *H. rotundifrons*, which, at a S/V ratio of 2.5/1, survives 10 hours desiccation without shelter at 14 ± 1°C and 70% humidity, loosing only 3.5% water weight/h, while a *Petrolisthes elongatus* with the same S/V ratio looses

5%/h and dies (fig. 3). At a S/V ratio of 1.7/l, *Heterozius rotundifrons* looses only 1%/h, while both grapsid species loose ≃ 5%/h, which approximates the lethal limit during a 10 h tolerance test.

Integument permeability. — On the basis of previous metabolic studies, weight loss due to metabolic carbon is not significant, as it is calculated to be < 1% (Herreid, 1969a; Scholander et al., 1953; Weymouth et al., 1944). According to Herreid (1969b), almost all water loss occurs directly through the integument from the body and legs with evaporation through gill chambers representing as little as 1% of the total evaporation. As we have seen in the preceding section, *Petrolisthes elongatus* looses nearly 1/3 more water/h at a given S/V ratio than *Heterozius rotundifrons*, and the two grapsid species loose almost 5× as much (but grow up to 10× as large, in terms of volume). The difference apparently results from *Petrolisthes elongatus*' and the two grapsids' relatively smaller skeletal mass and correspondingly thinner, more permeable integuments.

The role of temperature (an example). — During July, horizons between 0.0 and 0.7 m above the low tide level were occupied by two or more *Petrolisthes elongatus* with carapace widths < 5.0 mm (fig. 4). Individuals in this size range were present up to an elevation of 1.0 m above the low tide level. During August and September, as mean air temperatures rose from 8.9 to 12.0°C (and despite the year-round presence of 2.0-3.0 mm individuals in the sublittoral fringe), representation by *P. elongatus* at elevations between 0.2 and 1.0 m became restricted chiefly to individuals in the 5.0-10.0 mm size range (fig. 4). At a carapace width of 5.0 mm, *P. elongatus* has a surface area of 238 mm^2 and a volume of 95 mm^3. This corresponds to a S/V ratio of 2.5/l, compared with 0.9/l for a carapace width of 11.0 mm ($s = 900$ mm^2, $v = 1000$ mm^3). Individuals in the 10.0-11.0 mm size range can survive 10 h desiccation without shelter at 14 ± 1°C and 70% humidity with < 10% total water loss, while 5.0 mm individuals loose 30% of their water content within 6 hours and die (fig. 3). This relationship between surface area and volume seems to account for a shift, above the sublittoral fringe, to a higher minimum size range as the mean temperature increased during the spring season. Supportive evidence is provided by Herreid's (1969a) study of water loss in crabs, which demonstrates that evaporation loss increases with increasing temperature.

Seasonal variation. — From July through October, as the vertical extent of *Petrolisthes elongatus*' range became restricted, and its lower size limit rose, *Heterozius rotundifrons* increased in frequency (relative to *Petrolisthes elongatus*), especially in the 0.5-1.0 m level vacated by *P. elongatus* (fig. 5). During this time, at elevations between 0-0.5 m above the low tide level, where desiccation pressures were not as pronounced as higher on the shore, there was a well

defined shift of *Heterozius rotundifrons* from a mode (for lower size limit) of 5.0-10.0 mm carapace widths to carapace widths between 10.0-15.0 mm (fig. 4). In spite of the increasing frequency of *H. rotundifrons* in the lower midlittoral zone and sublittoral fringe (fig. 5), the lower size limit for individuals found in this region increased more noticeably than for individuals residing on horizons >0.5 m. This was most clearly illustrated during the month of October (fig. 4).

By then, the mean size of *Petrolisthes elongatus* in the 0-0.5 m region, due apparently to progressively increasing desiccation pressures, had increased. Possibly, the presence of *P. elongatus* is responsible for the disproportionate shift of the lower size limit for *Heterozius rotundifrons* in the 0-0.5 region. Thus, the size distribution of *H. rotundifrons* may be determined, in the upper extent of its range, by physical factors such as desiccation, and on the lower shore by the action of biotic factors such as the presence of another species with similar space requirements (for example, movement through gravel of a preferred grain size). Similar factors are apparently operant in the zonation of different species of barnacles (Knox, 1954; Connell, 1961); however, there remain unexplored possibilities, for example, food supply, which is complicated by the fact that the two species have different food requirements (Scott, 1958; Jones, 1978). The data are not yet sufficient to substantiate whether interspecies competition has been observed. As numbers of *Petrolisthes elongatus* found in the 0.5-1.0 m level declined from July through March, the frequency of *Heterozius rotundifrons* in that same region increased. *H. rotundifrons* seems simply to have moved into the space vacated by the anomuran species and replaced it during the warmer months.

In July, *Hemigrapsus edwardsi* as small as 6.5 mm were found as high as 1.3 m above the low tide level (fig. 4). From December through March, no individuals in the 6.5-10.0 mm range (corresponding to S/V ratios between 1.7/1 and 1.3/1) were found above 0.5 m. Above 0.8 m, only 4 individuals were found during this period (compared with 42 during the cooler months), and none of these measured <15.0 mm (corresponding to a S/V ratio of 0.85/1). Again, the summer size and range restrictions are probably set by surface area/volume relationships and desiccation pressures. Interestingly, from November through April, the frequency of *Hemigrapsus edwardsi* in the 0-0.4 m region, particularly individuals with carapace widths <15.0 mm, decreased (fig. 4). A similar increase in lower size limit for *Heterozius rotundifrons* residing in the 0-0.4 region was observed from August through November.

Cyclograpsus lavauxi was not recorded at elevations >1.4 m from November through March, and appears to have largely replaced *Hemigrapsus edwardsi* and *Petrolisthes elongatus* in the 0.7-1.1 m region (fig. 4).

Desiccation and zonation. — The evidence presented in this paper indicates a general pattern of retreat of small crabs (carapace widths between 5.0 and

10.0 mm; re. horizontal axis, fig. 4) from upper levels of their range in the intertidal zone during the warmer months. Desiccation experiments on crabs of known surface areas and volumes showed that evaporation water loss is greatest for small individuals with a high ratio of surface area to volume.

The effects of desiccation do not explain the virtual absence of *Cyclograpsus lavauxi* from the lower midlittoral zone (both grapsid species have survived among submerged rocks for >2 weeks in laboratory aquariums). Nor can desiccation directly account for the August through November shift of lower size limit for *Heterozius rotundifrons* in the 0-0.4 m region or the November through April reduction of *Hemigrapsus edwardsi* in the same region (which becomes most pronounced from February through April and appears to be tracked by *Cyclograpsus lavauxi* in fig. 4). There are apparently factors affecting distribution not examined in this study. For example, occupation of the sublittoral fringe and lower midlittoral zone by other species with similar space requirements (*Petrolisthes elongatus* and *Heterozius rotundifrons*) may restrict the frequency of the two grapsid species near the sublittoral fringe.

A species distinction becomes apparent when surface/volume ratios are compared against desiccation rates. For example, *Hemigrapsus edwardsi* and *Cyclograpsus lavauxi* both loose ≃ 4.5% water/h at a S/V ratio ≃ 1.65/l (corresponding to 188 mm^2/110 mm^3 and 200 mm^2/125 mm^3 respectively). By contrast, *Petrolisthes elongatus* looses only 1.2% water/h at a ratio of 1.7/l (corresponding to 765 mm^2/450 mm^3) and *Heterozius rotundifrons* survives with only 1.0% water loss/h at a S/V ratio of 1.7/l (corresponding to 1462 mm^2/850 mm^3). It is important to note here that if we ignore surface area and plot desiccation as a function of body weight (as did Herreid, 1969a) or volume alone, no interspecific difference is apparent (all four species loose ≃ 1.5% water weight/h at a volume ≃ 500 mm^3). Since surface areas are known, and a metabolic relationship is ruled out by the observation that desiccation rates remain constant after death, the difference would seem to be rooted in different integument permeabilities for the species studied. One would expect the two grapsid species, which reside higher on the beach than *Petrolisthes elongatus* and *Heterozius rotundifrons*, and which must tolerate longer periods of exposure, to have the least permeable exoskeletons; but the exact opposite appears to be true. This condition makes a rapid volumetric increase in *Hemigrapsus edwardsi* and *Cyclograpsus lavauxi* even more understandable, because these two species desiccate faster at given surface/volume ratios than *Petrolisthes elongatus* and *Heterozius rotundifrons* (fig. 3). The "reason" for a more permeable exoskeleton in *Hemigrapsus edwardsi* and *Cyclograpsus lavauxi* is unclear; but may be tied to such processes as evaporative cooling and/or the elimination of ammonia waste, which readily diffuses out through the cuticle (Prosser & Brown, 1961). Edney (1961, 1962) and Lewis (1963) have demonstrated that evaporation through the integument may reduce the body temperature of intertidal crabs by as much as 8°C below ambient temperature. Hence, the greater integu-

ment permeability of *Hemigrapsus edwardsi* and *Cyclograpsus lavauxi* may enable both species to withstand 6 to 12 hours exposure to summer daytime extremes as high as 23°C. Accordingly, the pressures of temperature and desiccation are interdependent, as suggested by Newell (1970); desiccation tolerance at given temperatures being limited by the ability to withstand up to 40 or 50% water loss, which is in turn dependent upon surface/volume relationships and the characteristic integument permeability of each species.

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RÉSUMÉ

Les changements saisonniers dans la distribution des tailles de quatre espèces de crustacés décapodes de Nouvelle-Zélande ont été évaluées comme une fonction de l'élévation croissante au-dessus du niveau de la marée basse.

Ces résultats ont été comparés aux données relatives à la dessication pour des représentants des mêmes espèces avec des surfaces et des volumes connus. Les surfaces ont été mesurées en appliquant une couche fine et mince d'aluminium (env. 20 Å d'épaisseur) sur les crabes et des feuilles de polythène de surface comme montées sur un support planétaire S.E.M. Les quantités d'aluminium recouvrant les crabes et les feuilles de polythène ont alors été mesurées à l'aide d'un spectromètre d'absorption atomique. Les données recueillies suggèrent que l'absence d'individus de moins de 6,5 mm (largeur de carapace) parmi les deux espèces de grapsides étudiées, les glissements saisonniers des tailles modales, et un retrait d'aspect général des niveaux supérieurs de la côte pendant les mois d'été peuvent être expliqués avant tout sur la base des pressions de dessication qui agissent sur les crabes dans des rapports donnés surface/volume. Ces constatations confirment l'hypothèse de relations exponentielles entre surface et volume, comme facteur limitatif principal dans le mouvement des crabes vers l'intérieur.

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