

Estimating biomass of benthic kelp forest invertebrates from body size and percent cover data

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Abstract The inability to compare different measures of species abundance (such as density and percent cover) or different metrics of species biomass (such as wet mass and ash-free dry mass) hampers quantitative studies of community dynamics, trophic interactions, energy flow and biodiversity. This has been especially problematic for the dynamic and highly productive communities inhabiting shallow reefs in temperate seas where varied metrics are commonly used to characterize the abundance and biomass of different suites of species. To facilitate the conversion of abundance data into common metrics of biomass, we developed quantitative relationships between wet mass and length and wet mass and percent cover, and conversion factors for transforming wet mass into dry mass, shell-free and decalcified dry mass, and ash-free dry mass for 84 species of benthic macroinvertebrates common to giant kelp forests in southern California. Regressions for all 84 species were highly significant, and regression fits were very good for most species. Interspecific differences between regression slopes and in the ratios used to convert one metric of mass into another varied by as much as an order of magnitude among species within the same taxonomic group indicating that caution should be used when attempting to

estimate biomass using generic relationships or ratios that were developed for other species, even if those species are closely related.

Introduction

The amount of living biomass and its allocation among different species defines the structure of natural communities, and there has been considerable research devoted to understanding how fluctuations in biomass across species influence the productivity and temporal stability of ecosystems (Tilman 1996; Cardinale et al. 2007; de Mazancourt et al. 2013; Hallett et al. 2014). Most research on this topic has involved terrestrial systems where the vast majority of biomass is distributed among plants. Our understanding of the ecological consequences of changes in species biomass across multiple trophic levels is relatively poor by comparison.

The highly productive and diverse communities of plants and animals inhabiting shallow reefs in temperate seas have the potential to offer novel insight into the ecological consequences of changes in biomass dynamics across multiple trophic levels. Unlike on land, the primary space holders on reefs (macroalgae and sessile suspension feeding invertebrates) occupy different trophic levels. Macroalgae are a phylogenetically diverse group of highly productive autotrophs that compete for space with heterotrophic sessile invertebrates that feed on suspended matter in the water column. Herbivorous and omnivorous invertebrates and fish feed on the benthic community of macroalgae and sessile invertebrates, and in turn are fed upon by invertebrate and fish predators.

Although temperate reefs have long served as model systems for developing and testing ecological theory and

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paradigms (Connell 1961; Paine 1966; Dayton 1971; Menge and Sutherland 1976; Underwood and Denley 1984), their potential for providing novel insight into the ecological consequences of alterations in the magnitude and distribution of biomass within and among trophic levels has yet to be fully realized. This is due in large part because species-specific data on biomass are extremely tedious to collect, especially if nondestructive sampling is required for time series analyses of permanent plots. As a result, the structure and dynamics of reef communities are most often evaluated in terms of species abundance that includes measurements of both numerical density and percent cover, depending on the life history and morphology of the species of interest (e.g., Estes and Duggins 1995; Fowler-Walker and Connell 2002; Wernberg et al. 2013; Menge et al. 2015). The inability to quantitatively compare such disparate measures of abundance hinders holistic analyses of community biodiversity (e.g., species diversity and evenness), primary and secondary production, energy flow, food web complexity and community dynamics. Species-specific information that enables density and percent cover data collected in situ to be converted to a common metric of biomass alleviates this constraint.

Relationships between length and mass have been developed for a variety of benthic marine species in a few regions to facilitate the conversion of size-specific density data into units of biomass (Taylor 1998; Reiss et al. 2005; Robinson et al. 2010). Such relationships, however, are not applicable to many reef macrophytes and sessile suspension feeding invertebrates with variable and complex morphologies that are difficult to identify as individuals and whose abundance is most often measured as percent cover. Relationships based on percent cover rather than size allow the conversion of abundance data of these species to biomass. There are relatively few reef species for which this has been done (Hatcher 1997; Shears and Babcock 2003; Harrer et al. 2013).

Here, we report quantitative relationships between wet mass and length or wet mass and percent cover for 84 species of benthic macroinvertebrates common to giant kelp forests in southern California. Several ongoing, multidecadal time series of species abundances exist for this system (Kenner et al. 2013; Kushner et al. 2013; Reed 2014a, b, c, d), and the ability to convert these data to a common metric of biomass offers great potential for exploring general ecological patterns and processes. We focus on benthic macroinvertebrates because previous studies have reported relationships between mass and length or mass and percent cover in this system for fishes (Quast 1968a, b; DeMartini et al. 1984; Love 2011) and macroalgae (Reed et al. 2009; Harrer et al. 2013). We also provide conversion factors for transforming wet mass into dry mass, shell-free and decalcified dry mass, and ash-free dry mass to facilitate

comparisons among studies using different metrics of mass, which are particularly useful in the analyses of large-scale spatial and temporal comparisons of secondary production and energy flow (Ricciardi and Bourget 1998).

Materials and methods

Field collections

The relationship between individual size and mass or aggregate percent cover and mass was determined for 84 species of benthic invertebrates found on shallow subtidal reefs in the Santa Barbara Channel. Specimens of all species were collected from 11 reefs (4- to 12-m depth) that are long-term study sites for the Santa Barbara Coastal Long Term Ecological Research program (see <http://sbc.lternet.edu/sites/sampling/> for detailed site descriptions). Specimens of common taxa were collected throughout the year over a 4-year period (April 2010–May 2014) to account for seasonal and interannual variation in body weight and composition; specimens of uncommon taxa were collected opportunistically. Species displaying large intra-annual variation in biomass due to seasonal gonadal development (e.g., sea urchins, crustaceans) were collected during nonspawning periods.

Specimens were collected using SCUBA, brought back to the laboratory in insulated coolers and placed in tanks supplied with running filtered seawater for 1–2 days before processing. This procedure allowed organisms to clear their digestive tract minimizing the contribution of gut contents to biomass. Species that could not be easily maintained in seawater tanks (e.g., sponges, hydroids) were processed immediately upon their arrival to the laboratory.

Measurements of body size and percent cover

Converting data on numerical abundance (i.e., density) to biomass requires information on the relationship between individual size and mass. For solitary species, individual size was measured as the length of a morphological trait specific for that species. Because our objective was to develop nondestructive methods for estimating standing biomass from abundance data collected in situ, only traits that were easily measured by divers without damaging the organism were used (e.g., total length, arm diameter, test diameter). Individuals of varying sizes were collected to generate relationships between length and wet mass for 53 species ($n = 6$ –207 individuals per species).

Percent cover is frequently used as a measure of abundance for many colonial species (e.g., compound ascidians, bryozoans, sponges) and small aggregating taxa that are often too numerous and indistinct for divers to efficiently

count (e.g., hydrozoans, anthozoans, polychaetes). Developing nondestructive methods for estimating standing biomass for these species thus requires information on the relationship between percent cover and mass. To obtain this information, divers measured the percent cover of a species within 10 cm × 10 cm quadrats using a uniform grid of 20 points. After data on percent cover were recorded, all tissues of the targeted species within the quadrat were collected by carefully removing it from the bottom or by collecting the substrate to which the species was attached and removing the tissue in the laboratory. Replicate quadrats containing varying amounts of percent cover were sampled to generate sufficient data for determining the relationship between percent cover and biomass for 31 species ($n = 9\text{--}40$ quadrats per species).

Measurements of body mass

Biomass can be reported using a variety of metrics. To facilitate interconversion among these various metrics, we estimated body mass as wet mass, dry mass, shell-free and decalcified dry mass and ash-free dry mass. To minimize the effects of water adhesion on wet mass measurements, specimens were removed from holding tanks and blotted dry with a clean paper towel or exposed in air at room temperature and allowed to desiccate for 1–2 min prior to being weighed (Dermott and Paterson 1974). Estimates of dry mass were obtained by placing specimens of known wet mass in a drying oven at 60 °C for several days until their mass remained constant. Water content was estimated as $[1 - (\text{dry mass}/\text{wet mass})] \times 100$.

After being measured and weighed wet, the calcareous shells of mollusks and the chitinous exoskeletons of crustaceans were separated from the soft tissue, and then dried and weighed separately to obtain estimates of dry mass (i.e., dried soft tissue + shell) and shell-free dry mass (i.e., dried soft tissue only). The separation of soft tissue from chitinous exoskeletons of crustaceans was facilitated by microwaving the specimen for 1–2 min. Specimens of species with calcified structures such as bryozoans, gorgonians and echinoderms were dried whole to measure dry mass and then treated with a 5 % HCl solution for 3–4 h to dissolve the calcified structures. Treatment with acid was repeated as necessary to remove all calcification. After full decalcification, the remaining soft tissue was carefully separated from the acidic solution, rinsed in deionized water and placed back into the drying oven until the mass remained constant. The dried soft tissue was then reweighed to obtain a measure of decalcified dry mass.

Dry mass samples of species without hard external structures and shell-free decalcified dry mass samples of species with hard structures were processed to obtain estimates of ash-free dry mass. Samples of known mass were placed in

aluminum trays and burned in a muffle furnace at 500 °C for 4 h to volatilize all organic materials (Holme and McIntyre 1984). The weight of the remaining ash was subtracted from the shell-free decalcified dry mass to obtain a value for the ash-free dry mass of the sample.

The relationship between length and wet mass was best explained by the power function $M = aL^b$ where M is wet mass in grams and L is length of the species-specific morphological trait used to estimate size in mm. Linear regression was performed on log-transformed values of length and mass to estimate the slope (b) and intercept (a) for each species. The antilog of the intercept was calculated for use in the power function. Smearing estimates (Duan 1983) were calculated to correct for biases caused by back-transformation of logged parameters, which can result in an underestimate of the response variable (Smith 1993). Residuals from the log–log regression between length and mass for each species were tested for homoscedasticity using White's General Test (SAS 9.4 Cary, NC, USA). A simple linear regression of the form $M = bC$ was used to describe the relationship between percent cover (C) and wet mass (M). Examination of residuals and graphical inspection showed that percent cover data met the assumptions of linear regression for all species examined.

Results and discussion

Residuals from the log–log regressions between length and mass were homoscedastic for 52 of the 53 species examined. The lone exception was the shelled gastropod *Tegula brunnea* (χ^2 13.92, $p = 0.001$), and the relationship between shell length and wet mass presented for this species should be viewed with caution. The regressions were significant ($p < 0.02$) for all species and highly significant ($p \leq 0.001$) for 79 of 84 species, regardless of whether the dependent variable was length or percent cover (Table S1). Most importantly, the regression fit for most species was very good ($r^2 \geq 0.7$ for 74 species and ≥ 0.8 for 63 species). The sizes of the six species with the poorest regression fit (i.e., $r^2 \leq 0.51$) were based on measurements of soft parts that readily expand and contract. Difficulties in accurately measuring the length of these species likely contributed to higher measurement error and lower coefficients of determination. The high coefficients of determination for *Chaceia ovoidea* and *Calliostoma tricolor* ($r^2 = 0.99$) were based on small sample sizes ($n = 6$). In the case of the common pholad clam *C. ovoidea*, the size range in siphon diameters of the six individuals used in the regression analysis (16–35 mm) largely encompassed the size range of nearly 1000 individuals measured in the field (14–46 mm) suggesting that the length–mass relationship developed for this species is quite robust over the wide range of sizes

encountered for this species. In contrast, the top snail *C. tricolor* is uncommon at our study sites. The six individuals used in the regression were the only ones that we encountered during our study and represent a relatively narrow size range (12–17 mm) causing more uncertainty in the general application of the length–mass relationship for this species. On average, relationships between wet mass and percent cover tended to be better than those between wet mass and length (mean $r^2 = 0.92 \pm 0.01$ SE vs. 0.79 ± 0.03 SE for cover and length, respectively; $F_{1,83} = 13.32$, $p = 0.0005$).

Species-specific conversion factors for converting different metrics of mass are provided in Table S2. As expected, body composition varied within and among phyla. The percent water mass averaged 61–72 % across all phyla except Mollusca, which averaged 44 % (Fig. 1a). The lower mean value for percent water in mollusks reflects the large number of shelled gastropods and bivalves in this group; in contrast, the water content of the three species of soft bodied mollusks averaged 84 %. Interspecific variation in the percent water within phyla was attributed largely to variation in the mass of calcified structures (shells and skeletons, Fig. 1b). The notable exception to this pattern was the tunicates, which lack calcification, but displayed considerable variability in their water content (50–93 %). The mean ash content of shell-free decalcified mass was highest in sponges (68 %) and tunicates (75 %, Fig. 1c). The high ash content of sponges undoubtedly reflects the mass associated with their spicules, which were silicious in four of the five species examined with the exception of *Leucilla*

nuttingi which has calcareous spicules. The tunicates examined in this study consisted entirely of ascidians, which do not have hard structures as their tunic is composed of proteins and complex carbohydrates. The blood of many ascidians does contain high concentrations of metals including vanadium and iron (Swinehart et al. 1974; Michibata et al. 1986), which may have contributed to the high ash content of this group.

Developing species-specific relationships between size (or percent cover) and mass or between different metrics of mass is tedious, and the use of common relationships that can be broadly applied to species within a larger taxonomic group has considerable appeal. Our results, however, suggest that estimating the mass of an organism from its size or percent cover using a relationship developed for a related species can be problematic as the slopes of the regressions varied considerably among species within some taxonomic groups (Table S1). For example, the slopes of the relationship between wet mass and percent cover for the four species of sponges examined differed by 12-fold; there was even a twofold difference in slopes between the morphologically similar congeneric bryozoans *Bugula californica* and *B. neritina*. By contrast, similar relationships between wet mass and length were observed among the five species of holothuroids (0.45-fold difference in slopes) and among the 11 species of shelled gastropods (0.74-fold difference), suggesting that use of a common relationship to estimate biomass from size may be possible for species in these groups. Ratios for converting one type of mass

Fig. 1 Box plots showing variation among species within phyla for: **a** percent of wet mass composed of water, **b** percent of dry mass composed of shell or other calcium carbonate structures and **c** percent ash in shell-free decalcified mass. The length of the box represents the interquartile range, the solid circle in the box denotes the mean, the horizontal line in the box represents the median and the whiskers extend to the minimum and maximum values

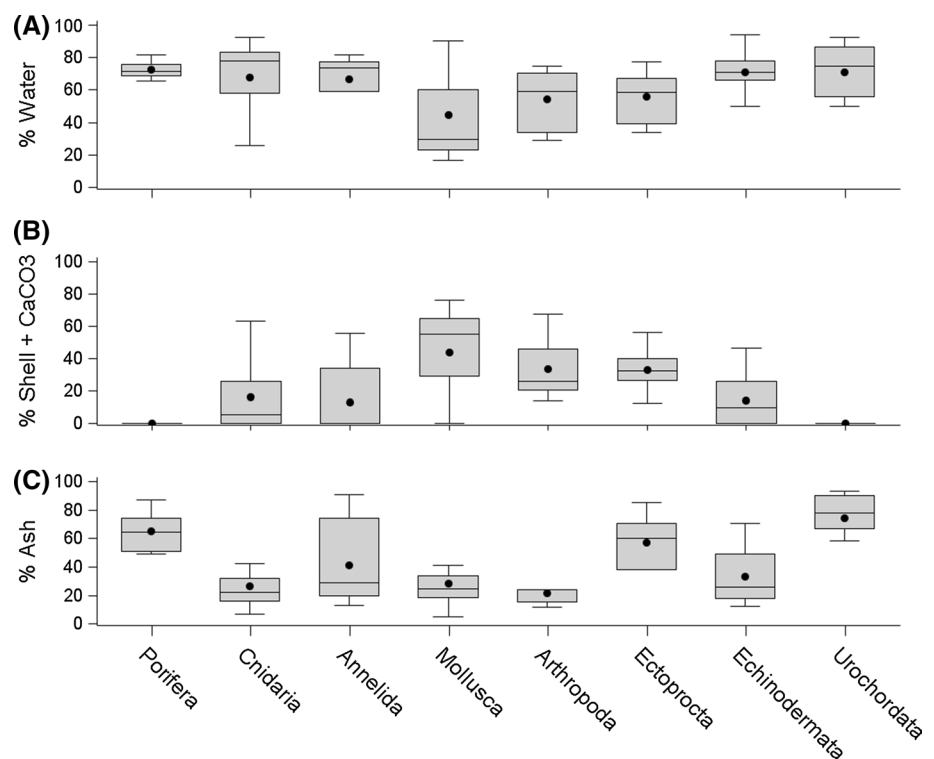


Table 1 95 % confidence limits for mass-to-mass conversion factors reported by Ricciardi and Bourget (1998) for major taxonomic groups and the percentage of species of kelp forest invertebrates within those confidence limits

	AFDM/WM		AFDM/DM		N
	CI	%	CI	%	
Porifera					
Demospongiae	9.3–12.1	0	37.8–56.4	50	4
Cnidaria					
Actiniaria	6.0–22.6	100	73.6–94.2	100	6
Annelida					
Polychaeta, Sedentaria	13.4–16.6	20	67.1–75.3	40	5
Mollusca					
Gastropoda, Prosobranchia	5.7–9.3	42			12
Gastropoda, Opisthobranchia			62.5–74.4	33	3
Bivalvia	5.2–6.4	0			6
Cephalopoda	13.6–29.2	100	81.3–97.1	100	1
Ectoprocta (Bryozoa)			28.4–53.4	0	5
Arthropoda					
Decapoda	14.6–18.4	0	62.9–70.9	0	3
Echinodermata					
Astroidea	7.1–15.3	50			6
Ophiuroidea	4.8–10	50			2
Echinoidea	1.4–5.6	33			3
Holothuroidea			35.0–64.2	43	
Tunicata					
Ascidacea			31.5–48.3	20	10

Ricciardi and Bourget (1998)

AFDM ash-free dry mass, WM wet mass, DM dry mass, N number of kelp forest species examined in each taxonomic group

into another also varied considerably among species within the same taxonomic group, even when accounting for differences in the presence of shells and calcified structures (Table S2). Moreover, the mass-to-mass conversion factors for the majority of the species that we examined fell outside the 95 % confidence interval reported by Ricciardi and Bourget (1998) for the broad taxonomic group to which they belonged (Table 1). Collectively, our findings indicate that considerable caution should be used when attempting to apply general biomass-related relationships that were developed for other species, even if they were closely related.

Tests of general ecological theory such as the relationship between biodiversity and ecosystem function are at present overwhelmingly conducted in terrestrial ecosystems, but work in marine systems has increased and helped shift focus toward inclusion of higher trophic levels in theoretical predictions (Gamfeldt et al. 2015). The data presented here will continue this trend by allowing

more holistic analyses of patterns in biomass allocation and energy flow in kelp forest communities of southern California. Conversion to a common currency of biomass facilitates spatiotemporal comparisons of biodiversity among morphologically and taxonomically disparate species occupying different trophic levels and enables investigations of the potential role of biodiversity in stabilizing fluctuations in community biomass (Gross et al. 2014). Kelp forests are highly diverse and productive ecosystems that are of conservation concern (Steneck et al. 2002; Schiel and Foster 2015) and can serve as a model for testing ecological theory in the oceans. New methods for nondestructively sampling these communities will help us bring them and other subtidal ecosystems into the mainstream of ecology.

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