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GROWTH IN MARINE GASTROPODS: A NON-DESTRUCTIVE TECHNIQUE FOR INDEPENDENTLY MEASURING SHELL AND BODY WEIGHT

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ABSTRACT

A technique is described for obtaining non-destructive measurements of shell weight and body wet weight in marine gastropods. Shell weight is obtained by weighing whole animals in seawater and using a regression between these values and destructively sampled dry weights of shell. This weight may then be subtracted from whole weight in air, to provide an estimate of body wet weight. Shell weights are more accurately estimated than body weights. However, the mean cumulative error of this technique for estimating body weights is 10.6% for *Thais lamellosa*, 4.9% for *T. canaliculata* and 4.8% for *T. emarginata*. The possible application of this technique to other carbonate skeleton-producing invertebrates is briefly discussed.

Key words: Gastropoda; non-destructive measurement; Mollusca; shells; growth; *Thais*; carbonate skeletons; weight.

INTRODUCTION

Growth in molluscs may be assessed using several different quantities (Wilbur & Owen, 1964), the most common of which is one or more caliper measurements of shell size (Branch, 1974; Frank, 1965; Kenny, 1977; Randall, 1964; Spight, 1974; Yamaguchi, 1977). Other techniques, including laser diffraction (Strömgren, 1975) and total weight (Stickle & Duerr, 1970; Walne, 1958) have also been used to assess mollusc size. A drawback to these measures is that they measure attributes primarily of the shell and only indirectly those of the animal residing within it. Where shell shapes and thicknesses are very similar, such measures of size or weight are usually adequate if animals are growing actively. However, body size changes are not always paralleled by changes in shell size: decreases in body weight due to spawning or starvation will not be accompanied by concomitant decreases in shell size; shell growth may continue in some molluscs in the absence of feeding (Revelle & Fairbridge, 1957: 267; Rhoads & Young, 1970: 163; Zischke et al., 1970); and the spires of gastropod shells can often erode with increasing age (Spight et al., 1974). In these situations, shell size measurements will not provide an accurate estimate of body size.

To circumvent these problems, I have developed a non-destructive technique to separate body growth from shell growth in marine prosobranch gastropods. This technique relies upon two weight measurements: 1) a weight of the whole animal immersed in seawater, which ultimately provides an estimate of shell weight (see Havinga, 1928, and Nishii, 1965, for immersed weight estimates of shell weight in oysters; and Bak, 1973, for application to corals; Lowndes, 1942, has applied a similar technique to a number of invertebrates and vertebrates), and 2) a weight of the entire animal, shell plus body, in air. Subtracting the estimated weight of the shell from the total weight provides an estimate of the body weight, and the animal is still intact. Below, I describe the application of this technique to three species of thaidid gastropods, *Thais lamellosa* (Gmelin, 1791), *T. canaliculata* (Duclos, 1832) and *T. emarginata* (Deshayes, 1839), all inhabitants of North American rocky intertidal shores from Alaska to California (Ricketts et al., 1968).

In essence, this technique takes advantage of the specific gravity differences between shell and tissue. By weighing intact animals in two mediums of differing specific gravity (air and seawater), it is possible to separate the relative contribution of each component to the animal's total weight. It further takes advantage of two convenient attributes of gastropod molluscs: 1) the mantle is not attached to the shell, thus extrapallial fluid is not irrevocably trapped, and 2) it is possible to remove a substantial amount of the pallial water without damaging the animal. Thus the whole weight may be reduced to shell plus body weight, with a minimal amount of residual extravisceral water.

MATERIALS AND METHODS

'Immersed weight,' or the weight of whole animals in seawater, was obtained by placing them on a 3 cm × 3 cm VEXAR® plastic screen platform, supported by and suspended from a fine copper wire that could be hooked directly to the underside of a Mettler P153 balance. The balance was placed on a stand that straddled the container of seawater in which the animals were to be weighed. By taring the balance to compensate for the weight of the suspended platform, actual weights of the immersed animals could be read with no correction. Snails were introduced individually using a pair of forceps and weights recorded to the nearest 0.001 g.

Because specific gravity differences were being used to separate shell weight from body weight, it was important to ensure that there was *no* air inside the mantle cavities of individuals prior to weighing them under water, otherwise shell weights could have been underestimated. A procedure used to minimize this possibility was to completely immerse the animals for 24–48 hours prior to weighing, since most animals appeared able to clear their mantle cavities of air over this period. Animals were also 'chased' into their shells with the tips of the forceps immediately prior to placing them on the immersed platform; this acted to squeeze much, though probably not all, of any residual air out of the mantle cavity. Air was detected as bubbles released by the withdrawing animal in fewer than 5% of the animals; these individuals were noted.

To obtain non-destructive estimates of shell weights from immersed weights, it was necessary to compute a regression of actual shell weight on immersed weight for all three species. For this purpose, I measured immersed weights for individuals from a size range of all three species. The shells were then broken open using a C-clamp to avoid uncontrolled shattering, and the fragments separated from the body and dried to constant weight at 80°C (Tables 2–4). The slopes of these regressions of destructively sampled shell dry weight on immersed weight (regressions 1–3, Table 1; Fig. 1) were then used to estimate actual shell weight from immersed

TABLE 1. Least squares linear regressions for shell and body weight estimates. Weights are measured in grams. N = number of individuals. See Figs. 1 and 2 for plots of the data for regressions 1–3 and 8–10 respectively.

Regression number	Species	N	Regression equation	R^2
Shell dry weight (Y) from immersed whole weight (X)				
1	*T. lamellosa*	27	Y = 1.572X + 0.0162	0.9998
2	*T. canaliculata*	21	Y = 1.558X − 0.0075	0.9995
3	*T. emarginata*	19	Y = 1.530X + 0.0032	0.9997
Body immersed weight (Y) from body dry weight (X)				
4	3 spp. pooled	16	Y = 0.202X − 0.0008	0.9946
Shell dry weight (Y) from corrected immersed whole weight (X)				
5	*T. lamellosa*	27	Y = 1.598X + 0.0174	0.9999
6	*T. canaliculata*	21	Y = 1.600X − 0.0013	0.9996
7	*T. emarginata*	19	Y = 1.605X + 0.0017	0.9993
Ash free dry weight (Y) from estimated body weight (whole wt.–shell wt.) (X)				
8	*T. lamellosa*	27	Y = 0.1043X + 0.0180	0.8050
9	*T. canaliculata*	21	Y = 0.1974X + 0.0141	0.9117
10	*T. emarginata*	19	Y = 0.2514X − 0.0029	0.9846
Log ash-free dry weight (Y) from log shell length (X)				
11	*T. lamellosa*	27	Y = 2.940X − 5.426	0.9277
12	*T. canaliculata*	21	Y = 2.709X − 4.743	0.9471
13	*T. emarginata*	19	Y = 3.304X − 5.440	0.9759

weight of the whole animal for each species. It is clear from the high R^2 values (0.9995–0.9998) that immersed weight can provide a very accurate, non-destructive estimate of actual shell weight.

Some care must be exercised in the application of a single regression to different species, however, since not all the weight of a snail immersed in seawater is due to the shell. The different slopes in regressions 1–3 (Table 1; Fig. 1) reflect differences in the amount of tissue. To assess the contribution of tissue weight to immersed weight, I separated a small number of individuals of all three species from their shells and measured the immersed weight of the bodies alone. These were then dried to constant weight at 80°C. Regression 4 (Table 1) describes how much a given dry weight of tissue weighs when immersed in seawater before it has been dried (dry weights were used here because they are much more accurate than attempting to uniformly towel-dry animals for wet weights in air). If the tissue dry-weight values of Tables 2–4 are multiplied by the slope of this regression, subtracted from the total immersed weights, and these corrected immersed weights (i.e. corrected for the contribution of body weight to immersed weight) regressed against destructively sampled shell dry weights, the differences between the three species disappear (regressions 5–7, Table 1). This is to be expected since the specific gravity of shell material should be essentially the same for all three species. However, since it is only changes in the amount of body weight *relative to the weight of the shell* that will affect the accuracy of the uncorrected estimate of shell weight, and also since the contribution of the entire body to immersed weight is at most 4% (4% for *T. emarginata*, less than 3% for *T. lamellosa* and *T. canaliculata*), such a correction will yield very slight differences in the estimated shell weights. In other words, since the entire body weight of an immersed animal amounts to less than 5% of the total

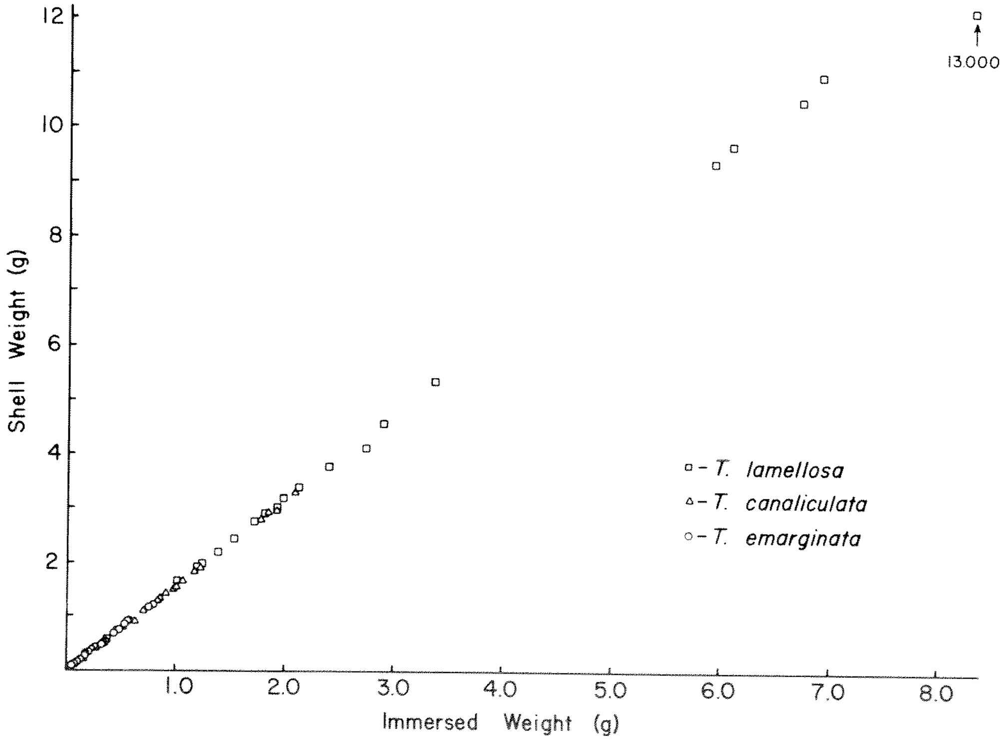

FIG. 1. The relationship between immersed weight of whole animals and destructively sampled dry weight of the shell for three species of *Thais*. The regression equations for these data are in Table 1, regressions 1–3. The high coefficients of determination (Table 1) indicate that shell weight is very accurately estimated from the weight of the whole animal immersed in seawater.

TABLE 2. Whole weights, immersed weights and error analysis for *Thais lamellosa*. Repeat whole weights were obtained on three successive days. Immersed weights were measured immediately prior to whole weights on the last two days. f = no penis. m = penis present.

		Whole weights (g)						Immersed weights (g)					Estimated body wt. (g)		
Shell length (mm)	Sex					Error					Error			Cum. error	
		1	2	3	Mean	Max.	%	1	2	Mean	Max.	%	1	Max.	%
58.2	f	17.992	17.661	17.461	17.681	0.261	1.46	8.277	8.272	8.274	0.005	0.06	4.681	0.266	5.68
56.0	f	15.181	14.840	14.702	14.908	0.341	2.25	6.721	6.699	6.710	0.022	0.33	4.453	0.363	9.41
55.1	f	14.506	14.780	14.806	14.697	0.274	1.89	6.666	6.617	6.642	0.049	0.74	4.184	0.323	7.72
53.9	f	13.784	13.047	13.544	13.458	0.737	5.35	6.084	6.103	6.094	0.019	0.31	3.786	0.756	19.97
52.9	m	14.701	15.215	12.956	12.945	0.514	3.50	6.904	6.892	6.898	0.012	0.17	4.025	0.526	13.07
52.0	m	13.154	13.673	12.679	13.169	0.994	7.27	5.923	5.909	5.916	0.014	0.24	3.840	1.008	26.25
41.2	m	7.369	7.224	7.449	7.347	0.225	3.11	3.374	3.364	3.369	0.010	0.30	2.019	0.235	11.64
39.1	m	6.252	6.133	6.214	6.200	0.119	1.90	2.898	2.888	2.893	0.010	0.35	1.667	0.129	7.74
37.0	m	5.478	5.355	5.619	5.484	0.264	4.93	2.395	2.383	2.389	0.012	0.50	1.712	0.276	16.12
36.9	m	4.609	4.548	4.738	4.632	0.190	4.18	2.119	2.109	2.114	0.010	0.47	1.306	0.200	15.31
36.1	f	4.488	4.645	4.654	4.596	0.157	3.50	2.129	2.120	2.125	0.009	0.42	1.239	0.166	13.40
35.3	f	4.169	4.210	4.194	4.191	0.041	0.98	1.996	1.987	1.992	0.009	0.45	1.015	0.050	4.93
35.2	m	4.107	4.126	4.011	4.081	0.115	2.79	1.937	1.930	1.934	0.007	0.36	1.105	0.122	11.04
33.9	m	3.640	3.643	3.671	3.651	0.028	0.77	1.738	1.730	1.734	0.008	0.46	0.893	0.036	4.03
32.6	f	4.014	3.948	3.992	3.985	0.066	1.64	1.831	1.817	1.824	0.014	0.76	1.112	0.080	7.19
32.6	f	3.149	3.108	3.078	3.112	0.041	1.30	1.382	1.377	1.380	0.005	0.36	0.931	0.046	4.94
32.5	f	5.449	5.595	5.553	5.532	0.146	2.68	2.581	2.566	2.574	0.015	0.58	1.449	0.161	11.11
30.5	m	3.037	3.057	3.026	3.040	0.031	1.01	1.526	1.529	1.528	0.003	0.20	0.624	0.034	5.45
28.9	m	2.491	2.483	2.457	2.477	0.026	1.05	1.241	1.242	1.242	0.001	0.08	0.507	0.027	5.33
27.9	f	1.991	1.976	1.960	1.976	0.016	0.81	0.977	0.978	0.978	0.001	0.10	0.439	0.017	3.87
27.7	f	2.351	2.301	2.315	2.322	0.050	2.13	1.149	1.148	1.149	0.001	0.09	0.498	0.051	10.04
27.5	m	2.102	2.110	2.051	2.088	0.059	2.80	1.013	1.015	1.014	0.002	0.20	0.487	0.061	12.53
27.1	m	2.355	2.338	2.355	2.349	0.017	0.73	1.196	1.196	1.196	0.000	0.00	0.455	0.017	3.74
25.9	m	1.969	1.986	1.955	1.970	0.031	1.56	1.004	1.006	1.005	0.002	0.20	0.274	0.033	12.04
17.1	?	0.570	0.570	0.569	0.570	0.001	0.18	0.291	0.292	0.292	0.001	0.34	0.117	0.002	1.71
16.6	?	0.530	0.532	0.522	0.528	0.010	1.88	0.271	0.271	0.271	0.000	0.00	0.100	0.010	10.00
14.0	?	0.300	0.313	0.303	0.305	0.013	4.33	0.156	0.160	0.158	0.004	2.56	0.052	0.017	32.69
					Means	0.177	2.44				0.009	0.30		0.188	10.63

TABLE 3. Whole weights, immersed weights and error analysis for *Thais canaliculata*. Repeat whole weights were obtained on three successive days. Immersed weights were measured immediately prior to whole weights on the last two days. f = no penis. m = average penis. 'm–' = small penis.

Shell length (mm)	Sex	Whole weights (g)						Immersed weights (g)					Estimated body wt. (g)		
						Error					Error			Cum. error	
		1	2	3	Mean	Max.	%	1	2	Mean	Max.	%	1	Max.	%
35.1	f	4.545	4.471	4.505	4.507	0.074	1.63	2.103	2.094	2.099	0.009	0.43	1.217	0.083	6.82
35.0	f	4.110	4.091	4.059	4.087	0.032	0.78	1.848	1.841	1.845	0.007	0.38	1.208	0.039	3.23
33.9	m	4.165	4.112	4.096	4.124	0.053	1.27	1.916	1.913	1.914	0.003	0.16	1.159	0.056	4.83
30.6	f	3.734	3.654	3.594	3.661	0.080	2.14	1.773	1.774	1.774	0.001	0.06	0.885	0.081	9.15
28.9	f	2.573	2.532	2.517	2.541	0.041	1.59	1.170	1.172	1.171	0.002	0.17	0.728	0.043	5.91
28.6	f	2.516	2.477	2.484	2.492	0.039	1.55	1.230	1.232	1.231	0.002	0.16	0.605	0.041	6.78
27.2	f	2.290	2.279	2.277	2.282	0.011	0.48	1.041	1.041	1.041	0.000	0.00	0.737	0.011	1.49
27.0	f	2.292	2.285	2.280	2.286	0.007	0.31	1.059	1.063	1.061	0.004	0.38	0.638	0.011	1.72
26.9	f	2.144	2.144	2.104	2.131	0.040	1.87	0.978	0.983	0.981	0.005	0.51	0.603	0.045	7.46
25.9	m	1.982	1.952	1.950	1.961	0.030	1.51	0.909	0.909	0.909	0.000	0.00	0.557	0.030	5.39
25.9	f	1.886	1.870	1.841	1.866	0.029	1.55	0.838	0.839	0.838	0.001	0.12	0.591	0.030	5.08
25.1	f	1.876	1.865	1.843	1.861	0.022	1.18	0.845	0.848	0.846	0.003	0.36	0.554	0.025	4.51
23.1	m	1.456	1.456	1.449	1.454	0.007	0.48	0.703	0.705	0.704	0.002	0.28	0.351	0.009	2.56
22.3	f	1.329	1.337	1.320	1.329	0.017	1.27	0.632	0.634	0.633	0.002	0.32	0.341	0.019	5.57
21.2	m	1.099	1.094	1.088	1.094	0.006	0.55	0.522	0.523	0.523	0.001	0.19	0.281	0.007	2.49
19.3	f	0.829	0.826	0.812	0.822	0.014	1.69	0.364	0.366	0.365	0.002	0.55	0.257	0.016	6.23
19.3	m–	0.937	0.942	0.941	0.940	0.005	0.53	0.467	0.468	0.468	0.001	0.21	0.200	0.006	3.00
16.5	m–	0.541	0.541	0.534	0.539	0.007	1.29	0.245	0.248	0.247	0.003	1.22	0.156	0.010	6.41
16.0	f	0.580	0.576	0.573	0.576	0.004	0.69	0.260	0.262	0.261	0.002	0.77	0.177	0.006	3.39
13.6	m–	0.340	0.342	0.341	0.341	0.002	0.59	0.165	0.165	0.165	0.000	0.00	0.083	0.002	2.41
13.5	?	0.346	0.349	0.345	0.347	0.004	1.15	0.161	0.164	0.162	0.003	1.86	0.093	0.007	7.53
					Means	0.025	1.15				0.003	0.38		0.027	4.86

TABLE 4. Whole weights, immersed weights and error analysis for *Thais emarginata*. Repeat whole weights were obtained on three successive days. Immersed weights were measured immediately prior to whole weights on the last two days. f = no penis. m = average penis. 'm–' = small penis.

		Whole weights (g)						Immersed weights (g)					Estimated body wt. (g)		
Shell length						Error					Error			Cum. error	
(mm)	Sex	1	2	3	Mean	Max.	%	1	2	Mean	Max.	%	1	Max.	%
27.2	f	1.991	1.964	1.951	1.969	0.027	1.36	0.800	0.799	0.800	0.001	0.13	0.749	0.028	3.74
25.7	m	1.836	1.829	1.822	1.829	0.007	0.38	0.766	0.765	0.765	0.001	0.13	0.656	0.008	1.22
22.7	f	1.182	1.187	1.159	1.176	0.028	2.36	0.493	0.495	0.494	0.002	0.34	0.422	0.030	7.11
22.3	m	1.339	1.335	1.333	1.336	0.004	0.30	0.581	0.583	0.582	0.002	0.34	0.433	0.006	1.39
22.3	f	1.245	1.245	1.235	1.242	0.010	0.80	0.542	0.543	0.543	0.001	0.18	0.401	0.011	2.74
21.8	m	1.296	1.289	1.274	1.286	0.015	1.16	0.569	0.571	0.570	0.002	0.35	0.397	0.017	4.28
21.2	f	1.104	1.112	1.096	1.104	0.016	1.44	0.455	0.456	0.456	0.001	0.22	0.417	0.017	4.08
20.2	f	0.889	0.886	0.877	0.884	0.009	1.02	0.363	0.363	0.363	0.000	0.00	0.327	0.009	2.75
20.0	f	0.816	0.811	0.804	0.810	0.007	0.86	0.331	0.330	0.331	0.001	0.37	0.304	0.008	2.63
19.9	f	0.779	0.774	0.768	0.774	0.006	0.78	0.322	0.322	0.322	0.000	0.00	0.280	0.006	2.14
18.0	m	0.636	0.635	0.635	0.635	0.001	0.16	0.271	0.270	0.271	0.001	0.37	0.218	0.002	0.92
17.2	m	0.528	0.528	0.519	0.525	0.009	1.70	0.222	0.222	0.222	0.000	0.00	0.180	0.009	5.00
16.9	f	0.583	0.576	0.576	0.578	0.007	1.20	0.244	0.246	0.245	0.002	0.82	0.199	0.009	4.52
15.6	m–	0.420	0.419	0.416	0.418	0.003	0.72	0.172	0.175	0.173	0.003	1.74	0.150	0.006	4.00
15.4	f	0.410	0.408	0.401	0.406	0.007	1.72	0.169	0.168	0.168	0.001	0.59	0.146	0.008	5.48
13.9	f	0.288	0.289	0.285	0.287	0.004	1.38	0.125	0.126	0.126	0.001	0.80	0.092	0.005	5.43
12.3	f	0.231	0.234	0.225	0.230	0.009	3.85	0.105	0.104	0.105	0.001	0.95	0.066	0.010	15.15
11.1	f	0.159	0.162	0.161	0.161	0.003	1.89	0.072	0.073	0.073	0.001	1.67	0.048	0.004	8.33
10.5	?	0.130	0.131	0.129	0.130	0.002	1.53	0.060	0.061	0.061	0.001	1.67	0.031	0.003	9.68
					Means	0.009	1.29				0.001	0.55		0.009	4.77

immersed weight, the fractional differences in body weights among animals with the same shell weight will be much less and hence introduce little error. As the ratio of shell to body weight decreases, however, this error will increase, thus for animals with slight shells this technique may be less accurate.

Whole weight in air ('whole weight' in Tables 2–4) was measured after several preparatory steps that removed most of the extravisceral water. In *Nucella lapillus* (Linné, 1758), this water may account for up to 39% of the total water of an attached animal (Boyle et al., 1979), and unless removed would be included as part of the body wet weight. Also, because animals will retract on their own to varying extents on different occasions, these preparatory steps permitted a much higher level of repeatability.

Snails were first arrayed aperture up on paper toweling in the order in which they were to be weighed. Each animal was then 'chased' back into its shell by stimulating the foot with a small modeling brush. A soft absorbent tissue (e.g. Kimwipe) was subsequently pressed firmly up against the retracted foot with a pair of forceps to squeeze out nearly all the remaining water. The animals were left on the toweling until all the shells in a group were visibly dry (approximately 20–40 min) and then weighed on top of a Mettler P153 balance to the nearest 0.001 g (Tables 2–4). This whole weight corresponded to shell plus tissue wet weight, plus any residual mantle water. The shell weight, as estimated from immersed weight (regressions 1–3, Table 1; Fig. 1), was then subtracted from the whole weight, thus providing an estimate of body tissue wet weight.

A more desirable correlation, though, was

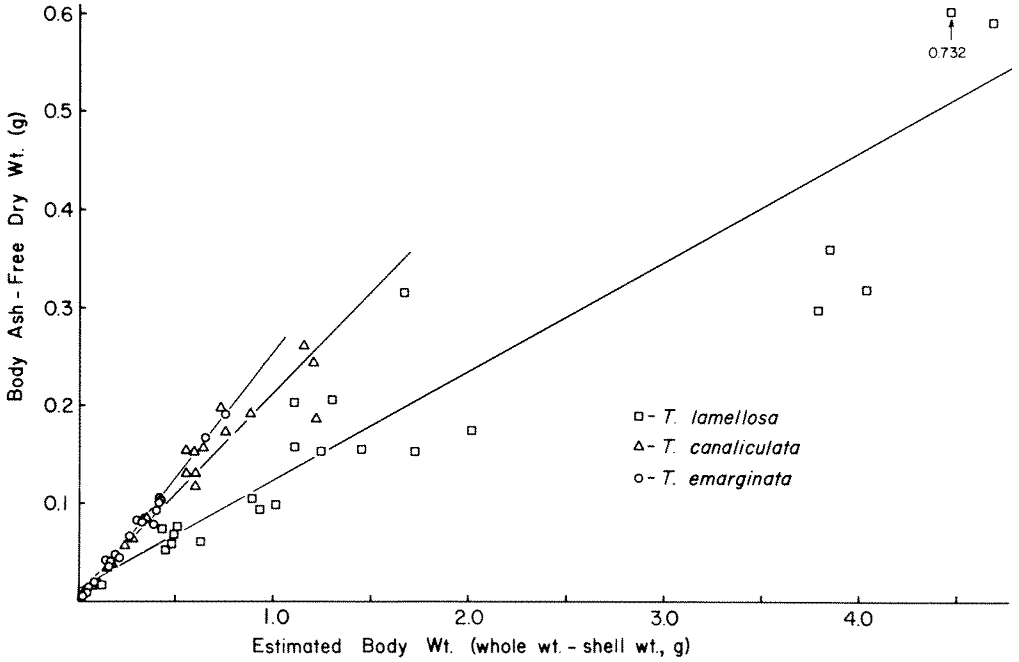

FIG. 2. The relationship between estimated body weight (the weight of the whole animal in air minus the weight of the shell) and destructively sampled ash-free dry weight of the body for three species of *Thais*. The regression equations for these data are in Table 1, regressions 8–10. As indicated by the coefficients of determination (Table 1), this relationship is least accurate for the largest species (*T. lamellosa*, squares) and most accurate for the smallest species (*T. emarginata*, circles). *T. canaliculata* (triangles), an intermediate-sized species, exhibits an intermediate level of variability. Much of the variation about these regressions appears due to differences among individuals in the percent water and percent ash of the body. The regressions of body *dry* weight on estimated body weight (whole weight minus shell weight) and of body *wet* weight on estimated body weight exhibit much less scatter: coefficients of determination (R^2) = 0.8591, 0.9217 and 0.9887 for body dry weight, and coefficients of determination (R^2) = 0.9770, 0.9871 and 0.9989 for body wet weight respectively for the three *Thais* species, *T. lamellosa, T. canaliculata* and *T. emarginata*.

between this value of estimated body weight (i.e. whole weight minus shell weight), and ash free dry weight, since ash free dry weight is a better estimate of metabolizing or metabolizable tissue. Regressions 8–10 (Table 1; Fig. 2) describe these relations for *Thais lamellosa, T. canaliculata* and *T. emarginata* respectively. Again, there is a close correspondence (R^2 values 0.8050–0.9846, Table 1), though not as precise as for shell weight. This two-step weighing procedure thus provides independent, non-destructive estimates of body and shell weight, allowing either to be used to measure growth.

The second step of this process, squeezing the water out of the mantle cavity, may traumatize the animal to some extent. However, in a field monitoring experiment involving all three species (Palmer, 1980), subgroups of each species were either 1) weighed as above in addition to being tagged and measured for shell length, or 2) only tagged and measured. There were no significant differences for any of the species between the proportion of animals recovered from the two treatment groups over the course of the following two weeks or after 2-1/2 months (Table 5), suggesting that the trauma associated with the weighing technique is slight for these species.

Immersed weight on the other hand involves little more disturbance than dislodgment of the animals from the bottom. If they have been immersed for a sufficient length of time prior to weighing, there is no need to force any air out of the mantle cavity and they may be placed directly on the submerged weighing platform. The entire operation, except for the brief transfer, takes place under water.

Another consideration regarding this technique is its repeatability. A comparison of R^2 values from regressions 1–3 with those of regressions 8–10 (Table 1) indicates that the replicability of immersed weights is greater than that for whole weights (Tables 2–4). For *Thais lamellosa* (Table 2) the mean maximum percent error for whole weight is 2.5%. Immersed weights of *Thais lamellosa* vary by less than 0.022 g between successive weighings and are in general much more accurate (mean percent error = 0.38%). For *Thais canaliculata* the mean maximum percent error is 1.15% for whole weights and 0.39% for immersed weights. For *Thais emarginata* these errors are about the same, 1.29% and 0.55% for maximum whole weight error and immersed weight error respectively. Tables 2–4 also indicate what the potential cumulative error might be when estimating body weight as described above.

DISCUSSION

The principal advantage to length as a measure of gastropod size is the comparative ease with which it may be obtained. Caliper measurements of shell length even to an accuracy of 0.1 mm require only a few seconds and with practice are repeatable to 0.2 mm. They are also readily obtainable in the field with a minimum of disturbance to the animals. Weight measurements, on the other hand, to be of sufficient accuracy (and hence utility), almost invariably require that animals be brought back to the laboratory, thereby increasing the disruption of the animal's normal activity as well as requiring additional time to return them to the field.

However, there are several limitations to shell length as a measure of animal size. First, as gastropod shells age, the spires begin to erode. Spight (1974) consistently observed negative "growth" (change in shell length) over the winter in *Thais lamellosa* at Shady Cove which he recognized as being due to spire erosion (see also Spight et al., 1974). Second, as animals increase in size there is a progressively smaller change in length for a given change in body weight so given the limit on resolution of length change imposed by the repeatability of caliper measurements (0.1–0.2 mm), changes in weight will be more readily detected than changes in length. Third, in mature gastropods, where shell growth is almost negligible, body weight may still vary seasonally in association with spawning, reduced activity over the winter or increases or decreases in the food supply. These body weight changes would pass undetected if only shell length is recorded. Finally, if populations differ from each other in shell shape, or if there is shape variation among individuals within a single population, then a given length change in animals of the same initial length will be associated with different changes in body weight.

In the final analysis, the choice of weight or length to measure growth, if not set by logistical constraints, is determined by the kind of information desired. The correlation between log shell length and log body weight is generally high for animals from a single population

TABLE 5. Proportions of marked animals recovered from each of two treatment groups on various days following release at Deadman Island, San Juan Islands, Washington, U.S.A. (48°27′N, 122°55′W). Marked animals were released on 4/26/78. SD = standard deviation. t = t value from paired t-tests.

Treatment	Number released	Proportion of released animals recovered												
		Date recovered (month/day)												
		5/4	5/5	5/6	5/7	5/9	5/11	5/12	5/13	5/15	7/16	Mean	SD	t_S
Thais lamellosa														
Length + weight	50	0.02	0.08	0.14	0.02	0.10	0.12	0.18	0.10	0.08	0.22	0.11	0.063	1.17
Length only	29	0.03	0.07	0.10	0.00	0.07	0.07	0.14	0.07	0.03	0.14	0.07	0.044	
Thais canaliculata														
Length + weight	50	0.28	0.42	0.46	0.42	0.40	0.34	0.34	0.36	0.42	0.62	0.41	0.092	0.18
Length only	262	0.28	0.30	0.40	0.40	0.38	0.47	0.47	0.50	0.41	0.50	0.41	0.076	
Thais emarginata														
Length + weight	50	0.62	0.62	0.50	0.70	0.70	0.78	0.80	0.80	0.86	0.80	0.72	0.111	1.70
Length only	139	0.55	0.58	0.58	0.66	0.70	0.80	0.78	0.78	0.69	0.58	0.67	0.095	

TABLE 6. Regressions of body weight change (Y) on shell length change (X). Shell lengths are in mm. Body weights are measured in grams. N = number of individuals. *T. lam.* = *Thais lamellosa*. *T. can.* = *T. canaliculata*. *T. em.* = *T. emarginata*.

Regression number	Species	Length change Mean	Length change Range	N	Regression equation	R^2
1	*T. lam.*[1]	−0.02	−0.5 to 1.6	11	$Y = 0.071X - 0.0425$	0.1985
2	*T. lam.*[2]	−0.02	−1.0 to 1.8	17	$Y = 0.072X - 0.0434$	0.3117
3	*T. lam.*[3]	6.43	3.3 to 10.3	27	$Y = 0.045X - 0.0024$	0.5635
4	*T. lam.*[4]	9.31	4.8 to 12.2	24	$Y = 0.057X - 0.0865$	0.7540
5	*T. can.*[1]	1.21	−0.3 to 4.1	28	$Y = 0.018X + 0.0785$	0.1178
6	*T. em.*[1]	1.24	−0.7 to 5.3	40	$Y = 0.039X + 0.0061$	0.7063
7	*T. em.*[2]	2.01	0.3 to 3.7	9	$Y = 0.025X - 0.0019$	0.7575

[1] Deadman Island, field growth.
[2] Point George, Lopez Island, field growth.
[3] Collected from False Bay, San Juan Island; grown in cages.
[4] Collected from Turn Rock, San Juan Islands; grown in cages.

(regressions 11–13, Table 1), indicating that length can provide a fairly reliable estimate of body weight. In addition, the correlation between *change* in length and *change* in body weight can also be relatively high for animals in the field and in cages, as long as they are increasing in size (regressions 3, 4, 6 and 7, Table 6; but note regression 5). Consequently, if growth rates are positive and of moderate magnitude relative to spire erosion, and if shell shapes are essentially the same, then length can provide an adequate measure of body size. If populations of different shape need to be compared, a single destructive correlation of body weight on length for each population can permit comparisons between them based on length measurements alone. If, on the other hand, there is a possibility that animals may lose weight and it is important to detect such a loss, or if there are significant differences in the rates of spire erosion among populations being compared, length measurement alone may lead to much lower resolution of growth rate differences.

In principle this technique would be applicable to any organism composed of two major components of differing specific gravity. Weights of the organism first in a medium whose specific gravity is very close to that of one of the components, and then in a second medium which may or may not be of similar specific gravity to the second component, will, via the appropriate regressions, permit independent estimates of both body components. In practice, such separation may be less feasible for other carbonate skeleton-producing invertebrates (sclerosponges, corals, brachiopods, bryozoans, bivalves and echinoderms), since for many the removal of extravisceral water will be difficult to accomplish reliably or without damaging the animal.

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