

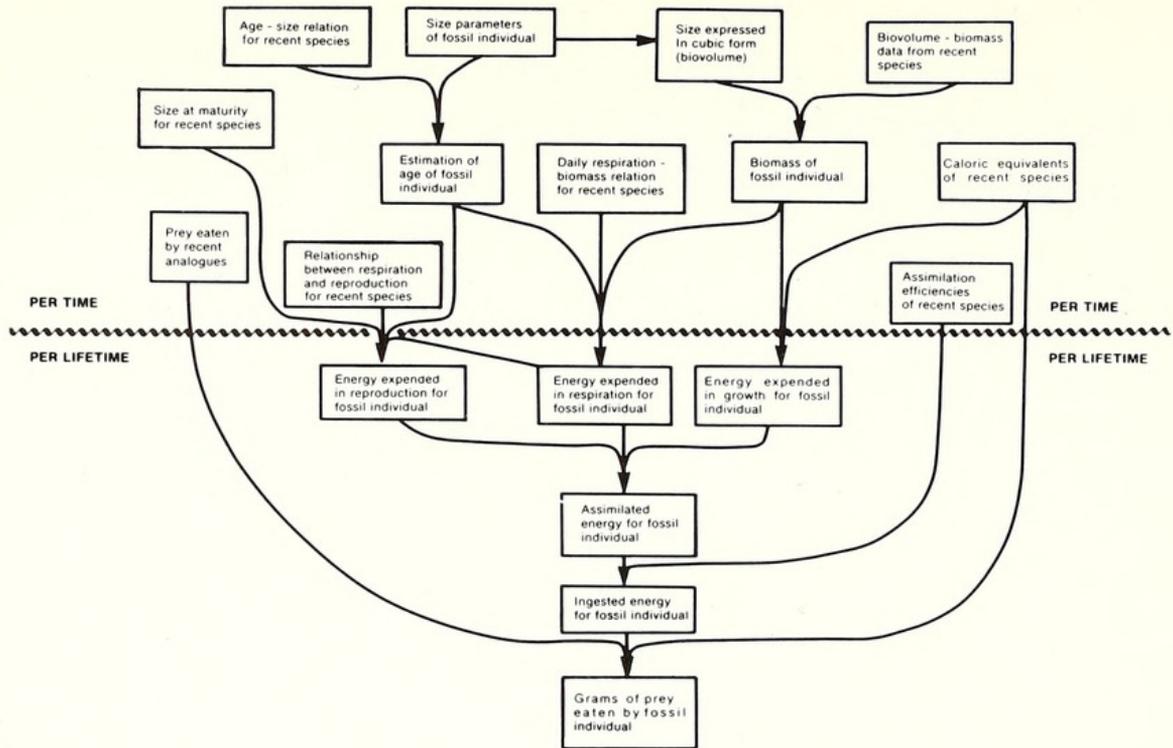
ESTIMATING BIOMASS AND ENERGY FLOW OF MOLLUSCS IN PALAEO-COMMUNITIES

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ABSTRACT. The reconstruction and interpretation of palaeo-community structure has been based largely on the taxonomic composition and relative abundance of the preserved species. An expanded and more precise understanding of some aspects of the palaeo-community can be deduced from information on the biomass and energy flow of its preserved components. The procedural steps to calculate energy flow in a palaeo-community require as input the size-frequency distribution of each species' population, the size-age relationship for each species, and certain parameters of energy flow that have been measured for living organisms. These parameters are used to: (1) estimate biomass from size, (2) convert biomass into its caloric equivalent, (3) estimate respiration from biomass and age, (4) estimate the energy cost of reproduction from respiration and size at maturity, and (5) calculate total assimilated energy from (2), (3), and (4) above. The quantity of food consumed by an individual or population can also be estimated because ingestion can be estimated from assimilation. These estimates must be summed over the individual's life span rather than evaluated on a yearly time scale, as is normally done in ecologic studies. Therefore, calculations of energy flow may differ substantially from those elucidated in studies of recent communities. The method is used to determine the energy flow in populations of four gastropods and one bivalve from the Stone City Formation (Eocene) of east-central Texas. The relative importance of species differs considerably if assessed by their numerical abundance, their biomass, or the amount of food ingested by them over their lifetimes. For example, *Hesperiturris nodocarinatus*, the least abundant species numerically, ingested the most prey biomass.

A CHRONIC problem in ecologic and palaeoecologic research is to adequately interpret community structure and dynamics from data consisting only of species composition and numerical abundance. Numerical abundance, however, may over-emphasize the importance in the living community of opportunistic species or species with particularly successful larval sets because of low juvenile survivorship (Thorson 1966) and frequently occurring disturbances (Gray 1977; Woodin 1978) in the community. Such species also may dominate the numerical abundance of the death assemblage (Levinton 1970; Powell *et al.* 1984) and the resulting fossil assemblage, so that the actual importance of other species may not be evaluated accurately from abundance data during community reconstruction. Stanton *et al.* (1981) discussed this problem in relation to the trophic reconstruction of palaeo-communities. In that case, use of abundance data over-emphasized the importance of naticid gastropods in the community's trophic structure (Stanton and Nelson 1980) because most of the individuals were small and contributed little biomass to, and had little predatory impact on, the total community. Stanton *et al.* (1981) argued that analysis of trophic structure based on biomass should be more accurate than on abundance, but they were constrained by the absence of a good procedure for determining biomass from size.

Odum and Smalley (1959) pointed out that, although the use of numerical abundance tends to over-emphasize the importance of small organisms, biomass tends to over-emphasize the importance of large organisms. Thus, Odum and Smalley (1959), Steele (1976), and others argued that energy flow provides the best method for interpreting the trophic structure of communities. Stanton *et al.* (1981) suggested that this should be true for palaeo-community reconstructions as well, but pointed out the primary difference between estimations of energy flow in ecology and palaeoecology. That is, energy flow in ecology is normally measured on a per area per year basis whereas energy flow in palaeoecology must be evaluated for an individual's entire lifetime. The absence of conversion equations to predict energy flow from size-frequency data prevented Stanton *et al.* (1981) from further investigation of this subject.



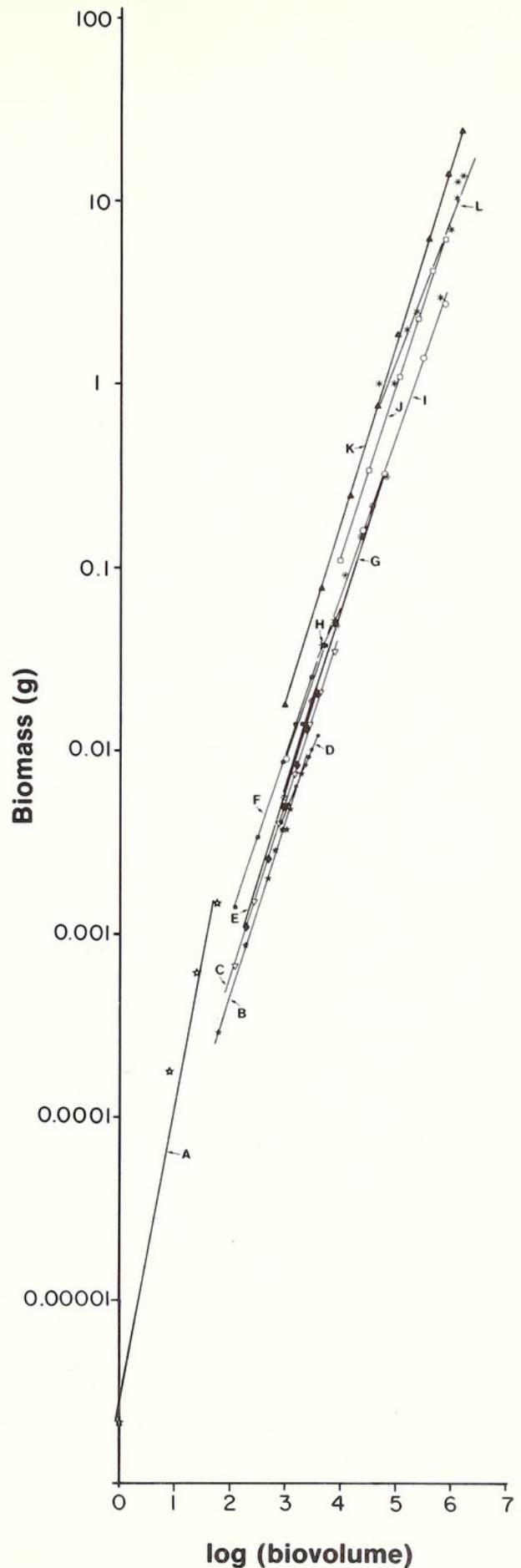
TEXT-FIG. 1. Steps in determining energy flow.

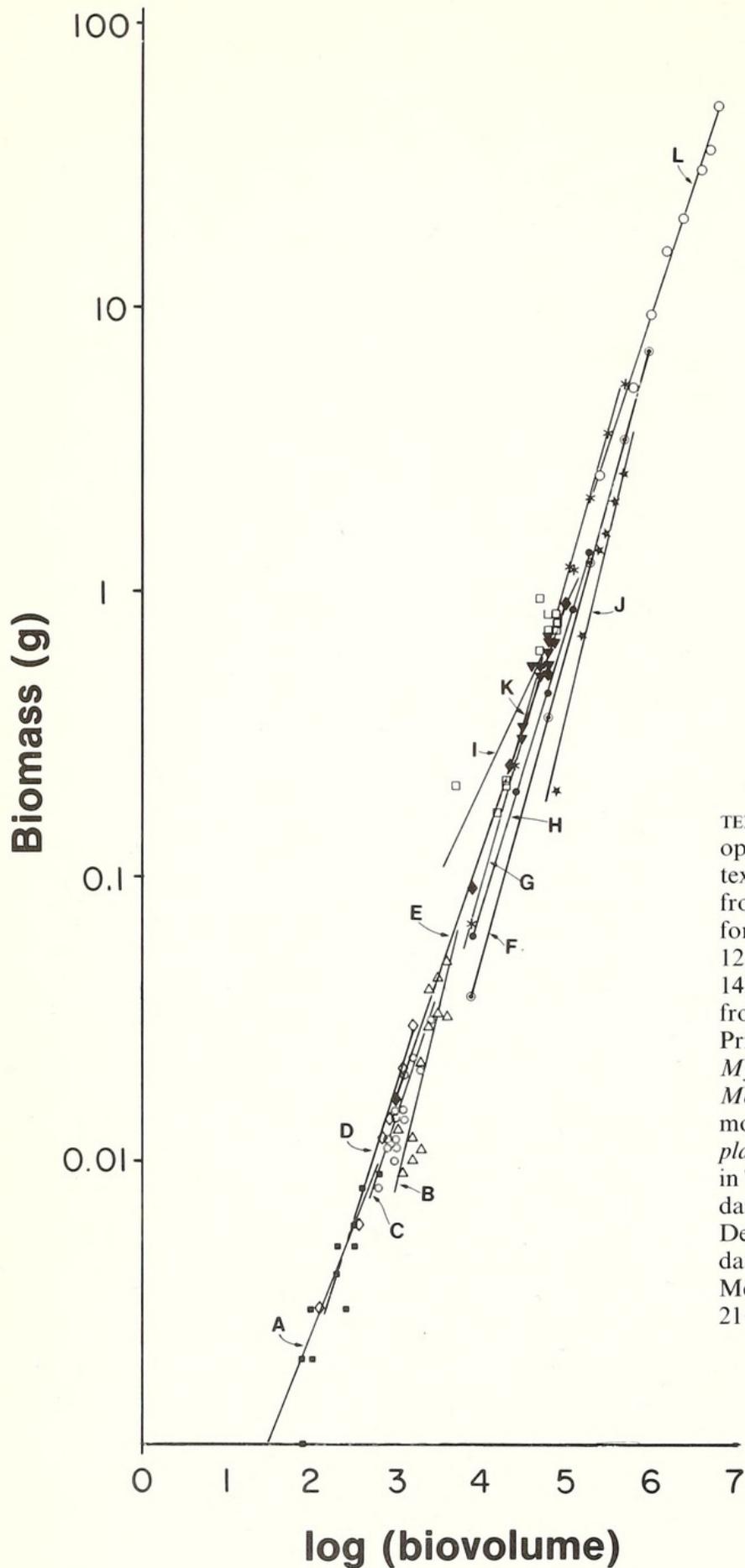
In this paper we present conversion equations for calculating biomass and energy flow from numerical abundance and size-frequency data, and discuss the assumptions behind these conversions. Similar approaches have been used for terrestrial vertebrates (Martin 1980; Scott 1982). To demonstrate the application of this method in palaeoecology, the parameters of energy flow will be evaluated for five of the species of Eocene molluscs discussed by Stanton *et al.* (1981) and Stanton and Nelson (1980). In deriving these equations, we have sought relatively simple procedures that require measurements of size commensurate with the quality of numerical abundance and size-frequency data normally available to palaeontologists. The data and equations deal specifically with molluscs. Although the method of conversion would be the same, different equations might be required for other phyla. Whenever possible we utilize one equation for molluscs as a whole or two equations, one for bivalves and one for gastropods. Although a higher degree of accuracy might be obtained, in some cases, by a series of equations for lower taxonomic levels, the data base available is not sufficiently large for this to be a viable alternative for many living taxa, and of course many extinct taxa have no recent analogues.

The steps in estimating biomass and energy flow are diagrammed in text-fig. 1. The biomass of a species' population in a community is the sum of the biomasses of all of the individuals in that population. It is determined, then, from (1) the number of individuals present, (2) the size-frequency distribution of the population, and (3) the relationship between size and biomass for each individual. In the following section we present simple equations for calculating biomass from shell dimensions for bivalves and gastropods. To do this, shell dimensions are converted by simple equations into operational biovolumes which subsequently can be converted to true biomass. The biovolumes are not true biovolumes as might be derived, for example, from displacement volume, but rather are simply shell dimensions transposed into a convenient cubic form.

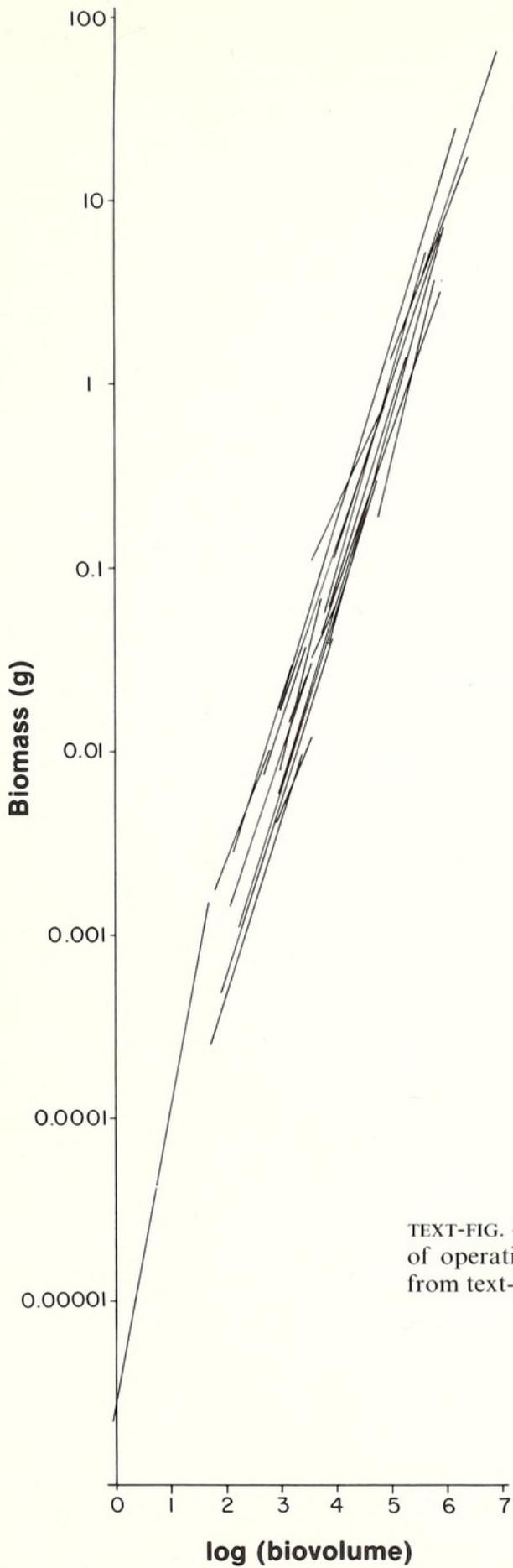
Assimilated energy is expended largely in growth, respiration, and reproduction. In the second section we present equations for the estimation of these parameters from the individual's biomass using relationships obtained from data on living molluscs. These relationships include a caloric equivalent of biomass, the daily respiration rate at a given biomass, and the amount of energy expended in reproduction relative to that expended in respiration. Energy expended in growth,

TEXT-FIG. 2. Regression lines of bivalve biomass versus log of operational biovolume (= cube of the maximum length). Additional bivalves are plotted in text-fig. 3. Data points indicate those data used from the individual data sets to calculate the final biomass-biovolume regression. In literature sources where regression lines were given but original data points were not, data points have been generated from these length-biomass regressions, and span the length range of the original data set. Information about the data sources is listed in the following order: taxon, reference, number of data points, comments, biomass measure (DW, dry weight; AFDW, ash-free dry weight; FDDW, freeze-dried dry weight; form, formalin preserved specimens; EtOH, alcohol preserved specimens; no designation, fresh or frozen specimens). A (☆): *Gemma gemma*, Green and Hobson (1970), 4, average length-DW regression for shelled animals and AFDW = 8.9% DW, AFDW. B (▼): *Abra nitida*, Wikander (1980), 7, from regression equation, AFDW. C (▽): *A. longicallus*, Wikander (1980), see B. D (●): *Spisula elliptica*, Ford (1925), 7, from Table III, DW EtOH. E (◆): *Nuculana minuta*, Ansell *et al.* (1978), 6, total wt-L³ regressions and DW = 4.88% total wt., DW. F (■): *Macoma balthica*, Bachelet (1980), 5, average of monthly regression equations, AFDW after decalcification. G (⊙): *Tagelus divisus*, Fraser (1967), 7, average of monthly regressions (for L > 2.5 cm) and single regression equation (for L < 2.5 cm) from Table 1, DW. H (★): *Cardium echinatum*, Ford (1925), 2, DW EtOH. I (○): *Mytilus californianus*, Fox and Coe (1943), 8, from Table 1, DW. J (□): *Mya arenaria*, Feder and Paul (1974), 7, from regression equation, DW. K (▲): *Tresus capax*, Breed-Willeke and Hancock (1980), 8, from Table 3, DW. L (✱): *Arctica islandica*, Ropes (1971) 9, from fig. 1, FDDW.





TEXT-FIG. 3. Regression lines of bivalve biomass versus log of operational biovolume (= cube of maximum length). See text-fig. 2 for format. A (■): unidentified venerid collected from Kahn Creek, Dubai, U.A.E., our data, 11, AFDW form. B (△): *Macoma balthica*, Beukema and DeBruin (1977), 12, from fig. 1, AFDW. C (○): *Mulinia lateralis*, our data, 14, AFDW. D (◇): *Tellina martinicensis*, Penzias (1969), 6, from fig. 5, DW. E (◆): *Cerastoderma edule*, Warwick and Price (1975), 5, from regression equation, AFDW. F (●): *Mya arenaria*, Warwick and Price (1975), see E. G (*): *Mercenaria mercenaria*, Hibbert (1977a), 7, average of monthly regressions in Table 2, AFDW. H (●): *Scrobicularia plana*, Hughes (1970), 5, from average of monthly regressions in Table 1, DW. I (□): *Anadara* sp., from Dubai, U.A.E., our data, 13, AFDW form. J (★): *Tagelus plebeius*, Holland and Dean (1977), 6, from fig. 4, DW. K (▼): *M. mercenaria*, our data, 10, AFDW. L (○): *Spisula solidissima*, Barker and Merrill (1967), 8, from fig. 3 using mean percentage solids of 21.4 to convert wet wt. to FDDW, FDDW.



TEXT-FIG. 4. Regression lines for bivalve biomass versus log of operational biovolume. Regression lines are combined from text-figs. 2 and 3.

respiration, and reproduction, however, are expressed in terms of the total energy used over the individual's life span because energy flow occurs throughout the individual's life and, for a fossil, the individual has completed its life span. For this reason, the age at sexual maturity, age at death, and a relationship between size and age also must be known. Then, by utilizing assimilation efficiencies of recent molluscs, we predict the quantity of food ingested over the individual's life span. In each step we list the sources of inaccuracy present in the calculation and, where possible, test the degree of accuracy by comparing independently published data with those predicted by our equations. In the last section we apply our results to the Stone City (Eocene) fauna in order to demonstrate the differences in interpretation that result from the use of biomass and energy flow rather than numerical abundance for trophic reconstruction of palaeo-communities.

BIOMASS

Biomass in a bivalve or gastropod is correlated with the volume of the body cavity within the shell. Thus, one could determine biomass for fossils from the relationships of size to biovolume, and biovolume to biomass for living molluscs. True biovolume is tedious to measure, however, so we chose, instead, to use an operational measurement of biovolume based on the conversion of easily measured shell parameters into cubic form. Regressions of true biovolume, obtained by filling shells with paraffin under vacuum, dissolving the shell in 10% HCl and weighing the paraffin, with operational biovolume for three species, *Thais haemastoma*, *Polinices duplicatus*, and *Littorina ziczac*, all had correlation coefficients above 0.95, proving the efficacy of this method. For bivalves, biomass is plotted in text-figs. 2-4 against the cube of the maximum (anterior-posterior) length, as suggested by Golightly and Kosinski (1981). For gastropods, the operational biovolume is the equation for the volume of a cone computed from maximum length and width, except for the limpet, in which case a formula for a general prismatoid is used. Gastropod biomass is plotted against operational biovolume in text-figs. 5-7. The equations for biomass in terms of operational biovolume derived from the regression lines for these plots are in the form:

$$\log_{10} B = m_B \log_{10} V + b_B \quad (1)$$

where V is operational biovolume in mm^3 and B is biomass in grams. They are:

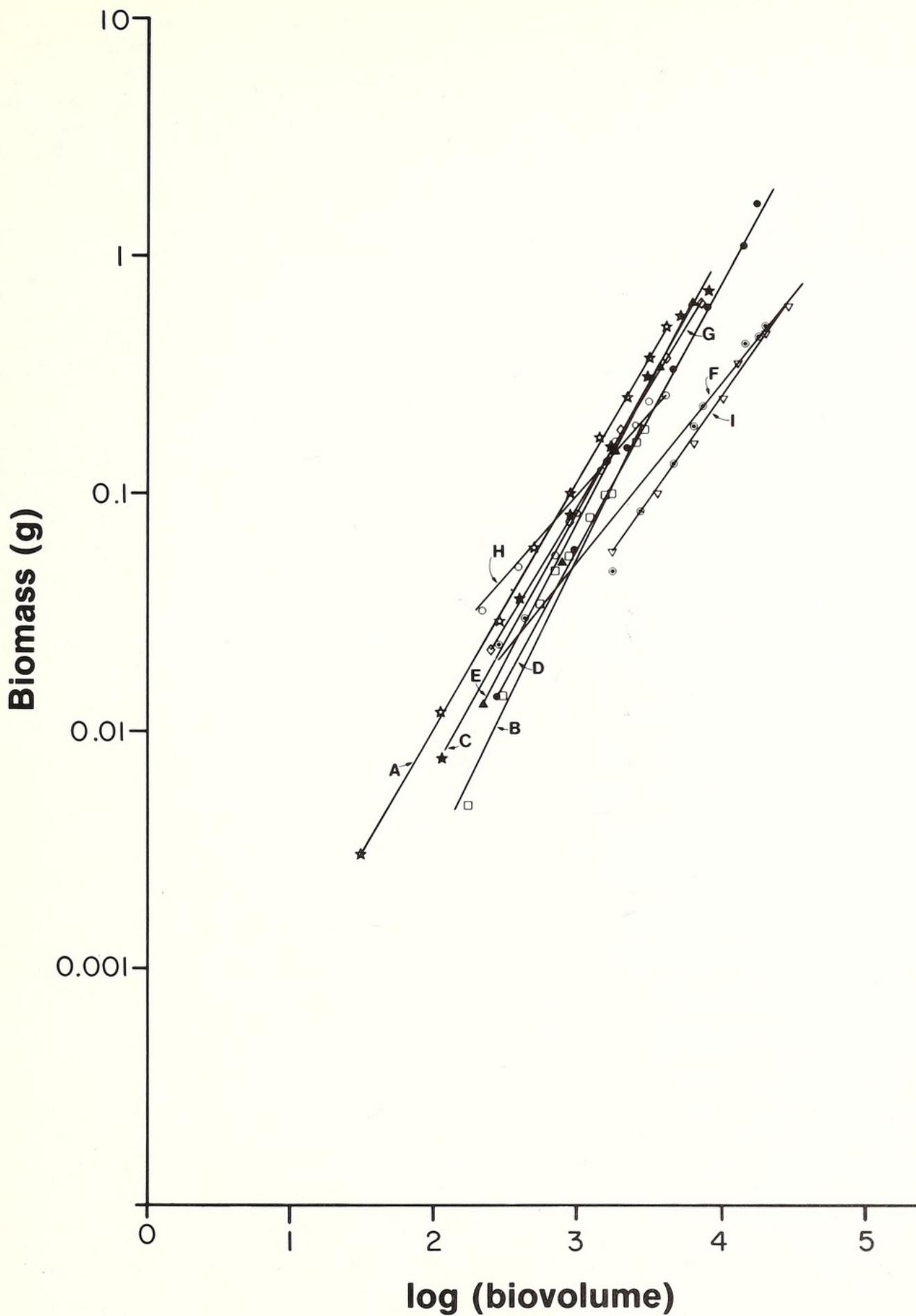
for bivalves,

$$\log B = (0.9576 \pm 0.0004) \log V + (-4.8939 \pm 0.0065) \quad r = 0.98 \quad (1a)$$

for gastropods,

$$\log B = (0.7708 \pm 0.0019) \log V + (-3.2421 \pm 0.0152) \quad r = 0.88 \quad (1b)$$

TEXT-FIG. 5 (*opposite*). Regression lines of gastropod biomass versus log of operational biovolume. Additional gastropod data are plotted in text-fig. 6. Except where noted, operational biovolume was computed from $V = \frac{1}{3} \cdot \pi \cdot (W/2)^2 \cdot L$, where W = maximum whorl width, and L = maximum apex-abapical tip length. W/L is estimated from cited figures in Abbott (1974) except where noted. See text-fig. 2 for format used below. A (☆): *Diloma novaezelandiae*, Logan (1976), 9, DW-shell diameter regression and $W/L = 0.97$ from figs. 8-9 in Cernohorsky (1974), DW. B (□): *Thais emarginata*, Palmer (1982), 10, L-body wt. from Table 2 and AFDW-body wt. regression Table 1 with $W/L = 0.77$ from fig. 1909, AFDW. C (★): *Fissurella barbadensis*, Hughes (1971a), 7, body wt.-shell length regression equation, calculation of biovolume used the equation for a general prismatoid $V = \frac{1}{6}L(B_1 + 4M + B_2)$ where L is dorsal-ventral shell height, B_1 , the area of a rectangle approximating the ventral base of the shell, M , the area of a rectangle at $L/2$, B_2 , the area of a rectangle at the apex (assumed $B_2 = 0$), relationship of B_1 , M , L to shell length from Abbott (1974), fig. 130, DW. D (●): *Nerita peloronta*, Hughes (1974b), 7, regression equation, assumed $W/L = 1.05$ from fig. 519, DW. E (▼): *N. tessellata*, Hughes (1971b), 5, see D, $W/L = 0.94$ from fig. 521. F (⊙): *T. lamellosa*, Palmer (1982), 10, see B, assumed $W/L = 0.63$ from fig. 1905. G (◇): *N. versicolor*, Hughes (1971b), see E, assumed $W/L = 1.0$ from fig. 520. H (○): *T. canaliculata*, Palmer (1982), see B, assumed $W/L = 0.60$ from fig. 1904. I (▽): *Polinices duplicatus*, Edwards, D. C. and Huebner (1977), 7, from AFDW-W regression and W-L regression, AFDW.



Text-figs. 4 and 7 contain all the individual regression lines for the bivalve and gastropod data respectively. The same lines are presented in text-figs. 2 and 3 (bivalves), and 5 and 6 (gastropods) at a larger scale so they can be examined in more detail. Some of the data points in text-figs. 2 and 3, and 5 and 6 were generated from the published regression lines if original data points were not given. Although these generated points cover the size range of individuals used by the original authors, the variability of our data is certainly less than that of the original data set. Therefore confidence limits and correlation coefficients are conditional. Data subsets used in text-figs. 2–7 are of similar size so that no one subset would be inordinately important in the regression.

The variability around the regression lines is smaller than one might anticipate, considering the wide array of shapes and sizes of bivalve and gastropod species included in the regressions. The gastropods used, for example, range in shape from naticids to muricids and columbellids; bivalves include cardiids, tellinids, and razor clams (*Tagelus*). Although a few taxa, such as the razor clam *Ensis* and some gastropods such as *Conus* or *Crepidula* may require different equations for operational biovolume (data for the limpet *Fissurella*, for example, fit the biomass curve when the equation for a prismatoid was used), these equations appear to be useful for the great majority of bivalves and gastropods.

The scatter of data points around the two main regression lines may be due in part to any of the following: (1) Seasonal reproductive cycles that can cause significant variability in biomass among individuals of the same species at a single location (see references in text-figs. 2–7). (2) Regional differences in shape and growth result in differences within a species in the biovolume to biomass relationship (Hamai 1938; Clark 1976; Eisma *et al.* 1976). (3) Differences in the methods used for measuring biomass; some are less accurate than others (Mills *et al.* 1982). (4) The equations for operational biovolume require measurements readily made from most fossils. More complex equations (Raup and Graus 1972; Kohn and Riggs 1975; Harasewych 1981) might estimate biovolume more accurately but would require measurements often not easily obtainable from fossils. Probably, the primary source of error in determining biomass is intraspecific variability. This will be difficult to eliminate. The range of variability among the gastropod regression lines is bracketed by regression lines for two samples of the same species, *P. duplicatus*, and by regression lines for two species of the same genus *Thais* and *Thais* (*Nucella*), for example. Thus, we use two general equations, 1a and 1b, to generate biomass rather than a larger number of equations derived from data sets each restricted to taxa of lower taxonomic level.

ENERGY FLOW

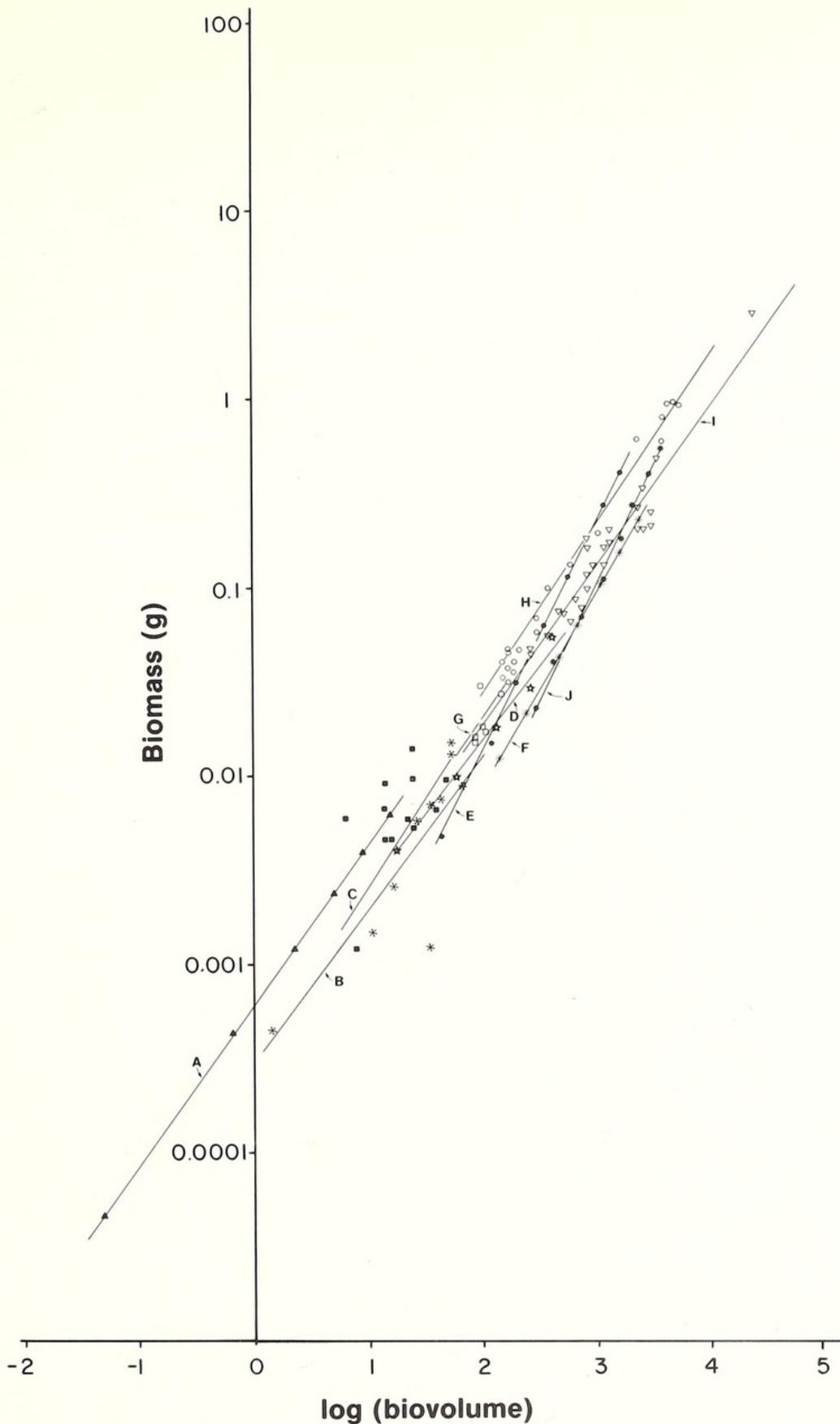
Assimilated energy (A) is expended largely in growth (P_g), respiration (R), and reproduction (P_r). The energy costs of excretion and secretion are assumed to be small by most referenced workers and will be assumed to be negligible here. Energy flow is calculated in ecology in terms of $\text{cal} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$. Energy flow can only be calculated in palaeoecology, however, for an organism's life span ($\text{cal} \cdot \text{lifetime}^{-1}$) because the data base consists of dead shells, which obviously have completed their life spans. Each of these energy uses—growth, respiration, and reproduction—varies with the size and age of the organism. Therefore, in order to estimate the amount of energy used in an organism's lifetime, both an individual's age and size must be known.

Estimation of age

An estimate of age can be obtained using the general logarithmic relationship between size and age (Levinton and Bambach 1970).

$$S = s_T \log_{10}(T + 1) \quad (2)$$

where S is a linear measurement of size; s_T , a species-specific constant, and T , the elapsed time since birth, or age at death. Ideally age would be determined more specifically for each individual by some means such as daily or annual shell banding (Tevesz 1972; Jones 1980), but this may not be practical



TEXT-FIG. 6. Regression lines of gastropod biomass versus log of operational biovolume. See text-figs. 2 and 5 for format. A (\blacktriangledown): *Potamopyrgus jenkinsi*, Simpson (1978), 6, average of all L-organic carbon regressions Table 1 and organic carbon-DW regressions Table 2, assumed $W/L = 0.54$ from pl. 10.3, McMillan (1968), DW. B ($*$): *Anachis avara*, our data, 11, W/L measured, AFDW. C (\blacksquare): *Littorina ziczac*, our data, 13, W/L measured, AFDW. D (\star): *L. planaxis*, North (1954), 5, from fig. 7, assumed $W/L = 0.74$ from fig. 553, DW. E (\bullet): *Tegula funebris*, Paine (1971), 8, from regression equation for total of 1965 and 1966 Table 2, assumed $W/L = 0.87$ from fig. 385, DW. F ($*$): *Nucella lapillus*, Hughes (1972), 7, from average of monthly regressions Table 1, assumed $W/L = 0.56$ from fig. 1903, DW. G (\square): *Nassarius vibex*, our data, 5, W/L measured, AFDW. H (\odot): *Polinices duplicatus*, our data, 21, W/L measured, AFDW. I (∇): *Thais haemastoma*, our data, 27, W/L measured, AFDW. J (\star): *L. littorea*, Grahame (1973a), 8, from DW-shell height regression, assumed $W/L = 0.76$ from fig. 549, DW.



TEXT-FIG. 7. Regression lines for gastropod biomass versus log of operational biovolume. Regression lines are combined from text-figs. 5 and 6.

for many species. In the equations to follow, however, equation 2 can be replaced by any other equation relating size to age should a more accurate one be known.

To determine T from this equation, s_T must be known for each species in question. This requires at least one known age-size relation. In some cases this might be obtained by actually determining the age at death for a few individuals, by counting growth lines, for example. Barring this capability, an alternative approach would be to relate maximum age and maximum size because maximum size data are commonly available for fossil species. This approach is used here. Maximum size in any fossil assemblage, however, is not necessarily equivalent to the maximum size of the species because poor survival may prevent individuals of a species from growing to their maximum size in many areas. Thus, a literature search is essential to verify true maximum size for the species. Maximum age data for modern analogues of many palaeo-species can be found in Comfort (1957), Peterson (1979), and other works, some of which are summarized in Table 1. Within-taxon variability in maximum age may be considerable. Also, sexual dimorphism and environmentally determined differences in growth rate may contribute additional uncertainty (Wilbur and Owen 1964; Fotheringham 1971; Franz 1971). Consequently, for calculations of energy flow of taxa in the Stone City Formation, we use a range of ages at maximum size that available data suggest will bracket the true maximum age. If age-size information is not available, percentage maximum age (using maximum size from the literature as 100% maximum age) might be used (Stanton *et al.* 1981). Use of this method is discussed later.

Energy expended in growth

The amount of energy expended in growth during the animal's lifetime (P_{glt}) can be calculated by converting biomass at death to its energy equivalent in calories. Conversion factors are reviewed by Cummins and Wuycheck (1971) (see Tyler 1973 for additional values). The conversion factors used for subsequent calculations of energy expended in growth are:

$$\begin{aligned} \text{Gastropods: } & 5675 \text{ cal} \cdot \text{g AFDW}^{-1} \\ \text{Bivalves: } & 4452 \text{ cal} \cdot \text{g AFDW}^{-1} \end{aligned}$$

Energy expended in respiration

Daily respiration. Energy expended in respiration depends upon the biomass of the individual and of the temperature at which it lives (Prosser 1973). These relations are expressed by the regression lines in text-fig. 8 for species of gastropods and bivalves. Each individual line is for a particular species, observed at a particular temperature. For simplicity, we have divided the data into three temperature ranges, 10 ± 5 , 20 ± 5 , and 30 ± 5 °C, denoted by the three line weights. Respiration is usually measured in terms of oxygen consumption. The caloric conversion used in the literature ranges from 4.75 to 5.0 cal·ml⁻¹ O₂, depending on the author. The mean of values from Hughes (1971a), Thompson and Bayne (1974), and Bernard (1974), 4.86 cal·ml⁻¹, is used to generate the data in text-fig. 8. The resulting equations relating respiration to biomass are in the form:

$$\log_{10} R = m_R \log_{10} B + b_R \quad (3)$$

where B is biomass in grams and R is respiration in calories per day. Regression equations for the data in text-fig. 8 for each temperature range are:

$$10 \pm 5 \text{ °C: } \log R = (0.8573 \pm 0.0101) \log B + (1.4984 \pm 0.0179) \quad r = 0.89 \quad (3a)$$

$$20 \pm 5 \text{ °C: } \log R = (0.9142 \pm 0.0042) \log B + (1.7587 \pm 0.0133) \quad r = 0.95 \quad (3b)$$

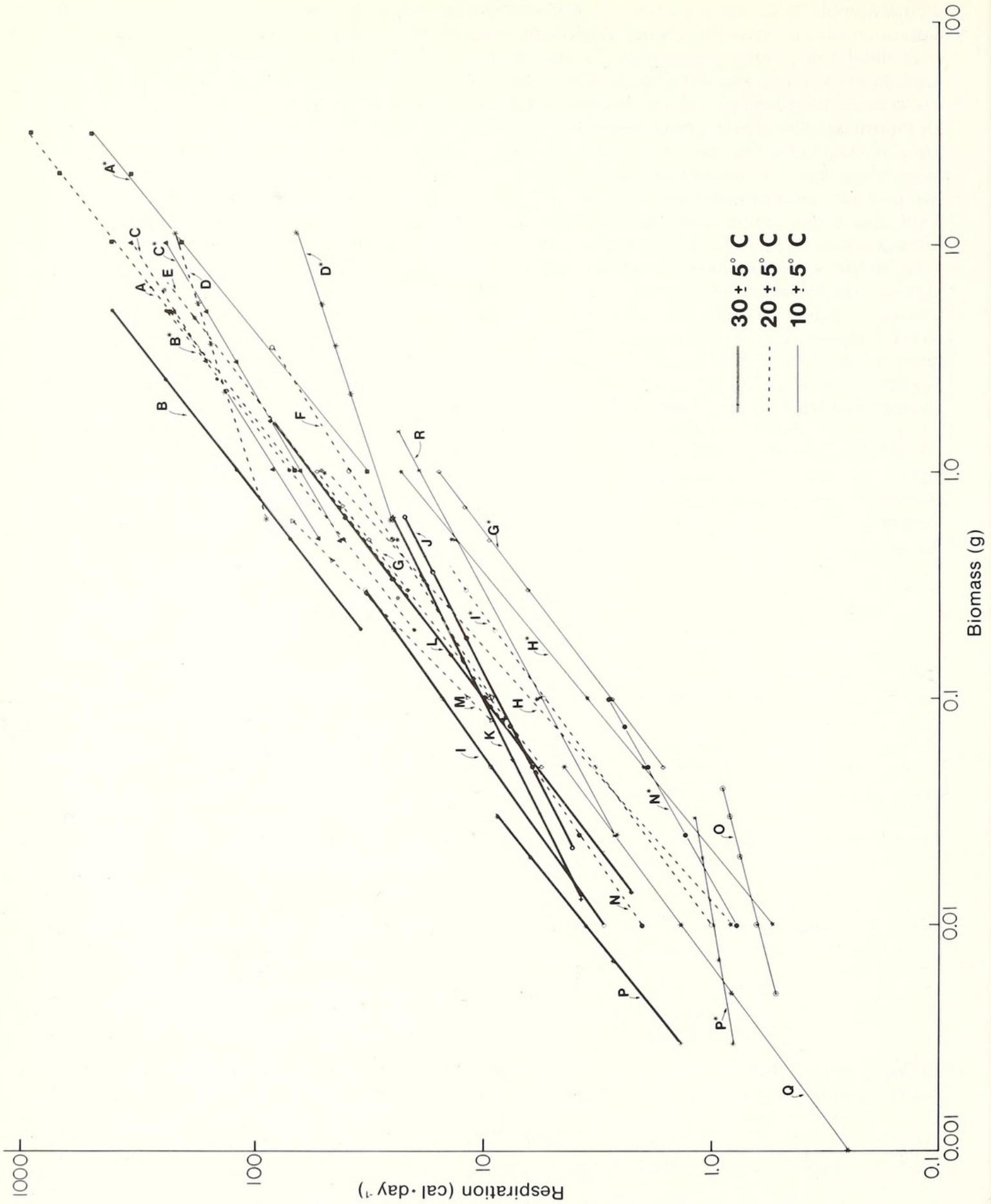
$$30 \pm 5 \text{ °C: } \log R = (0.7736 \pm 0.0073) \log B + (1.8943 \pm 0.0169) \quad r = 0.95 \quad (3c)$$

The data for 20 and 30 °C overlap to a considerable extent, whereas the data for 10 °C are clearly below the other two (text-fig. 8). Combining the 20 and 30 °C data sets yields:

$$\log R = (0.8375 \pm 0.0029) \log B + (1.8152 \pm 0.0087) \quad r = 0.94 \quad (3d)$$

If all three data sets are combined, the regression is:

$$\log R = (1.0054 \pm 0.0072) \log B + (1.7421 \pm 0.0155) \quad r = 0.82 \quad (3e)$$



Because the data used are selected subsets of considerably larger data sets, confidence limits and correlation coefficients for the regressions are conditional. Differences in the regression lines for individual species might result from the following: (1) The temperature effect, as discussed above. (2) Salinity (Lange *et al.* 1972), food concentration (Thompson and Bayne 1974), oxygen concentration (Staalnd 1972), and seasonal cycles. (3) Differences in the amount of activity of the organism during the time respiration was measured (e.g. quiescent vs. active animals—Newell and Pye 1971) and (4) differences in the temperatures of acclimation, acclimatization, and experimentation. The range of values about the 10, 20, and 30 °C regression lines is small, indicating that only temperature is a major source of variability. Furthermore, combining the 20 and 30 °C data does not affect the resulting regression substantially—however, adding the 10 °C data produces a marked change. Thus, it appears reasonable in palaeoecology to use the 10 °C equation for cold-water faunas and the combined 20 and 30 °C equation for temperate-tropical faunas.

These equations can be used to estimate respiration rates for most molluscan species encountered in palaeo-communities. The accuracy of this procedure can be evaluated by comparing calculated values with measured values of respiration (Table 2) for species not included in any of the data sets used for the previous equations. The calculated values of biomass for four such species (Table 2) are within a factor of 1.4 of the measured values. The combined 20 °C + 30 °C respiration equation more accurately predicts respiration at 20 °C than does the 20 °C equation in most cases, whereas the 10 °C + 20 °C + 30 °C equation is clearly inferior. Respiration rates predicted from the 20 °C + 30 °C, or the 10 °C equation are all within a factor of 1.7 of the actual values. Thus, respiration rate can be effectively predicted from shell dimensions using equations 1 and 3.

Lifetime respiration. In palaeoecology, the total energy expended in respiration during the organism's lifetime (R_{lt}) must be determined. This is daily respiration rate (R of equation 3) integrated over the organism's life span, taking into account the change in respiration rate with size as the animal grows.

Age and biovolume are related by the equation.

$$V = S^3 = [s_T \log(T + 1)]^3 \quad (4)$$

TEXT-FIG. 8 (*opposite*). Regression lines of respiration rate (in calories per day) versus biomass (in grams) on a log-log scale. Biomass data have been selected to cover the range of biomass used in the referenced data set. The following explanations are ordered as follows: species, source, temperature(s) plotted (lower temperature indicated by *), comments. A (■), A* (■): *Patinopecten yessoensis*, Fuji and Hashizume (1974), 22 °C, 9 °C, data from fig. 2. B (●), B* (●): *Brachidontes demissus plicatulus*, Read (1962), 28.2 °C, 22 °C, from regression equations Table 4. C (▼), C* (▼): *Mytilus edulis*, Read (1962), 19.8 °C, 12 °C, from regression equations Table 2. D (*), D* (*): *Mercenaria mercenaria*, Hibbert (1977b), 20 °C, 10 °C, from regression equation relating respiration to length and temperature and the length biomass regression of Hibbert (1977a). E (☆): *Polinices duplicatus*, Huebner and Edwards, D. C. (1981), 22.7 °C, data from regression of shell-less wet wt.-respiration and diameter-wet wt. Table 1 using AFDW-diameter regression from Edwards and Huebner (1977). F (○): *Mytilus perna*, Bayne (1967), 20 °C, from regression of respiration-DW. G (◇), G* (◇): *Scrobicularia plana*, Hughes (1970), 22.5 °C, 9.5 °C, from regression equation. H (★), H* (★): *Tegula funebris*, Paine (1971), 17 °C, 10 °C from fig. 1. I (○), I* (○): *Fissurella barbadensis*, Hughes (1971a), 30.2 °C, 21 °C, from regression equations. J (★): *Nerita versicolor*, Hughes (1971b), 30 °C, from respiration-L and L-DW regressions. K (+): *N. tessellata*, Hughes (1971b), see J. L (◇): *N. peloronta*, Hughes (1971b), see J. M (▽): *Modiolus demissus*, Kuenzler (1961), 20 °C, from fig. 6. N (●), N* (●): *Mya arenaria*, Kennedy and Mihursky (1972), 20 °C, 10 °C, regression for individuals acclimated to experimental temperature Table 2, young only. O (*): *Macoma balthica*, Kennedy and Mihursky (1972), 10 °C, see N Table 5. P (*), P* (*): *Mulinia lateralis*, Kennedy and Mihursky (1972), 30 °C, 10 °C, see N Table 7. Q (★): *Spisula subtruncata*, Møhlenberg and Kiørboe (1981), 11-14 °C, used regression of respiration to wt. for fed animals. R (X): *Chlamys delicatula*, Mackay and Shumway (1980), 10 °C, used DW-VO regression equation.

TABLE 1. Maximum ages for selected bivalves and gastropods reported since Comfort (1957) exclusive of Peterson (1979).

Species	Suggested maximum age	Source	Species	Suggested Maximum age	Source
Gastropoda			Bivalvia		
Haliotidae			Nuculanidae		
<i>Haliotis iris</i>	> 10 yr.	Poore (1972)	<i>Nuculana minuta</i>	7-8 yr.	Ansell, <i>et al</i> (1978)
Patellidae			<i>Nuculana pernula</i>	5 yr.	Ansell, <i>et al</i> (1978)
<i>Acmaea digitalis</i>	8 yr.	Zaika (1970)	Arcidae		
<i>Patella aspera</i>	12 yr.	Thompson, G. B. (1979)	<i>Senilia senilis</i>	9 yr.	Okera (1976)
Trochidae			Mytilidae		
<i>Margarita helicina</i>	1-67 yr.	Zaika (1970)	<i>Crenomytilus grayanus</i>	88 yr.	Selin (1980)
<i>Tegula funebris</i>	24-30 yr.	Cockcroft and Forbes (1981)	<i>Mytilus galloprovincialis</i>	12 yr.	Zaika (1970)
Lacunidae			Ostreidae		
<i>Lacuna pallidula</i>	< 1 yr.	Zaika (1970)	<i>Ostrea edulis</i>	20 yr.	Rodhouse (1978)
Littorinidae			Leptonidae		
<i>Littorina saxatilis</i>	1 yr.	Burke and Mann (1974)	<i>Mysella planulata</i>	4 yr.	Franz (1973)
Rissoidae			Cardiidae		
<i>Rissoa parva</i>	0-75 yr.	Wigham (1975)	<i>Cardium edule</i>	11 yr.	Evans and Tallmark (1977)
<i>Rissoa splendida</i>	1 yr.	Zaika (1970)	<i>Cerastoderma edule</i>	14 yr.	Boyden (1972)
Hydrobiidae			<i>Cerastoderma glaucum</i>	7 yr.	Boyden (1972)
<i>Hydrobia neglecta</i>	1-5 yr.	Lassen and Clark (1979)	Mactridae		
<i>Hydrobia ventrosa</i>	1-5 yr.	Lassen and Clark (1979)	<i>Spisula elliptica</i>	1 yr.	Zaika (1970)
<i>Hydrobia ulvae</i>	> 2 yr.	Lassen and Clark (1979)	<i>Spisula solidissima</i>	25 yr.	Jones (1980)
Potamididae			Tellinidae		
<i>Cerithidea decollata</i>	3-9 yr.	Cockcroft and Forbes (1981)	<i>Macoma balthica</i>	9 yr.	Evans and Tallmark (1977)
Cerithiidae			<i>Macoma balthica</i>	> 7 yr.	Warwick and Price (1975)
<i>Cerithium atratum</i>	1 yr.	Houbrick (1974)	<i>Macoma litoralis</i>	> 5 yr.	McLachlan (1974)
<i>Cerithium eburneum</i>	1 yr.	Houbrick (1974)	<i>Tellina martinicensis</i>	2 yr.	Penzias (1969)
<i>Cerithium lutosum</i>	1 yr.	Houbrick (1974)	<i>Tellina tenuis</i>	> 7 yr.	Trevallion (1971)
<i>Cerithium muscarum</i>	1 yr.	Houbrick (1974)	Semelidae		
<i>Diaostoma varium</i>	1-5 yr.	Marsh (1976)	<i>Abra ovata</i>	3-4 yr.	Zaika (1970)
Naticidae			Solecurtidae		
<i>Polinices duplicatus</i>	4-7 yr.	Hunter and Grant (1966)	<i>Tagelus divisus</i>	2-5 yr.	Fraser (1967)
Muricidae			Arcticidae		
<i>Ocenebra poulsoni</i>	> 9 yr.	Fotheringham (1971)	<i>Arctica islandica</i>	~ 70 yr.	Jones (1980)
<i>Shaskyus festvus</i>	> 10 yr.	Fotheringham (1971)	Veneridae		
<i>Urosalpinx cinerea</i>	> 4 yr.	Franz (1971)	<i>Anomalocardia squamosa</i>	2-5 yr.	Morton (1978)
Buccinidae			<i>Dosinia hepatica</i>	6 yr.	McLachlan (1974)
<i>Neptunea antiqua</i>	> 10 yr.	Pearce and Thorson (1967)	<i>Mercenaria mercenaria</i>	25-40 yr.	Loesch and Haven (1973)
Nassariidae			<i>Tapes japonica</i>	~ 3 yr.	Ohba (1959)
<i>Nassarius reticulatus</i>	> 15 yr.	Tallmark (1980)	Myidae		
Retusidae			<i>Mya arenaria</i>	> 17 yr.	Warwick and Price (1975)
<i>Retusa obtusa</i>	1 yr.	Smith (1967)	<i>Mya arenaria</i>	12 yr.	Evans and Tallmark (1977)

TABLE 2. Comparison of calculated with measured biomass and respiration values for four bivalves not included in either the biomass or respiration regressions. Predicted values use length as the input datum.

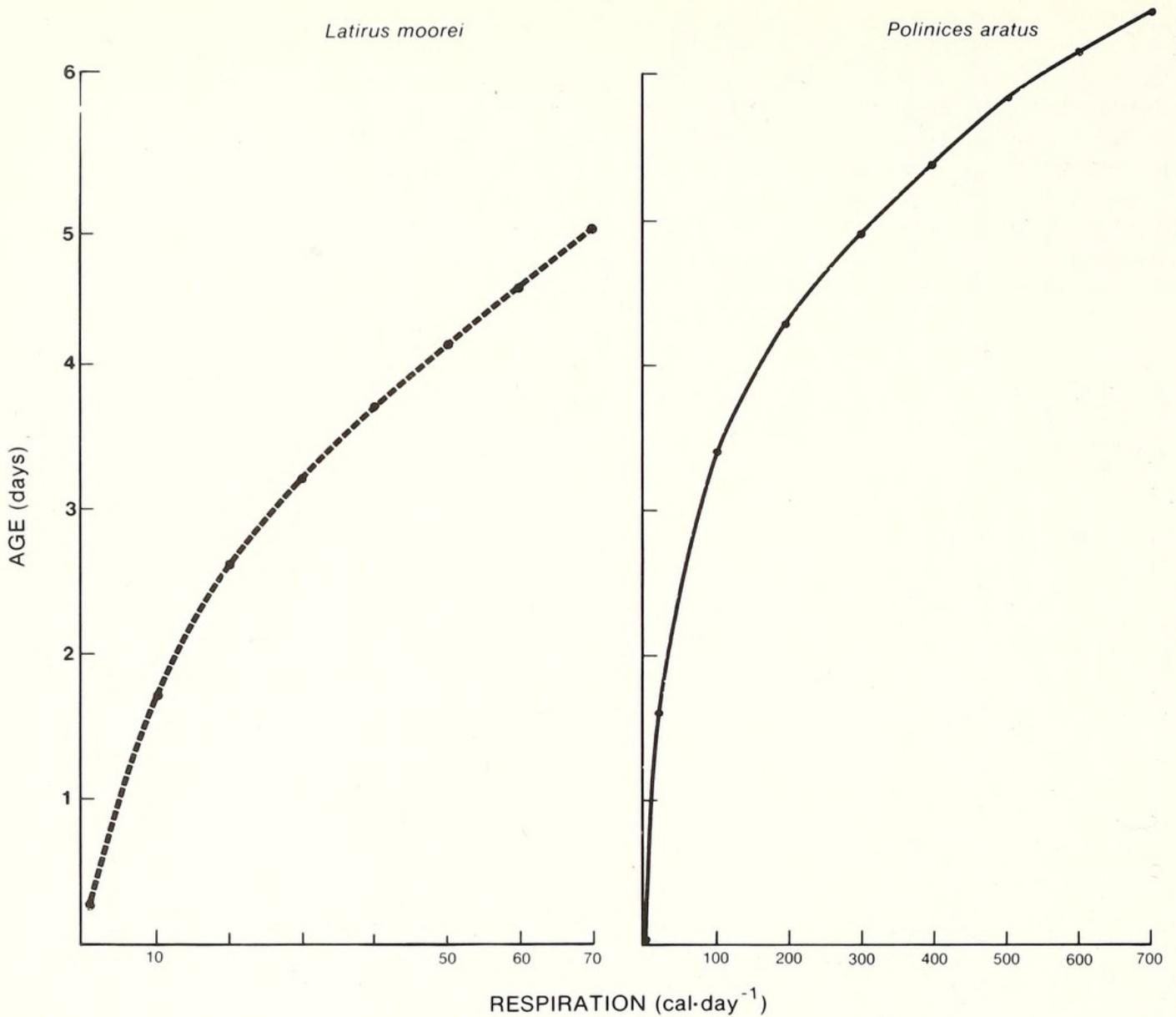
Species	Measured values			Calculated values			Source for measured data, and comments
	Length (mm)	Biomass (g)	Temperature (°C) at which respiration measured	Respiration (cal/day)	Biomass (g)	Respiration (cal/day) At measured temperature equation	
<i>Donax serra</i>	21.8	0.1	20	14.93	0.089	6.28	Dye (1979) Measured values for respiration and length from author's biomass regression equations Same as for <i>D. serra</i>
			10	7.00		3.96	
<i>Donax sordidus</i>	24.8	0.1	20	15.40	0.129	8.82	Dye (1979)
			10	6.42		5.44	
<i>Aulacomya ater</i>	25.0	0.094	12.5	3.65	0.132	5.55	Griffiths, C. L. Measured values from length regressions assuming predicted <i>R</i> is in $\mu\text{l O}_2\text{hr}^{-1}$ (as in Fig. 4) rather than $\text{ml}\cdot\text{hr}^{-1}$ as stated. Predicted values of <i>R</i> at measured temperature use 10 °C regression equation
<i>Choromytilus meridionalis</i>	25.0	0.110	18	10.41	0.132	9.01	Griffiths, R. J. (1981) Measured values from (1) regression equation Table 1 for B.L.W.S. at 12 °C + 18 °C; and (2) Avg. of DW-length regressions in Griffiths, R. J. and Buffenstein (1981). Predicted values of <i>R</i> at measured temperature were calculated using 20 °C and 10 °C regression equations
			12	7.39		5.55	

TABLE 1. Maximum ages for selected bivalves and gastropods reported since Comfort (1957) exclusive of Peterson (1979).

Species	Suggested maximum age	Source	Species	Suggested Maximum age	Source
Gastropoda			Bivalvia		
Haliotidae			Nuculanidae		
<i>Haliotis iris</i>	> 10 yr.	Poore (1972)	<i>Nuculana minuta</i>	7-8 yr.	Ansell, <i>et al</i> (1978)
Patellidae			<i>Nuculana pernula</i>	5 yr.	Ansell, <i>et al</i> (1978)
<i>Amaea digitalis</i>	8 yr.	Zaika (1970)	Arcidae		
<i>Patella aspera</i>	12 yr.	Thompson, G. B. (1979)	<i>Senilia senilis</i>	9 yr.	Okeru (1976)
Trochidae			Mytilidae		
<i>Margarita helicina</i>	1-67 yr.	Zaika (1970)	<i>Crenomytilus grayanus</i>	88 yr.	Selin (1980)
<i>Tegula funebris</i>	24-30 yr.	Cockcroft and Forbes (1981)	<i>Mytilus galloprovincialis</i>	12 yr.	Zaika (1970)
Lacunidae			Ostreidae		
<i>Lacuna pallidula</i>	< 1 yr.	Zaika (1970)	<i>Ostrea edulis</i>	20 yr.	Rodhouse (1978)
Littorinidae			Leptonidae		
<i>Littorina saxatilis</i>	1 yr.	Burke and Mann (1974)	<i>Mysella planulata</i>	4 yr.	Franz (1973)
Rissoidae			Cardiidae		
<i>Rissoa parva</i>	0-75 yr.	Wigham (1975)	<i>Cardium edule</i>	11 yr.	Evans and Tallmark (1977)
<i>Rissoa splendida</i>	1 yr.	Zaika (1970)	<i>Cerastoderma edule</i>	14 yr.	Boyden (1972)
Hydrobiidae			<i>Cerastoderma glaucum</i>	7 yr.	Boyden (1972)
<i>Hydrobia neglecta</i>	1-5 yr.	Lassen and Clark (1979)	Maclridae		
<i>Hydrobia ventrosa</i>	1-5 yr.	Lassen and Clark (1979)	<i>Spisula elliptica</i>	1 yr.	Zaika (1970)
<i>Hydrobia ulvae</i>	> 2 yr.	Lassen and Clark (1979)	<i>Spisula solidissima</i>	25 yr.	Jones (1980)
Potamididae			Tellinidae		
<i>Cerithidea decollata</i>	3-9 yr.	Cockcroft and Forbes (1981)	<i>Macoma balthica</i>	9 yr.	Evans and Tallmark (1977)
Cerithiidae			<i>Macoma balthica</i>	> 7 yr.	Warwick and Price (1975)
<i>Cerithium atratum</i>	1 yr.	Houbrick (1974)	<i>Macoma litoralis</i>	> 5 yr.	McLachlan (1974)
<i>Cerithium eburneum</i>	1 yr.	Houbrick (1974)	<i>Tellina martinicensis</i>	2 yr.	Penzias (1969)
<i>Cerithium lutosum</i>	1 yr.	Houbrick (1974)	<i>Tellina tenuis</i>	> 7 yr.	Trevallion (1971)
<i>Cerithium muscarum</i>	1 yr.	Houbrick (1974)	Semelidae		
<i>Diastoma varium</i>	1-5 yr.	Marsh (1976)	<i>Abra ovata</i>	3-4 yr.	Zaika (1970)
Naticidae			Solecurtidae		
<i>Polinices duplicatus</i>	4-7 yr.	Hunter and Grant (1966)	<i>Tagelus divisus</i>	2-5 yr.	Fraser (1967)
Muricidae			Arcticidae		
<i>Ocenebra poulsoni</i>	> 9 yr.	Fotheringham (1971)	<i>Arctica islandica</i>	~ 70 yr.	Jones (1980)
<i>Shaskyus festivus</i>	> 10 yr.	Fotheringham (1971)	Veneridae		
<i>Urosalpinx cinerea</i>	> 4 yr.	Franz (1971)	<i>Anomalocardia squamosa</i>	2-5 yr.	Morton (1978)
Buccinidae			<i>Dosinia hepatica</i>	6 yr.	McLachlan (1974)
<i>Neptunea antiqua</i>	> 10 yr.	Pearce and Thorson (1967)	<i>Mercenaria mercenaria</i>	25-40 yr.	Loesch and Haven (1973)
Nassariidae			<i>Tapes japonica</i>	~ 3 yr.	Ohba (1959)
<i>Nassarius reticulatus</i>	> 15 yr.	Tallmark (1980)	Myidae		
Retusidae			<i>Mya arenaria</i>	> 17 yr.	Warwick and Price (1975)
<i>Retusa obtusa</i>	1 yr.	Smith (1967)	<i>Mya arenaria</i>	12 yr.	Evans and Tallmark (1977)

TABLE 2. Comparison of calculated with measured biomass and respiration values for four bivalves not included in either the biomass or respiration regressions. Predicted values use length as the input datum.

Species	Measured values				Calculated values				Source for measured data, and comments	
	Length (mm)	Biomass (g)	Temperature (°C) at which respiration measured	Respiration (cal/day)	Biomass (g)	Respiration (cal/day)				
						At measured temperature	20° + 30° equation	10° + 20° + 30° equation		
<i>Donax serra</i>	21-8	0-1	20 10	14-93 7-00	0-089	6-28 3-96	8-62	4-85	Dye (1979)	Measured values for respiration and length from author's biomass regression equations. Same as for <i>D. serra</i> .
<i>Donax sordidus</i>	24-8	0-1	20 10	15-40 6-42	0-129	8-82 5-44	11-76	7-05	Dye (1979)	
<i>Aulacomya ater</i>	25-0	0-094	12-5	3-65	0-132	5-55		7-21	Griffiths, C. L. and King (1979b)	Measured values from length regressions assuming predicted <i>R</i> is in $\mu\text{l O}_2\text{hr}^{-1}$ (as in Fig. 4) rather than $\text{ml}\cdot\text{hr}^{-1}$ as stated. Predicted values of <i>R</i> at measured temperature use 10 °C regression equation.
<i>Choromytilus meridionalis</i>	25-0	0-110	18 12	10-41 7-39	0-132	9-01 5-55	11-99	7-21	Griffiths, R. J. (1981)	Measured values from (1) regression equation Table 1 for B.L.W.S. at 12 °C + 18 °C; and (2) Avg. of DW-length regressions in Griffiths, R. J. and Buffenstein (1981). Predicted values of <i>R</i> at measured temperature were calculated using 20 °C and 10 °C regression equations.



TEXT-FIG. 9. The change in respiration rate (in $\text{cal} \cdot \text{day}^{-1}$ estimated using equation 6), with age (in days estimated using equation 2 and Table 5), for two species from Stone City.

Combining equation 4 with equations 1 and 3 yields:

$$\log R = m_R(m_B \log\{[s_T \log(T+1)]^3\} + b_B) + b_R \quad (5)$$

Taking the antilog and rearranging the constants yields:

$$R = ((s_T)^{3m_R m_B})(10^{m_R b_B + b_R})([\log(T+1)]^{3m_R m_B}) \quad (6)$$

Equation 6 relates respiration to age at any specified age [in days because R is measured in $\text{cal} \cdot \text{day}^{-1}$ (equation 3)]. The relationship of respiration to age as predicted by this equation is shown in text-fig. 9. Respiration increases with age as the individual grows, but at a decreasing rate because growth rate decreases with age.

To calculate the total respiration during an organism's life span, equation 6 is integrated from birth, t_0 , to death, t_n :

$$R_{It} = \int_{t_0}^{t_n} \{(s_T)^{3m_R m_B}(10^{m_R b_B + b_R})([\log(T+1)]^{3m_R m_B})\} dT \quad (7)$$

Equation 7 cannot be solved directly unless $3m_R m_B$ is an integer. When using equations 1a, b and 3a-e, it is not. Therefore we calculated R_{lt} by summing consecutive values of R from t_0 to t_n , using a computer and one-, ten-, or thirty-day time-steps depending on the age of the individual. The estimation of R_{lt} depends on the accuracy with which age can be estimated from size and will be less accurate for older than for younger individuals because age increments are represented by smaller and smaller size increments as growth rate declines with age.

Energy expended in reproduction (P_r)

Energy expended in reproduction can be estimated if the size at maturity and a relationship between P_r and either P_g or R are known. Data on energy used for reproduction are less numerous and probably less accurate than data on energy used for growth or for respiration. Available data for bivalves and gastropods, and their size at maturity as a percentage of maximum size, are presented in Table 3. Maturity is defined as age at initial gonadal development, rather than age at first spawning. Most values for size at maturity are between 40 and 70% of maximum size and average 44 and 51% for bivalves and gastropods respectively. This difference is not significant ($\alpha = 0.5$, Student's t -test).

Energy expended in reproduction, as a value equivalent to a percentage of the energy expended in respiration, ranges from 3 to 40% for bivalves, but most values are between 10 and 30%, averaging 18%. Values range from 2 to 26% for gastropods, with most values below 10%, averaging 6.8%. The difference between bivalves and gastropods is significant ($0.05 < P < 0.10$; Student's t -test). The data, however, are insufficient to determine whether this difference is real or merely a result of a small data base. In the following calculations the average values for the two classes are used.

The energy expended by an animal in reproduction in its lifetime (P_{rlt}) is equivalent to a percentage of the energy expended in respiration during that part of its life subsequent to attaining sexual maturity. Thus,

$$P_r = 18 \text{ or } 6.8 \% \text{ of } \left[\int_{t_0}^{t_n} R \, dR - \int_{t_0}^{t_m} R \, dR \right] \quad (8)$$

where t_0 is age at birth; t_n age at death; t_m age at maturity. The first integral corresponds to R_{lt} from equation 7.

Caveats associated with the data in Table 3 include the following: (1) differences in food supply affect fecundity (Spight and Emlen 1976). (2) Taxa which produce more than two clutches per year are not included. Equation 8 may not apply to such species (Borkowski 1971). (3) We assume that both males and females utilize energy at the same rate, although this is not always the case (Grahame 1973a). (4) Iteroparous species may differ from semelparous species (Browne and Russell-Hunter 1978); most species in Table 3 reproduce in more than one year. (5) The transition from immaturity to maturity in long-lived species may be gradual over a period of years, during which time reproductive output gradually increases to adult levels. This transition period is not included in equation 8, which treats reproduction as an all or nothing phenomenon beginning at 44 or 51% maximum size. (6) Many values in Table 3 are means of populations including non-reproducing juveniles as well as reproducing adults. This is not likely to be a significant factor in most cases because adult respiration is significantly greater per individual than juvenile respiration, and the data are presented as a percentage of respiration—however, the data of Paine (1971) and Hibbert (1977b) illustrate the potential error introduced from this source.

Estimation of energy assimilated (A)

The total assimilated energy during an individual's lifetime (A_{lt}) is:

$$A_{lt} = P_{glt} + R_{lt} + P_{rlt} \quad (9)$$

Estimation of ingestion (I)

Ingestion during an organism's lifetime (I_{lt}) can be estimated using an assimilation efficiency (A/I):

$$I_{lt} = A_{lt} \cdot (A/I)^{-1} \quad (10)$$

TABLE 3. The amount of energy expended per year in reproduction as a percentage of that expended in respiration (i.e. 40% indicates that the energy expended in reproduction was equivalent to 40% of that expended for respiration during the year studied) and the size at maturity as a percentage of maximum size in molluscs.

Species	Size at maturity	Energy expended in reproduction	Comments	Source
Bivalvia				
<i>Aulacomya ater</i>	18%	—	—	Griffiths, C. L. and King (1979a)
<i>Choromytilus meridionalis</i>	54%	0, 40, 37, 36, 35%. Avg. yrs. 2-5 = 37%	From Table 2. Energy expended is for age classes 1, 2, 3, 4, 5 yr. respectively	Griffiths, R. J. (1981)
<i>Crassostrea virginica</i>	40%	12%	Average of monthly surveys, Table 2, for a population with > 50% juveniles	Dame (1976)
<i>Mercenaria mercenaria</i>	43%	0, 0, 25, 32, 28, 28, 26, 29%. Avg. of 8 = 21%; of last 6 = 28%	Energy expended is for age classes (from left to right, top to bottom) 1, 2, 3, 4, 5, 6, 7, 8 yr.	Hibbert (1977b)
<i>Modiolus demissus</i>	—	7.8%	Population mean with most biomass as adults although ~ 25% of the individuals were juveniles	Kuenzler (1961)
<i>Mytilus californianus</i>	42%	7, 7, 6%	Energy expended for age classes 1, 2, 3 yr. respectively	Fox and Coe (1943)
<i>Ostrea edulis</i>	—	24, 27, 35, 35%. Avg. = 30%	Energy expended for age classes 5, 10, 15, 20 yr respectively	Rodhouse (1978)
<i>Patinopecten yessoensis</i>	—	3, 10, 15%. Avg. of 3 = 9%; of last 2 = 13%	Energy expended for age classes 1, 2, 3 yr. respectively	Fuji and Hashizume (1974)
<i>Scrobicularia plana</i>	—	13.4, 7.6%. Avg. = 11%	Population means of two separate populations	Hughes (1970)
<i>Tagelus divisus</i>	37%	—	—	Fraser (1967)
<i>Tellina martinicensis</i>	77%	—	—	Penzias (1969)
<i>Tellina tenuis</i>	—	9.7, 21.8%. Avg. = 15.8%	Population means of one population in consecutive years.	Trevallion (1971)
Bivalve average	44%	18.0%	Using all averaged data excluding yrs. 1 and 2 of Hibbert (1977b) and yr. 1 of Fuji and Hashizume (1974)	
Gastropoda				
<i>Fissurella barbadensis</i>	33%	3.8%	Population mean with most individuals adults	Hughes (1971b)
<i>Littorina littorea</i>	40%	—	—	Grahame (1973a)
<i>Nassarius reticulatus</i>	50%	—	—	Tallmark (1980)
<i>Neptunea antiqua</i>	73%	—	—	Pearce and Thorson (1967)
<i>Nerita peloronta</i>	45%	2.2, 2.9%. Avg. = 2.6%	Population means of two separate populations, left population has more juveniles than right population	Hughes (1971b)
<i>Nerita tessellata</i>	56%	3.9%	Population mean of population with ~ 50% adult individuals	Hughes (1971b)
<i>Nerita versicolor</i>	64%	1.8%	Population mean of population with ~ 50% adult individuals	Hughes (1971b)
<i>Nucella lapillus</i>	57%	33, 18.3%. Avg. = 26%	Population means of two separate populations in which most individuals were adults	Hughes (1972)
<i>Petella aspera</i>	34%	—	—	Thompson (1979)
<i>Tegula funebris</i>	54%	0.2, 2.9%	Population means of two separate populations: left with 93% of individuals juveniles; right with 17% juveniles	Paine (1971)
<i>Thais emarginata</i>	63%	—	—	Spight and Emlen (1976)
<i>Thais lamellosa</i>	40%	—	—	Spight and Emlen (1976)
Gastropod average	51%	6.8%	Using all averaged data but excluding 0.2% of Paine (1971)	

Assimilation efficiencies that have been measured for living molluscs are presented in Table 4; they are nearly equal for bivalves and gastropods, averaging 0.53 and 0.54 respectively. The data do not support Welch's (1968) suggestion that carnivores have a higher assimilation efficiency than herbivores-detritivores although information on carnivorous molluscs is scarce. Caveats concerning the data in Table 4 include the following. (1) Assimilation efficiency varies with food concentration and food quality (Thompson and Bayne 1974; Kofoed 1975). (2) Some values have been determined

TABLE 4. Assimilation efficiencies for bivalves and gastropods.

Species	Assimilation efficiency	Comments	Source
Bivalvia			
<i>Choromytilus meridionalis</i>	0.18, 0.15, 0.16, 0.16, 0.16. Avg. = 0.16	From Table 2, for age classes 1, 2, 3, 4, 5 yr, respectively	Griffiths, R. J. (1981)
<i>Mercenaria mercenaria</i>	0.39	Population mean	Hibbert (1977b)
<i>Mytilus californianus</i>	0.8, 0.77, 0.78. Avg. = 0.78	For age classes 1, 2, 3 yr, respectively	Fox and Coe (1943)
<i>Mytilus californianus</i>	0.59	Table 5	Elvin and Gonor (1979)
<i>Mytilus edulis</i>	0.39	Value at peak number of calories assimilated—values varied from 0.20 to 0.90	Thompson, R. J. and Bayne (1974)
<i>Patinopecten yessoensis</i>	0.79, 0.65, 0.68. Avg. = 0.71	For age classes 1, 2, 3 yr, respectively	Fuji and Hashizume (1974)
<i>Scrobicularia plana</i>	0.61, 0.60. Avg. = 0.61	Population means	Hughes (1970)
<i>Spisula subtruncata</i>	0.60	Average of Table 4	Møhlenberg and Kjørboe (1981)
All bivalves	0.60		Edwards, R. R. C. (1973)
Average bivalves	0.53		
Gastropoda			
<i>Fissurella barbadensis</i>	0.34	Population mean	Hughes (1971a)
<i>Hydrobia ventrosa</i>	0.53	Average value from Table 1	Kofoed (1975)
<i>Littorina irrorata</i>	0.45		Odum and Smalley (1959)
<i>Littorina littorea</i>	0.86	Mean of values for cal. (%), Table 2	Grahame (1973b)
<i>Nerita tessellata</i>	0.40	Population mean	Hughes (1971b)
<i>Nerita peloronta</i>	0.41, 0.43. Avg. = 0.42	Population means	Hughes (1971b)
<i>Nerita versicolor</i>	0.39	Population mean	Hughes (1971b)
<i>Polinices duplicatus</i>	0.70, 0.61, 0.74. Avg. = 0.68	For age classes 1-2, 2-3, 3-4 yr, respectively	Huebner and Edwards, D. C. (1981)
<i>Tegula funebris</i>	0.71, 0.70. Avg. = 0.70	Population means	Paine (1971)
All gastropods	0.60		Edwards, R. R. C. (1973)
Average gastropods	0.54		
Average total	0.54		
Other			
All carnivores	0.58		Welch (1968)
All herbivores-detritivores	0.43		Welch (1968)

from measurements in mg(%), others in cal(%). (3) Few values include reproduction; of those that do, some are population means that include juveniles as well as adults. (4) Few data are available for carnivores, deposit feeders, or species with short (≤ 1 yr) life spans. Nevertheless, the available data indicate that ingestion can be predicted within 30% of the measured values using $A/I = 0.54$ for the two classes of molluscs.

Accuracy of estimation

Essentially no data exist in the ecologic literature for the parameters P_{rit} , R_{lt} , A_{lt} , and I_{lt} ; thus a check of the accuracy of these estimations is difficult beyond that considered in Table 2. Alimov (1983), however, from an admittedly sparse data base, suggested that the energy utilized during postlarval development by invertebrates should be about 2.5 times the adult biomass (expressed in energy units). Our calculations of energy flow can be compared to Alimov's (1983) prediction by taking biomass at sexual maturity calculated from equation 1 and Table 3 as adult biomass and using the

TABLE 5. Age, biomass, and energy-flow parameters for populations of four gastropods and one bivalve from the Stone City Formation. P_{rit} is energy expended in growth, lifetime; R_{it} , energy expended in respiration, lifetime; P_{rit} , energy expended in reproduction, lifetime; A_{it} , assimilated energy, lifetime; I_{it} , ingested energy, lifetime. Value for total number of individuals collected is from Stanton and Nelson (1980). Total biomass is the sum of individual biomasses as determined by equations 1a and 1b. Biovolumes for calculating biomass are computed using $V = \frac{1}{3} \cdot \pi \cdot (W/2)^2 \cdot L$ for *Polinices aratus*, *Latirus moorei*, and *Hesperitarris nodocarinatus*, $V = \pi(W/2)^2 \cdot L$ for *Retusa kellogii*, and $V = L^3$ for *Notocorbula texana*. The L and W used are the mean length and width for each size class because the size class intervals were small (Bergh 1974). Maximum sizes are from a compilation of data in Stanton *et al.* (1981), Gardner (1945), Harris (1937), and Palmer, K. V. W. (1937). Estimates for maximum age (T) attained by each species are from Table 1 and Peterson (1979). For the turrid and fasciolariid they are based on the assumption that most neogastropods have ten to fifteen years maximum ages; for the corbulid, that most bivalves of this size and opportunistic life-style (Zarkanelas 1979; Rainer 1982) live less than five years; for the naticid, that its maximum size is less than most *Polinices*, and, therefore, that its maximum age may also be below values in Table 1. The individuals surviving to reproductive age are those that reach 44% of maximum size (bivalves) and 51% of maximum size (gastropods). R_{it} , P_{rit} , A_{it} , and I_{it} , because they are summed over the lifetime of the organism, depend strongly upon the age of each individual. Maximum age in each case, however, is not well known; therefore calculations are made using the probable range limits (T) of maximum age for each species. Energy expended in respiration (R_{it}) is based on the 20 °C + 30 °C regression. Calculation of P_{rit} uses the percentages of 6-8% for gastropods and 18% for bivalves from equation 8. Ingestion (in calories) (I_{it}) is determined from A_{it} using an assimilation efficiency (A/I) of 0.54. Ingestion is converted from calories to grams using the gram/calorie conversions from Cummins and Wuycheck (1971) taking into account the probable diet of each species: *P. aratus*—molluscan prey (Stanton and Nelson 1980) at 5492 cal·g AFDW⁻¹; *L. moorei*—mostly molluscan and annelidan prey (Paine 1963) at 5033 cal·g AFDW⁻¹; *H. nodocarinatus*—annelidan prey (Maes 1983) at 4700 cal·g AFDW⁻¹; *R. kellogii*—microconsumer prey (Smith 1967) at 4958 cal·g AFDW⁻¹; *N. texana*—algal prey at 4469 cal·g AFDW⁻¹.

Species	Total number of individuals collected	Biomass (g)	P_{rit} (cal)	Maximum size (mm)	Maximum age (yr.)	Number surviving to reproductive age	R_{it} (cal)	P_{rit} (cal)	A_{it} (cal)	I_{it} (cal)	I_{it} (g)
<i>Polinices aratus</i>	881	3.12	17 696	8.5 (Stanton <i>et al.</i> 1981)	2.5-5.0	22	{ $T = 2.5$ 13 389 $T = 5.0$ 24 598	735	31 820	58 926	10.73
<i>Latirus moorei</i>	152	1.41	7985	38.0 (Gardner 1945)	10.0-15.0	0	{ $T = 10.0$ 2336 $T = 15.0$ 2809	0	10 321	19 113	3.80
<i>Hesperitarris nodocarinatus</i>	137	0.53	3009	17.0 (Stanton <i>et al.</i> 1981)	10.0-15.0	19	{ $T = 10.0$ 45 299 $T = 15.0$ 67 873	2993	51 301	95 002	20.20
<i>Retusa kellogii</i>	191	0.72	4067	7.5 (Stanton <i>et al.</i> 1981)	1.0-2.0	126	{ $T = 1.0$ 6050 $T = 2.0$ 10 947	320	10 437	19 328	3.90
<i>Notocorbula texana</i>	1140	1.29	5733	11.5 (Gardner 1945)	1.0-5.0	321	{ $T = 1.0$ 4462 $T = 5.0$ 15 862	643	10 838	20 070	4.49
								2538	24 133	44 691	10.00

TABLE 5. Age, biomass, and energy-flow parameters for populations of four gastropods and one bivalve from the Stone City Formation. P_{git} is energy expended in growth, lifetime; R_{it} , energy expended in respiration, lifetime; P_{rit} , energy expended in reproduction, lifetime; A_{it} , assimilated energy, lifetime; I_{it} , ingested energy, lifetime. Value for total number of individuals collected is from Stanton and Nelson (1980). Total biomass is the sum of individual biomasses as determined by equations 1a and 1b. Biovolumes for calculating biomass are computed using $V = \frac{1}{3} \cdot \pi \cdot (W/2)^2 \cdot L$ for *Polinices aratus*, *Latirus moorei*, and *Hesperiturris nodocarinatus*, $V = \pi(W/2)^2L$ for *Retusa kellogii*, and $V = L^3$ for *Notocorbula texana*. The L and W used are the mean length and width for each size class because the size class intervals were small (Bergh 1974). Maximum sizes are from a compilation of data in Stanton *et al.* (1981), Gardner (1945), Harris (1937), and Palmer, K. V. W. (1937). Estimates for maximum age (T) attained by each species are from Table 1 and Peterson (1979). For the turrid and fasciolarid they are based on the assumption that most neogastropods have ten to fifteen years maximum ages; for the corbulid, that most bivalves of this size and opportunistic life-style (Zarkanellas 1979; Rainer 1982) live less than five years; for the naticid, that its maximum size is less than most *Polinices*, and, therefore, that its maximum age may also be below values in Table 1. The individuals surviving to reproductive age are those that reach 44% of maximum size (bivalves) and 51% of maximum size (gastropods). R_{it} , P_{rit} , A_{it} , and I_{it} , because they are summed over the lifetime of the organism, depend strongly upon the age of each individual. Maximum age in each case, however, is not well known; therefore calculations are made using the probable range limits (T) of maximum age for each species. Energy expended in respiration (R_{it}) is based on the $20^\circ\text{C} + 30^\circ\text{C}$ regression. Calculation of P_{rit} uses the percentages of 6.8% for gastropods and 18% for bivalves from equation 8. Ingestion (in calories) (I_{it}) is determined from A_{it} using an assimilation efficiency (A/I) of 0.54. Ingestion is converted from calories to grams using the gram/calorie conversions from Cummins and Wuyccheck (1971) taking into account the probable diet of each species: *P. aratus*—molluscan prey (Stanton and Nelson 1980) at 5492 cal·g AFDW⁻¹; *L. moorei*—mostly molluscan and annelidan prey (Paine 1963) at 5033 cal·g AFDW⁻¹; *H. nodocarinatus*—annelidan prey (Maes 1983) at 4700 cal·g AFDW⁻¹; *R. kellogii*—microconsumer prey (Smith 1967) at 4958 cal·AFDW⁻¹; *N. texana*—algal prey at 4469 cal·g AFDW⁻¹.

Species	Total number of individuals collected	Biomass (g)	P_{git} (cal)	Maximum size (mm)	Maximum age (yr.)	Number surviving to reproductive age	R_{it} (cal)	P_{rit} (cal)	A_{it} (cal)	I_{it} (cal)	I_{it} (g)
<i>Polinices aratus</i>	881	3.12	17 696	8.5 (Stanton <i>et al.</i> 1981)	2.5-5.0	22	13 389 24 598	735 1422	31 820 43 716	58 926 80 956	10.73 14.74
<i>Latirus moorei</i>	152	1.41	7985	38.0 (Gardner 1945)	10.0-15.0	0	2336 2809	0 0	10 321 10 794	19 113 19 989	3.80 3.97
<i>Hesperiturris nodocarinatus</i>	137	0.53	3009	17.0 (Stanton <i>et al.</i> 1981)	10.0-15.0	19	45 299 67 873	2993 4437	51 301 75 319	95 002 139 480	20.20 29.68
<i>Retusa kellogii</i>	191	0.72	4067	7.5 (Stanton <i>et al.</i> 1981)	1.0-2.0	126	6050 10 947	320 605	10 437 15 619	19 328 28 924	3.90 5.83
<i>Notocorbula texana</i>	1140	1.29	5733	11.5 (Gardner 1945)	1.0-5.0	321	4462 15 862	643 2538	10 838 24 133	20 070 44 691	4.49 10.00

value of I_{1t} from birth until sexual maturity as the energy utilized during postlarval development. We have used data for the five species from Stone City discussed subsequently (Table 5) to compute the energy utilized during postlarval development from our equations. The values predicted from these equations are consistently within a factor of 1.8 or less of those predicted using Alimov's (1983) method. The fact that Alimov's (1983) method of calculation and data set are completely different from those used here, but yield similar conclusions, suggests that the accuracy of our estimates is substantially better than the sum of the potential errors of each step would suggest. Although none of the individual calculations is error free, the least accurate estimations are, almost certainly, s_T , the species-specific constant relating size to age, and P_{rlt} , the energy expended in reproduction. Increased accuracy in the latter requires a substantially increased data base, whereas increased accuracy in the determination of s_T requires the use of methods for determining age at any size for fossil molluscs that are substantially better than the maximum age–maximum size relation used here.

APPLICATION OF ENERGY FLOW—THE STONE CITY FORMATION (EOCENE)

Introduction

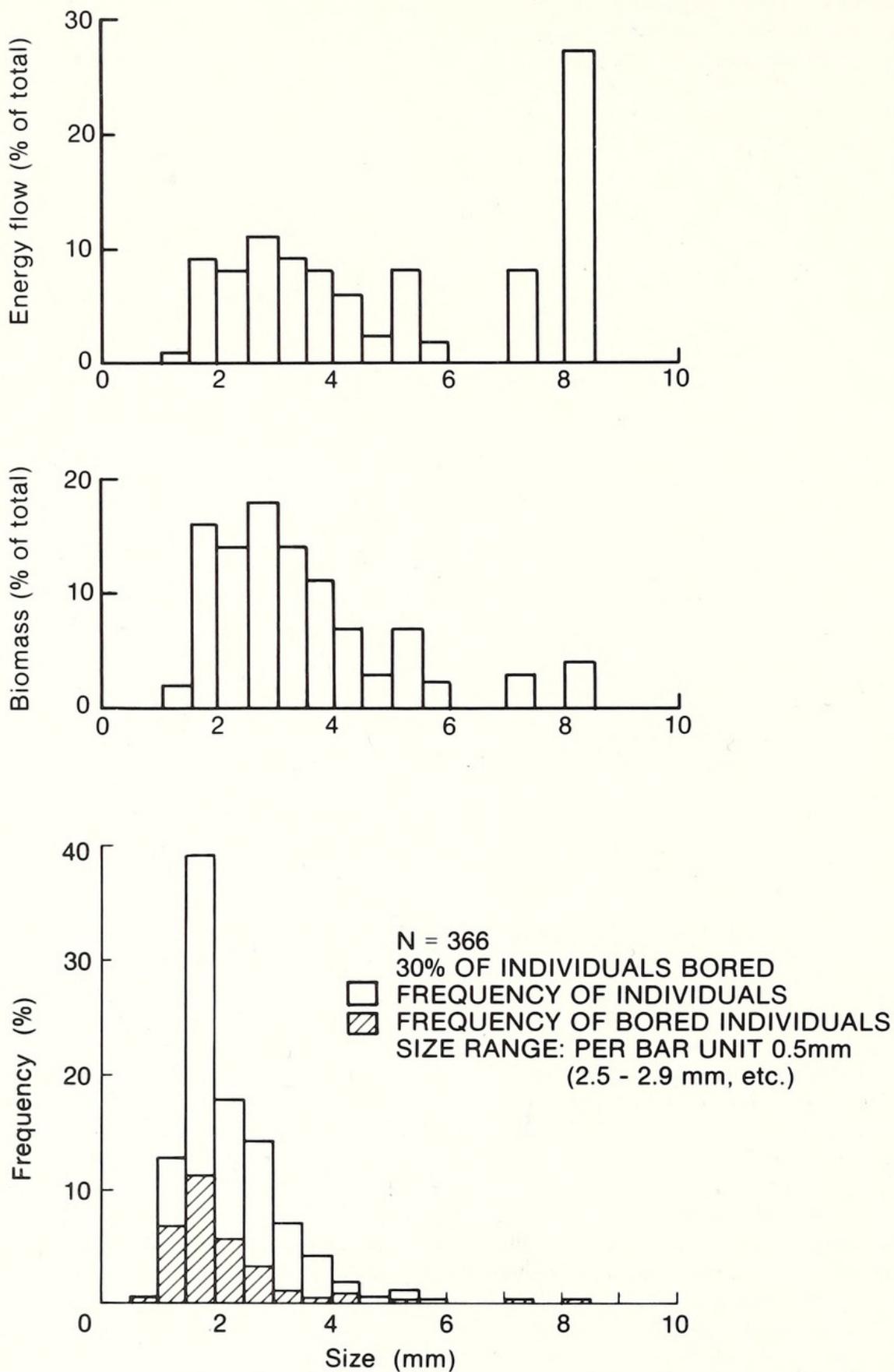
Four carnivorous gastropods and one bivalve from the Stone City Formation were analysed to demonstrate the application of energy flow in describing and interpreting palaeo-communities. The species are (1) *P. aratus*, a naticid gastropod characterized by high abundance, a relatively short life span and a high juvenile mortality rate in this assemblage (text-fig. 10); (2) *Latirus moorei*, a fasciolariid, and *H. nodocarinatus*, a turrid; common large gastropods that attained maximum sizes and, probably, maximum ages considerably greater than that of *P. aratus*, and which have relatively high percentages of larger individuals in the size–frequency distributions (text-figs. 11, 12); (3) *Retusa kellogii*, a small, short-lived, retusid gastropod with a high percentage of relatively large individuals in its size–frequency distribution (text-fig. 13); and (4) *Notocorbula texana*, an abundant corbulid bivalve that was an important food source for *P. aratus* (text-fig. 14). Stanton and Nelson (1980) discussed the location of the outcrop, method of collection and initial data analysis. Previous trophic reconstructions of the Stone City community were based on the numerical abundance of the species present (Stanton and Nelson 1980) and their biovolume (Stanton *et al.* 1981).

Calculations of energy flow

Age, biomass, and energy flow parameters for these five species (Table 5) have been calculated by the procedures described in the first part of this paper. Two sets of calculations are made for each species to bracket the range of probable maximum ages. The size–frequency distributions and the percentages of total biomass and energy flow in each size class for each species are presented in text-figs. 10–14. The relative importance of the species differs greatly, depending on whether numerical abundance, biomass, or energy flow data are used. Ranking of the species by numerical abundance yields: (1) *N. texana*, (2) *P. aratus*, (3) *R. kellogii*, (4) *L. moorei*, and (5) *H. nodocarinatus*. The ranking by biomass is (1) *P. aratus*, (2) *L. moorei*, (3) *N. texana*, (4) *R. kellogii*, (5) *H. nodocarinatus*. Both *P. aratus* and *L. moorei* are less abundant than *N. texana* but have a greater total biomass because biomass per individual is considerably greater. Ranking of the species by the biomass of prey ingested yields: (1) *H. nodocarinatus*, (2) *P. aratus*, (3) *N. texana*, (4) *R. kellogii*, (5) *L. moorei*. *H. nodocarinatus* had the fewest individuals and smallest biomass, but a number of the individuals lived to near maximum age, reproducing, respiring, and consuming prey for ten plus years. These few individuals consumed as much prey as the more numerous, but shorter-lived individuals of *P. aratus*. Individuals of *L. moorei* grew as large as those of *H. nodocarinatus*, but none reached reproductive age. Consequently, energy expended on growth (P_{gl}) was similar for the two species, but respiratory and reproductive energy expenditures by *L. moorei* were well below that of *H. nodocarinatus*. *R. kellogii*, though small and short lived, had a 66% survival to reproductive age. Consequently, because of the greater energy expended in respiration and reproduction, its estimated prey consumption is comparable to that of *L. moorei* in spite of its smaller size. *P. aratus* was abundant, but consisted

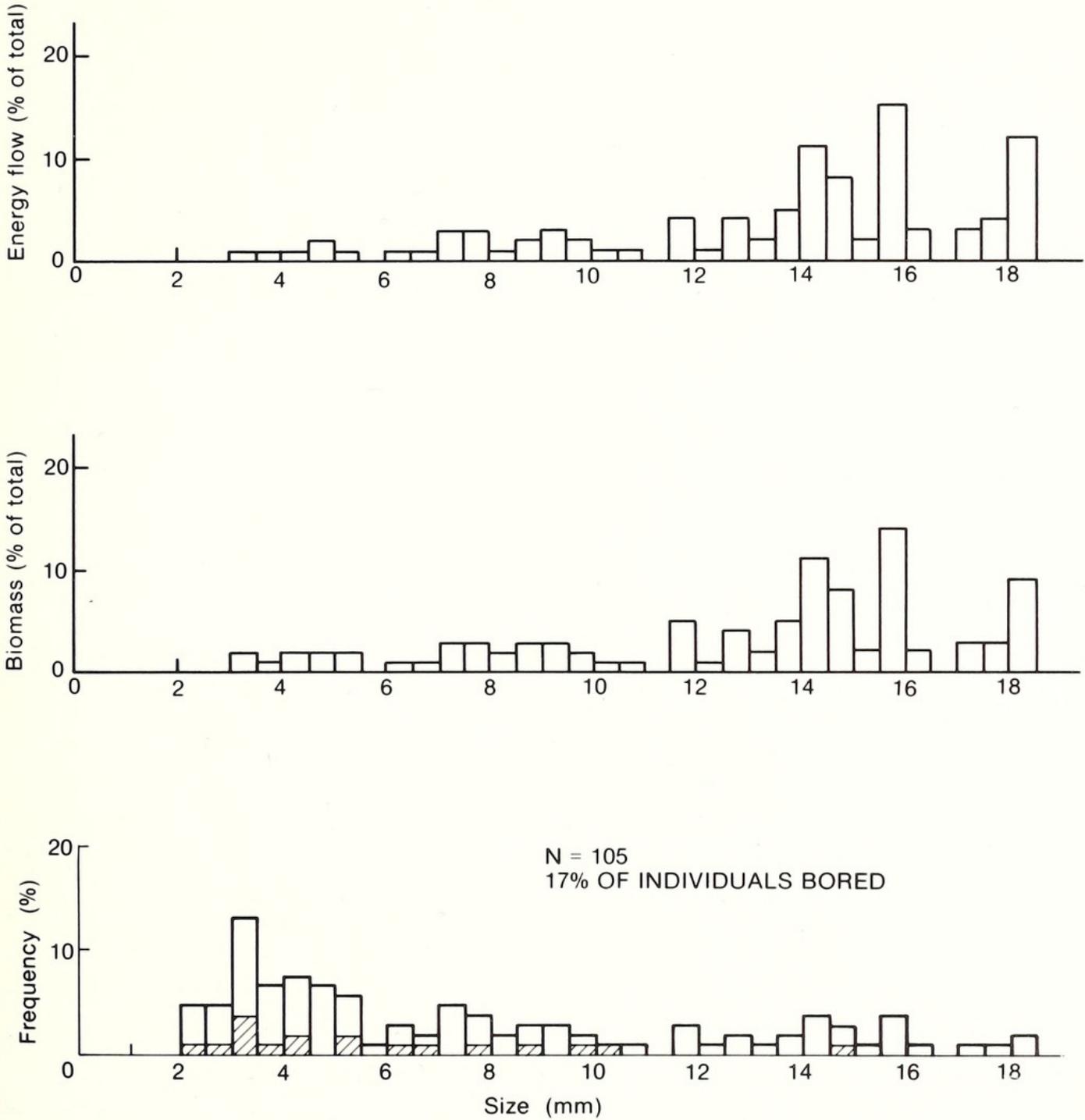
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Polinices aratus
(naticid gastropod)

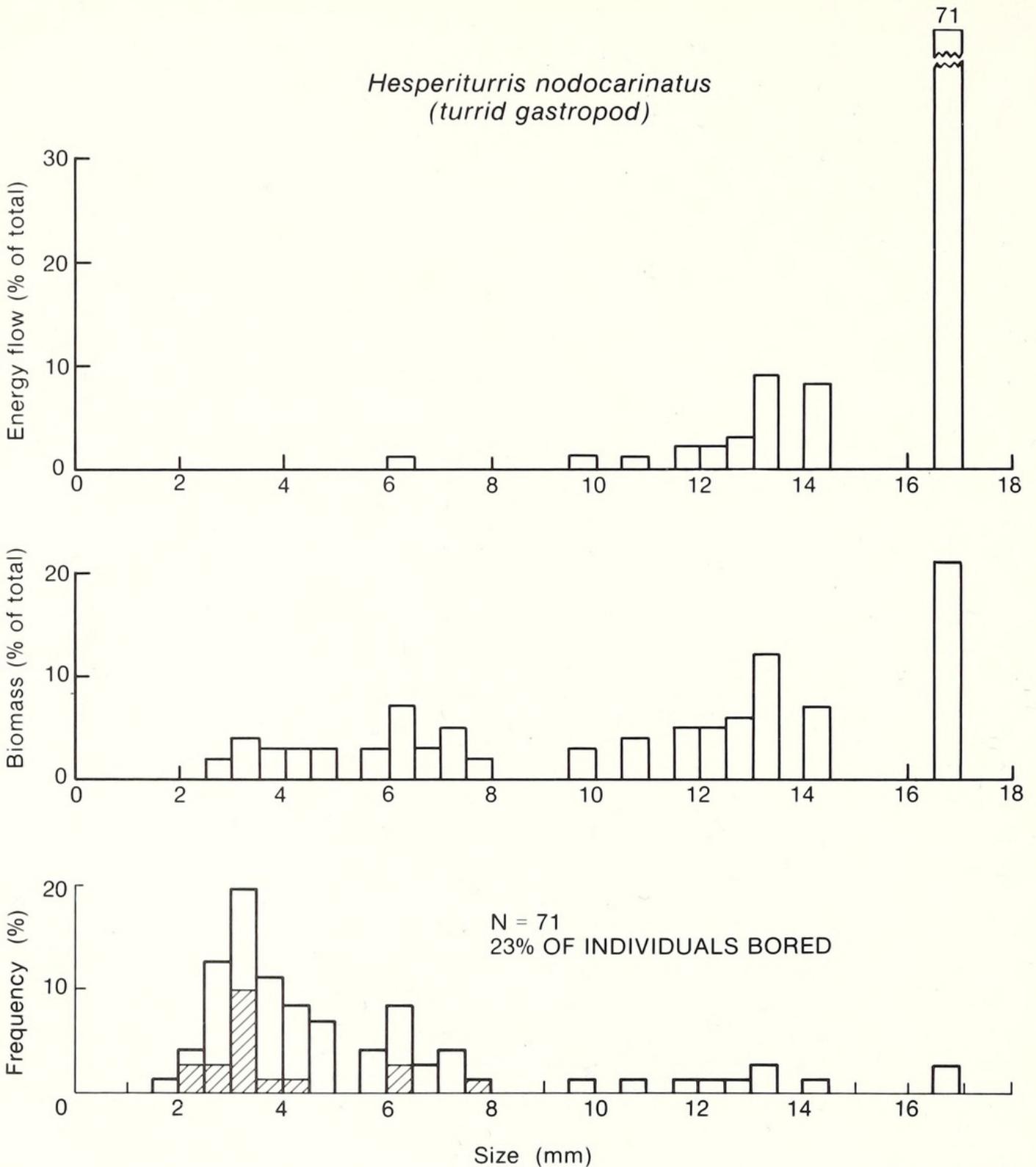


TEXT-FIG. 10. Lower, size-frequency distribution from Stanton *et al.* (1981); middle, percentage of total biomass in each size class; and upper, percentage of total population energy flow (= percentage of total prey ingested) in each size class for the naticid gastropod, *Polinices aratus*.

Latirus moorei
(fasciolariid gastropod)

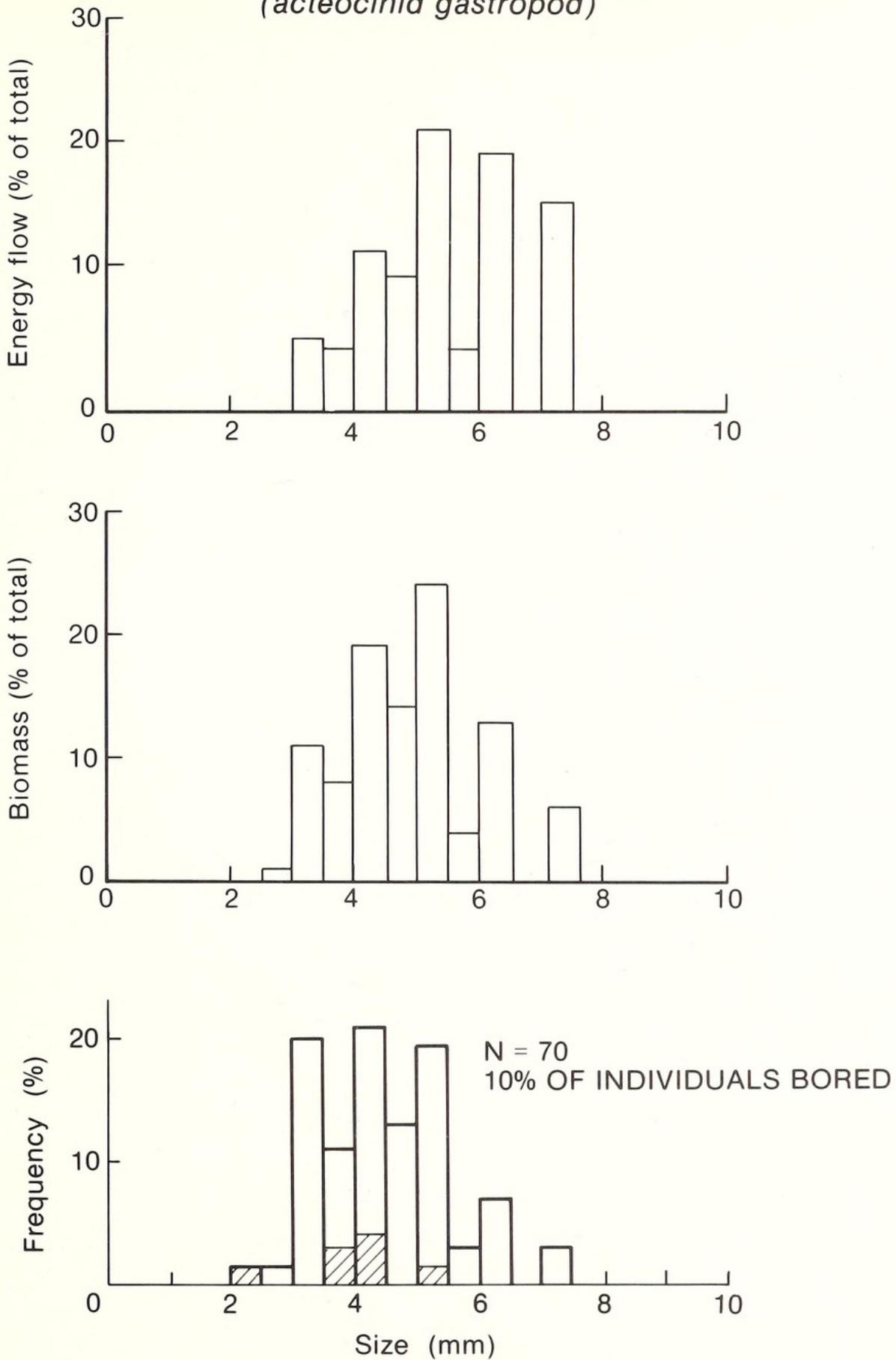


TEXT-FIG. 11. Lower, size-frequency distribution from Stanton *et al.* (1981); middle, percentage of total biomass in each size class; and upper, percentage of total population energy flow (= percentage of total prey ingested) in each size class for the fasciolariid gastropod, *Latirus moorei*.



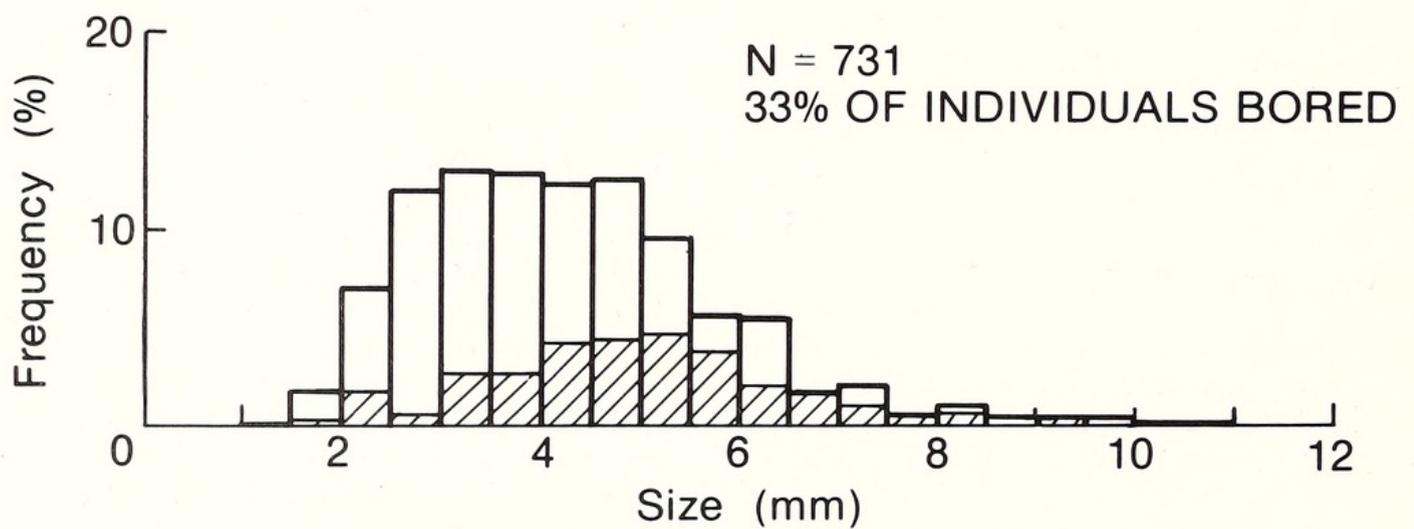
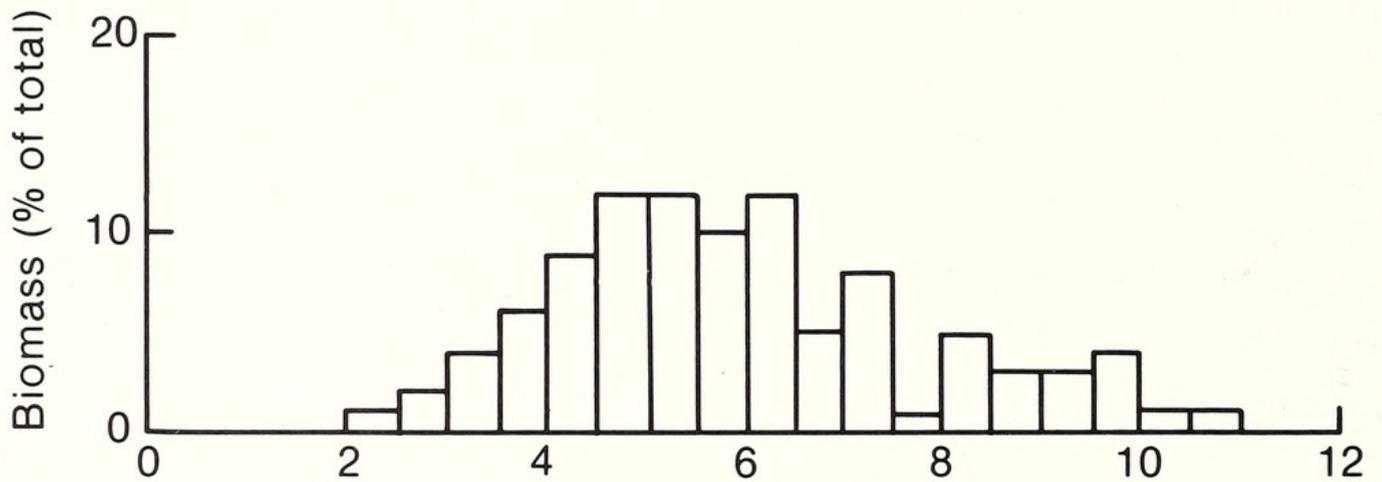
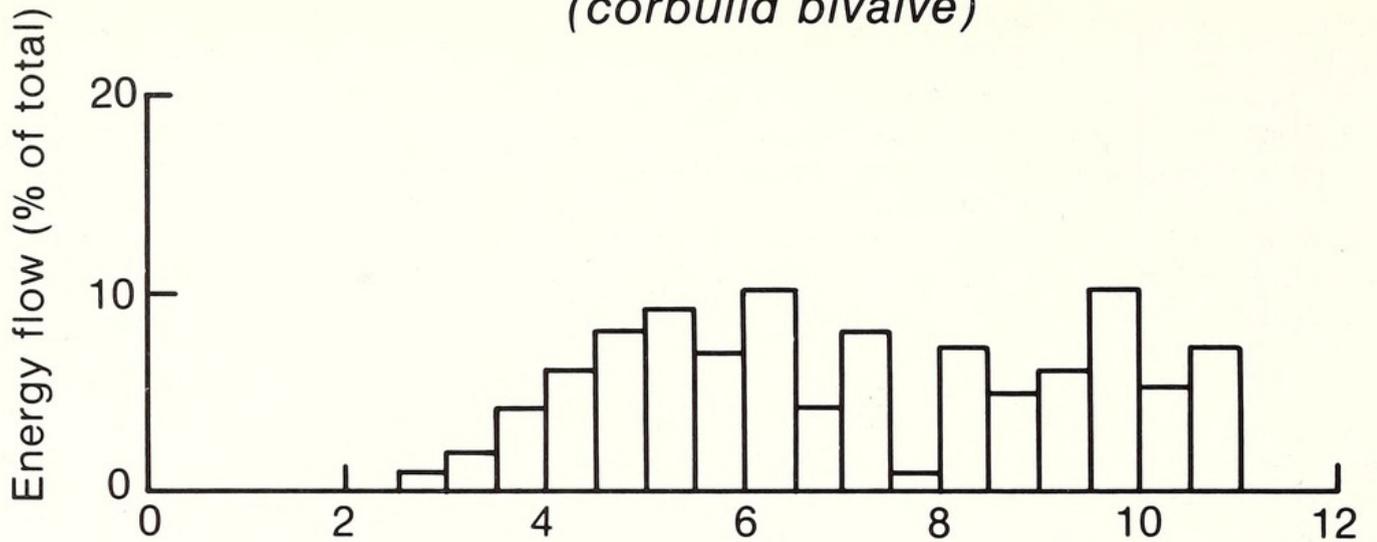
TEXT-FIG. 12. Lower, size-frequency distribution from Stanton *et al.* (1981); middle, percentage of total biomass in each size class; and upper, percentage of total population energy flow (= percentage of total prey ingested) in each size class for the turrid gastropod, *Hesperiturris nodocarinatus*.

Retusa kellogii
(acteocinid gastropod)



TEXT-FIG. 13. Lower, size-frequency distribution from Stanton *et al.* (1981); middle, percentage of total biomass in each size class; and upper, percentage of total population energy flow (= percentage of total prey ingested) in each size class for the retusid gastropod, *Retusa kellogii*.

Notocorbula texana
(corbulid bivalve)



TEXT-FIG. 14. Lower, size-frequency distribution from Stanton *et al.* (1981); middle, percentage of total biomass in each size class; and upper, percentage of total population energy flow (= percentage of total prey ingested) in each size class for the corbulid bivalve, *Notocorbula texana*.

largely of small, non-reproducing individuals; yet a few individuals also lived to approximately maximum age. The large amount of energy expended in growth by the many juveniles plus the large amount of energy expended in respiration by the long-lived individuals results in a large predicted prey consumption, second only to that of *H. nodocarinatus*.

This brief analysis of these five species from Stone City indicates how species-specific differences in abundance, size-frequency distribution, survivorship, and maximum age can produce rankings based on energy flow that are very different from those based on numerical abundance or biomass. Trophic reconstructions based on abundance (Hoffman *et al.* 1978; Stanton and Nelson 1980) or on the trophic nucleus as determined from abundance (Antia 1977; Stanton *et al.* 1981) provide a limited view of the community. The relative importance of the various size classes shifts markedly if biomass or energy flow is used rather than abundance (text-figs. 10–14). Use of biomass emphasizes the larger individuals at the expense of the usually more abundant smaller individuals. Conversion to energy flow emphasizes the larger individuals even more. In species such as *H. nodocarinatus*, where some individuals reached near-maximum age, the bulk of the energy flow is accounted for by the largest few size classes.

Thus, the largest, oldest individuals, although numerically of minor importance, are of overwhelming importance in the community's trophic structure. This not only illustrates the danger of depending on numerical abundance data in palaeoecology, but also emphasizes the significance of the larger individuals, which may be most likely to survive taphonomic destruction. For the five species in Table 5, for example, if taphonomic processes had reduced by one-half the number of individuals that were smaller than 50% of the largest size found in the assemblage, the values of energy flow would have been reduced by less than 20%.

Palaeoecologic efficiencies

Stanton *et al.* (1981) discussed the possibility that trophic reconstructions can be used to examine the importance of that portion of the community that is not preserved. In most communities, most of the individuals will not be preserved because they do not have mineralized skeletons (Stanton 1976; Schopf 1978) or because taphonomic processes preferentially destroy some that do (Powell *et al.* 1982). Comparison of the amount of prey consumed by preserved predators with the amount of prey species found in the assemblage permits an estimation of the minimum amount of biomass present at the next lower trophic level that was not preserved. Stanton and Nelson (1980) and Stanton *et al.* (1981) considered abundances, ecologic efficiencies, and total biovolumes of preserved species to make this estimation. Estimations based on energy flow, however, are superior. For example, we can deduce from Table 5 that at least 20 g of non-preserved annelidan prey had to be present to feed the individuals of *H. nodocarinatus*. This is a lifetime requirement, however, so that the 20 g of prey were not present at any one time. Probably, in fact, the predators also were not present simultaneously, because time-averaging affects the fossil assemblage. Trophic reconstructions in palaeoecology differ from those in ecology in that they encompass entire life spans and perhaps many generations, and do not imply simultaneous presence of all components in the community.

Ecologic efficiencies are commonly stated to be between 10 and 20% between higher trophic levels and to be generally lower between trophic levels one and two. Table 6 presents ecologic efficiencies as the ratio NP_n/NP_{n-1} where NP (net production) = $P_g + P_r$ (growth + respiration, although in most cases only P_g has been measured so that $NP = P_g$). Ecologic efficiencies average 7% between trophic levels one and two and 16% between levels two and three. If the ratio of net production to biomass is similar for the two trophic levels, then about five to twenty times more prey biomass than predator biomass should be present. Thus, because predators usually are larger than their prey, predators should be relatively rare in communities. Curiously, predatory gastropods are numerically dominant in the Stone City Formation, a fact that led Stanton and Nelson (1980) to use ecologic efficiency to estimate the amount of prey not preserved. Ecologic efficiencies, however, are based on data computed per area per year, whereas fossil assemblages must be treated on a per-lifetime basis. Therefore, the prey biomass that must be present to feed a predator is a function not only of their number and biomass, but also of the relative life spans of both predator and prey. If the predator lives

TABLE 6. Ecologic efficiency expressed as the ratio net production at one trophic level to the net production at the next lower trophic level (NP_n/NP_{n-1}).

Trophic levels	NP_n/NP_{n-1}	Comments	Source
1-2	0.021	—	Teal (1962)
2-3	0.064		
1-2	0.16		
2-3	0.05	—	Odum, H. T. (1957)
3-4	0.09		
1-2	0.11		
2-3	0.28	—	Baird and Milne (1981)
1-2	0.04		
2-3	0.21		
1-2	0.005	Los Maritas site—without meiofauna, benthos only, trophic level 2	Edwards, R. R. C. (1973)
2-3	0.20		
1-2	0.005	San Luis site—benthos only, trophic level 2	
2-3	0.20		
Avg. 1-2	0.07		
2-3	0.16		

significantly longer than the prey, then the total biomass of prey required to feed a given biomass of predator over the predator's life span must be higher than if their life spans were similar. Thus, predators should be very rare in fossil assemblages relative to their prey.

In the Stone City example, *P. aratus* consumed 11–15 g of prey to produce 3 g of biomass, an efficiency of 20–27%, and *N. texana* consumed 5–10 g of food to produce 1.3 g, an efficiency of 13–26%, but the much longer-liver *H. nodocarinatus* expended a much higher percentage of its energy in respiration, so that 20–30 g of prey were required to support 0.53 g of predator, an efficiency of only 2–3%. *H. nodocarinatus* has a poor palaeoecologic efficiency, not because the daily assimilation efficiencies were low, but because gross growth efficiency declines with age (Calow 1977). Older individuals, while consuming more, produce much less. For *H. nodocarinatus*, most of the energy flow of the population is contributed by a few older individuals.

Ecologic efficiencies, such as those in Table 6, are difficult to apply in palaeoecology because they are not based on the individuals' life spans. Thus, palaeoecologic efficiencies and the inferences made from them may be considerably different from their ecologic countertypes discussed by Kozlovsky (1968) and others.

Percent maximum age

Calculation of energy flow requires an age–size relationship for each species. If this cannot be established, a relationship between size and percent maximum age might be used. In this case the maximum size would be assigned an arbitrary age in equation 2. Two methods might be used. (1) All maximum sizes could be given the same age. Most molluscs have life spans in the range of one to twenty years, so an age of five years, for example, could be used. Table 5 shows the variability that results in data on energy flow even when realistic ages are used to bracket the real age. In cases where the age structure of the population includes individuals near maximum size, the discrepancies are large. For example, values for *N. texana* differ by 50%; for *H. nodocarinatus* and *P. aratus*, 33%, although the range of maximum ages used was about five years. Assigning each species the same maximum age rewards the short-lived species in the analysis and penalizes those long-lived species with good survivorship. (2) A value of $s_T = 1$ might be used so that the age determination is based on a single growth curve. This method rewards larger species regardless of their survivorship. Stanton *et al.* (1981) discussed the implications of this method (see fig. 14 in Stanton *et al.* 1981); using it, they predicted that *L. moorei* was the predominant predator in the Stone City assemblage. This is not the

case (Table 5) because *L. moorei* never reached reproductive age. Neither of these two alternatives yields a realistic estimate of energy flow. Some species will be penalized, others rewarded, and often substantially so. There is no substitute for knowledge of the individual's actual age.

CONCLUSIONS

The interpretation of the community in palaeoecology has been largely based on taxonomic composition and relative abundance and on structural measures such as diversity and equitability. Reconstruction of the trophic relationships within the community may provide information about the environment as well as about the evolution of ecosystems through geologic time. Trophic reconstruction has been difficult, however, because abundance does not provide a satisfactory picture of the trophic importance of a species in the community.

This paper describes a simple procedure to resolve this problem by determining energy flow through each population. Consequently, the relative trophic importance of each species can be determined. In addition, non-preserved components of the trophic web can be included in the trophic reconstruction by estimating the amount of prey consumed by the preserved components. Analysis of the community in terms of energy flow brings into sharper focus the influence of taphonomy and time-averaging in determining the composition of the fossil assemblage. Their role in the formation of the fossil assemblage must be ascertained and evaluated if the trophic structure of a palaeo-community is to be viewed in the same terms as the trophic structure of an ecologic community.

We have described the steps necessary to determine energy flow within a fossil community. Before the procedure is applied in palaeoecology, the potential user must be convinced that the fossil assemblage provides a reasonable representation of the original community. We believe that in many, but not all, cases this is true and the analysis will provide useful information.

Two basic categories of data are necessary for the analysis: (1) size and age information for each population in the community, and (2) energy parameters, which are based on measurements from living organisms. We have pointed out sources of error in these two categories, and have also shown the effect differences in these input data will have on the final results. Improvement of the estimations in both categories is clearly desirable, but present uncertainties in them are small enough that their use can improve substantially trophic analysis of palaeo-communities.

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