

Allometric scaling of mortality rates with body mass in abalones

Marisa Rossetto · Giulio A. De Leo ·
Daniele Bevacqua · Fiorenza Micheli

Received: 22 November 2010 / Accepted: 4 October 2011
© Springer-Verlag 2011

Abstract The existence of an allometric relationship between mortality rates and body mass has been theorized and extensively documented across taxa. Within species, however, the allometry between mortality rates and body mass has received substantially less attention and the consistency of such scaling patterns at the intra-specific level is controversial. We reviewed 73 experimental studies to examine the relationship between mortality rates and body size among seven species of abalone (*Haliotis* spp.), a marine herbivorous mollusk. Both in the field and in the laboratory, log-transformed mortality rates were negatively correlated with log-transformed individual body mass for all species considered, with allometric exponents remarkably similar among species. This regular pattern confirms previous findings that juvenile abalones suffer higher mortality rates than adult individuals. Field mortality rates were higher overall than those measured in the laboratory, and the relationship between mortality and body mass tended to be steeper in field than in laboratory conditions for all species considered. These results suggest that in the natural environment, additional mortality factors, especially linked to predation, could significantly contribute to

mortality, particularly at small body sizes. On the other hand, the consistent allometry of mortality rates versus body mass in laboratory conditions suggests that other sources of mortality, beside predation, are size-dependent in abalone.

Keywords Body mass · *Haliotis* spp. · Marine invertebrates · Size-dependent mortality · Survival

Introduction

Identifying the relative importance of factors that control mortality rates is fundamental to understanding and predicting dynamics of natural populations (Gulland 1987). Mortality, as most vital rates, is governed by a combination of physiological and environmental factors, and has been shown to be related to body mass and temperature for a wide range of organisms (Blueweiss et al. 1978; Calder 1983; Lorenzen 1996; Byström et al. 2006).

Theoretical and empirical studies suggest that an allometric relationship of the form, $\mu = aM^b$ where a is a normalization constant and b is a negative scaling exponent, exists between mortality rate (μ) and body mass (M) at different levels of biological organization (Peterson and Wroblewski 1984; McGurk 1986; Lorenzen 1996; Brown et al. 2004; Savage et al. 2004; Marbà et al. 2007; McCoy and Gillooly 2008). Among taxa, the allometry of mortality versus body mass is thought to result from the body size scaling of individual metabolic rate, which fosters faster aging in small organisms (West et al. 1997; Brown et al. 2004). Empirical studies of the size dependence of mortality rates across taxa suggest negative scaling exponents around -0.25 that agree with theoretical expectations (Savage et al. 2004; Marbà et al. 2007;

Communicated by Marc Mangel.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-011-2163-1) contains supplementary material, which is available to authorized users.

M. Rossetto (✉) · G. A. De Leo · D. Bevacqua
Dipartimento di Scienze Ambientali, Università degli Studi di
Parma, Parco Area delle Scienze 33A, 43100, Parma, Italy
e-mail: marisa.rossetto@nemo.unipr.it

G. A. De Leo · F. Micheli
Hopkins Marine Station, Stanford University, Pacific Grove,
CA 93950, USA

McCoy and Gillooly 2008). At the intra-specific level, in contrast, the size dependence of mortality rates is likely to originate from ecological factors (Peterson and Wroblewski 1984; Dickie et al. 1987), and analyses restricted to a single species or a group of closely related species suggest more negative exponents up to -0.46 (McGurk 1986, 1996; Lorenzen 1996, 2000; Bevacqua et al. 2011). Indeed, body size affects mortality in natural environments by offering resistance to environmental stressors and by influencing individual competitive abilities and susceptibility to predators (Charnov 1993; Kozłowski and Weiner 1997; Sogard 1997; Taborsky et al. 2003; Tilman et al. 2004). In addition, negative relationships between mortality and body size can be related to trade-offs in energy allocation between growth and maintenance (West et al. 2001; Moses et al. 2008). Young, fast-growing individuals can have a lower investment in processes such as immunological competence, resistance to physiological stressors, or developmental stability (Mangel and Stamps 2001; Hou et al. 2008), thereby suffering greater mortality compared to later stages.

In this study, we investigate the intra-specific allometric relationship between mortality rates and body mass in seven species of abalones *Haliotis* spp., which are marine mollusks characterized by a broad geographic distribution. In most marine invertebrates, mortality rates are size-dependent, with smaller individuals having lower survival probabilities than larger individuals (Seager 1982; Berg and Alatalo 1985; Gosselin and Qian 1997). In abalones, high juvenile mortality has been observed in the field (Shepherd and Breen 1992). Young abalones are expected to be more exposed to different sources of mortalities compared to adults given their weaker shells and a weaker power of attachment to the substratum (Prince et al. 1988). Predation, in particular, can be a major driver of higher natural mortality of young abalones compared to adult individuals (Hines and Pearse 1982; Tegner and Butler 1985), as larger individuals may attain a refuge from predation because of their stronger foot muscles, thicker shells, and the difficulty that predators have in handling them (Leaf et al. 2007). Because abalones have high commercial value and support both wild capture fisheries and aquaculture operations in several nations, a suite of laboratory and field studies have investigated mortality rates and their relationship with individual size or age. The plethora of published field and laboratory studies conducted on this molluskan genus provides an opportunity to: (1) compare the relationship between mortality rates and body mass among different species, and (2) compare this relationship between field and laboratory conditions. In particular, we address the questions (1) do mortality rates scale with body mass in abalone species and (2) does the relationship between mortality and body mass differ between natural and laboratory conditions?

Materials and methods

Dataset

Estimates of age-specific, length-specific or mass-specific mortality rates of abalones obtained in the field and under laboratory condition were searched both in peer-reviewed and grey literature. Data presented in graphs were extracted using the software Plot Digitizer 2.5. All measures of survival and mortality were converted into instantaneous yearly mortality rates μ (y^{-1}). Estimates of abalone mortality were collected for seven species, i.e. the pink (*Haliotis corrugata* Gray), green (*H. fulgens* Philippi) and red (*H. rufescens* Swainson) abalones (found in California, USA, and Baja California, Mexico); the two Australian species, blacklip (*H. rubra* Leach) and greenlip (*H. laevigata* Leach) abalones; the Japanese Ezo abalone (*H. discus hannai* Ino); and the green ormer (*H. tuberculata tuberculata* Linnaeus and *H. tuberculata coccinea* Reeve).

For estimates of mortality rates in the field, all experiments that monitored natural or transplanted populations of given age or size in the natural environment were included in the analysis (Table S1). With the exception of *H. tuberculata*, mortality data were available for multiple populations of the same abalone species (Table S1). Only 8% of the studies reported the initial body weight of individuals. When body weight was not available, we derived it from shell length through published length–mass relationships. In addition, in about 20% of cases, shell length was derived from individual age through the Von Bertalanffy growth equation. Length–age and length–mass relationships, when available, were extracted from the same data source; otherwise, they were selected from studies carried out in the nearest location. In total, 101 data points reporting mass-specific mortality rates in the field were collected from 27 studies (Table S1).

For estimates of mortality rates in the laboratory, we reviewed experiments conducted in closed systems under controlled conditions; studies that exposed individuals to different diet, light, density or temperature treatments were included (see Table S2), while studies in which abalones were starved or exposed to infectious agents as part of the experiments were excluded from the analysis. The initial weight of individuals was reported in 54% of laboratory experiments; in all other cases, the mass was calculated from the shell lengths of reared individuals using published length–mass relationships (Table S2). In total, 274 data points reporting mortality rates at different body sizes in the laboratory were extracted from 46 studies (Table S2).

Temperatures experienced by individuals in field and laboratory studies were recorded from the source publications, when available. For field studies in which temperature was not reported, the geographic coordinates of the

study location were used to derive a 30-year average of sea surface temperature estimated from the NCEP real-time Marine database (NCEP Marine data provided by the NOAA/OAR/ESRL PSD, Boulder, CO, USA, from their Web site at <http://www.esrl.noaa.gov/psd/>).

A summary of data reporting the range of mortality rates, sizes, and temperatures for each *Haliotis* species and condition is presented in Table 1.

Statistical analysis

The significance of the relationship between log-transformed mortality rates and log-transformed body mass was tested for each species both in the field and in the laboratory using ordinary least-square regression. Analysis of covariance (ANCOVA) was then used to test whether the relationship between body mass and mortality rates varied among species and between natural and laboratory conditions. The model included log-transformed mortality rates ($\ln\mu$) as the response variable and three explanatory variables with all first order interactions and multiplicative terms: log-transformed body mass $\ln M$ (covariate); species (seven levels: *H. corrugata*, *H. discus hannai*, *H. fulgens*, *H. rufescens*, *H. laevigata*, *H. rubra*, *H. tuberculata*); and condition (two levels: laboratory and field conditions).

As temperature is known to strongly influence vital rates, including mortality rates, we also tested linear models including temperature. In particular, empirical and theoretical studies conducted at intra- and inter-specific levels, basing their arguments on the theoretical framework of Gillooly et al. (2001) and Brown et al. (2004), suggest that mortality rates scale with the inverse of temperature as:

$$\mu \propto \exp\left(-\frac{E}{kT}\right)$$

where k is Boltzmann’s constant (8.62×10^{-5} eV/K), T is temperature in K, and E is the activation energy to be

estimated on available data. First, the temperature effect was tested for each species both in the field and in the laboratory by fitting a multiple linear model of the form:

$$\ln \mu \propto \text{const} + \alpha \ln M - \frac{\beta}{kT}.$$

Then, we tested the effect of temperature on mortality rates in laboratory and field conditions assuming a common temperature dependence of mortality rates among all species, by adding the explanatory variable $1/kT$ to the ANCOVA.

In our dataset, the range of laboratory studies included much smaller animals than those in the wild population studies (Table 1), potentially influencing our comparison of mass–mortality relationships between field and laboratory conditions. In order to check the robustness of our results, we therefore performed ANCOVAs on a subset of laboratory data that only included the range in body masses reported in the field studies.

Finally, a sensitivity analysis was carried out to assess how uncertainty in parameters of the Von Bertalanffy growth equations and of length–mass relationships affects final estimates of the allometric exponent (see Electronic Supplementary Materials).

Results

Log-transformed mortality rates in the field were negatively correlated with individual log-transformed body mass for all seven species considered (Fig. 1; Fig. S1a). The relationship was significant for *H. corrugata* ($p < 0.05$, $r^2 = 0.76$, $n = 6$), *H. discus hannai* ($p < 0.001$, $r^2 = 0.69$, $n = 14$), *H. laevigata* ($p < 0.05$, $r^2 = 0.38$, $n = 16$), *H. rubra* ($p < 0.001$, $r^2 = 0.68$, $n = 31$), *H. rufescens* ($p < 0.001$, $r^2 = 0.46$, $n = 23$); nearly significant for *H. fulgens* ($p = 0.064$, $r^2 = 0.53$, $n = 7$); and not significant for *H. tuberculata* ($p = 0.121$, $r^2 = 0.77$, $n = 4$).

Table 1 Summary of the dataset reporting the range of mortality rates, sizes and temperatures for each species and type of study

Species	Field studies				Laboratory studies			
	No. studies	Mortality range (year ⁻¹)	Mass range (g)	Temperature range (°C)	No. studies	Mortality range (year ⁻¹)	Mass range (g)	Temperature range (°C)
<i>H. corrugata</i>	2	0.20–1.05	9.8–459.3	16.5	5	0.29–22	2×10^{-7} –7.2	16.8–20
<i>H. discus hannai</i>	5	0.22–16.04	0.0054–18.23	4.4–17	12	0.05–36.78	8.3×10^{-6} –25	3.9–22.3
<i>H. fulgens</i>	3	0.11–3.04	0.97–459.1	16.5–18.7	10	0.04–43.70	6×10^{-7} –3.7	16–28
<i>H. laevigata</i>	4	0.31–8.20	0.36–231.8	15–17.20	7	0.09–18.07	4×10^{-7} –10	16.9–20
<i>H. rubra</i>	9	0.09–37.29	0.029–308.5	13–22	4	0.32–60.95	4.01×10^{-6} –3.39	16.9–19.2
<i>H. rufescens</i>	5	0.05–4.61	7.7–829.5	12.35–17	7	0.05–19.16	1.7×10^{-6} –99.23	11.1–22
<i>H. tuberculata</i>	1	0.14–1.70	0.67–179.9	14	6	0.12–6.96	8×10^{-7} –18.35	13–24.6

Mean estimates of allometric exponents in the field ranged from -0.52 for red abalone to -0.30 for blacklip abalone (Fig. 2). Estimated intercepts ranged from -0.11 for Ezo abalone to 2.09 for red abalone (Fig. 2), corresponding to mortalities at unit weight of 0.89 and 8.01 y^{-1} , respectively.

Log-transformed mortality rates in the laboratory also scaled negatively with individual log-transformed body mass (Fig. 1; Fig. S1b). Allometric relationships were highly significant for all seven species considered: $p < 0.001$, $r^2 = 0.93$ for *H. corrugata* ($n = 29$); $p < 0.001$, $r^2 = 0.68$ for *H. discus hannai* ($n = 73$); $p < 0.001$, $r^2 = 0.54$ for *H. fulgens* ($n = 38$); $p < 0.001$, $r^2 = 0.46$ for *H. laevigata* ($n = 29$); $p < 0.05$, $r^2 = 0.33$ for *H. rubra* ($n = 23$); $p < 0.001$, $r^2 = 0.52$ for *H. rufescens* ($n = 51$) and $p < 0.001$, $r^2 = 0.62$ for *H. tuberculata* ($n = 31$). Mean allometric exponents ranged from -0.32 for Ezo abalone to -0.15 for blacklip abalone (Fig. 2). Estimated intercepts ranged from -1.58 for green ormer to 0.30 for blacklip abalone (Fig. 2), corresponding to mortalities at unit weight of 0.20 and 1.35 y^{-1} , respectively.

The scaling of mortality with body mass in the field was very similar across the seven species considered (Fig. 1), with estimates of allometric exponents having widely overlapping confidence intervals (Fig. 2). In the laboratory, the slopes of the log–log relationships were also similar across species (Fig. 1), and confidence intervals of estimated allometric exponents overlapped with the only exception of *H. discus hannai* (Fig. 2). In the analysis of covariance (Table 2), the significant interaction term between $\ln M$ and species ($p < 0.05$) was entirely driven by the Japanese species, which showed more negative scaling

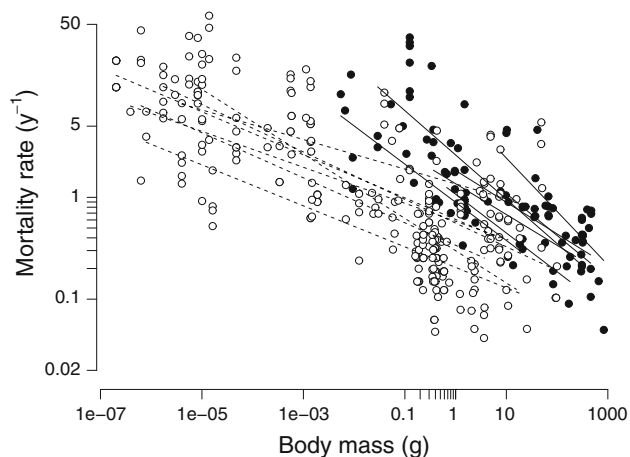


Fig. 1 Scatter plot of mortality rate versus body mass (both natural log-transformed) for seven species of abalone (*Haliotis* spp.), along with the fitted regression line for each species, for laboratory studies (white circles, dashed lines) and for field studies (black circles, solid lines). Data presented here are not temperature corrected; however, temperature correction has little effect on the regression lines that are displayed (see “Results”)

in laboratory conditions with respect to the other species. For all seven species considered, mean estimates of allometric exponents were consistently more negative in natural than in laboratory conditions (Fig. 2). Although the differences in allometric exponents between field and laboratory conditions were not significant at the species level (with the exception of *H. rubra*), the estimated slopes in the laboratory were significantly lower than those estimated in natural conditions, as indicated by the significant interaction term between $\ln M$ and condition (Table 2). Common allometric exponents were -0.40 (95% CI -0.47 , -0.34) in the field and -0.21 (95% CI -0.26 , -0.16) in the laboratory.

The intercepts of the log–log relationships estimated in the field, representing the log-mortality rate at unit weight, were significantly different among species ($p < 0.001$, Table 1), indicating that individuals of the same body size belonging to different abalone species experience different mortality rates. The intercepts of allometric relationships estimated in the laboratory were smaller than the estimates obtained in field conditions (Table 2), indicating that mortality rates at unit weight are generally higher in the field than in the laboratory (Fig. 2). The interaction term between species and condition was near to the significance levels ($p = 0.10$), suggesting that the differences in mortality rates at unit weight between laboratory and natural conditions are variable among species. This indicates that species with relatively high mortality in the field do not necessarily also have relatively high mortality in the laboratory.

Within single species, temperature had relatively little or no effect on the scaling of mortality rate, being not significant in 10 of 14 cases. For laboratory studies, temperature was significant in three of the seven species considered, with values of E ranging from 7.01 (95% CI 1.62 , 12.41) eV for *H. rubra* to 1.83 (95% CI 1.12 , 2.56) eV for *H. rufescens* and 0.45 eV (95% CI 0.06 , 0.85) for *H. tuberculata*. In natural conditions, temperature was significant only for *H. rubra*, with E equal to 1.18 eV (95% CI 0.42 , 1.94) (in two cases, for *H. tuberculata* and *H. corrugata*, we could not test the temperature effect given the low number of data; see Table 1). Among species, instead, temperature effect was highly significant ($p < 0.001$; Table 2). Mortality increased with temperature with activation energy of 0.62 eV (95% CI 0.36 , 0.89). When temperature was included in the model, however, variability was only marginally reduced, with significant differences in mortality at unit weight among species still remaining (Table 3). Common allometric exponents obtained when adding $1/kT$ to the model remained very similar to previous estimates, being -0.37 (95% CI -0.45 , -0.30) and -0.22 (95% CI -0.24 , -0.20) in the field and laboratory, respectively.

Fig. 2 Estimates of **a** slopes and **b** intercepts of linear regressions of the logarithm of mortality rate versus the logarithm of body mass for abalone species along with 95% confidence intervals in the laboratory (*white circles*) and in the field (*black circles*). *Diamonds* represent common estimate of allometric exponents for laboratory (*white*) and field (*black*) studies with 95% confidence intervals. As intercepts were significantly different among species (see “Results”), we did not compute common intercepts for laboratory and field condition

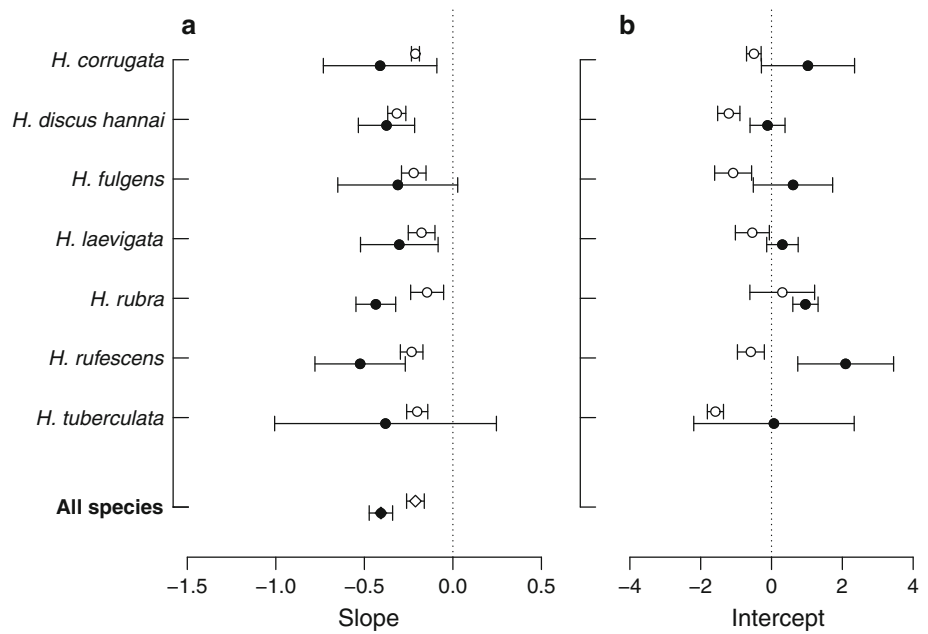


Table 2 ANOVA table for the statistical model relating log-transformed mortality rate ($\ln\mu$) to variation in log-transformed body mass ($\ln M$), species (seven levels: *H. corrugata*, *H. discus hannai*, *H. fulgens*, *H. rufescens*, *H. laevigata*, *H. rubra*, *H. tuberculata*), and condition (two levels: laboratory and field conditions)

Source of variation	<i>df</i>	Sum sq	<i>F</i>	<i>p</i>
$\ln M$	1	476.39	508.75	<0.001
Species	6	42.56	7.58	<0.001
Cond	1	59.04	63.05	<0.001
$\ln M$:species	6	16.98	3.02	<0.01
$\ln M$:cond	1	18.68	19.95	<0.001
Species:cond	6	10.04	1.79	0.101
$\ln M$:species:cond	6	4.85	0.86	0.522
Residuals	347	324.93		

Table 3 ANOVA table for the statistical model relating log-transformed mortality rate ($\ln\mu$) to variation in inverse temperature ($1/kT$), log-transformed body mass, species, and condition

Source of variation	<i>df</i>	Sum sq	<i>F</i>	<i>p</i>
$1/kT$	1	19.26	21.29	<0.001
$\ln M$	1	422.97	467.60	<0.001
Species	6	39.20	7.22	<0.001
Cond	1	66.52	73.54	<0.001
$\ln M$:species	6	9.85	1.81	0.09
$\ln M$:cond	1	15.11	16.71	<0.001
Species:cond	6	11.37	2.09	0.05
$\ln M$:species:cond	6	3.96	0.73	0.626
Residuals	332	300.31		

The results of the ANCOVA (with and without temperature) performed on the reduced dataset, that excluded 35% of laboratory data outside the body mass range of field data, remained unchanged compared to the full dataset with respect to the significance levels of the explanatory variables and the magnitude of estimated regression coefficients (see Tables S3 and S4 in the ESM).

Discussion

Results of our analyses show that body mass is an important predictor of mortality rates both at the intra-specific level and among closely related species of *Haliotis* spp. First, mortality decreases significantly with individual body mass both in natural and laboratory conditions, indicating the size-dependence of different sources of mortality for abalone. Second, allometric exponents are remarkably similar among seven species of the same genus. Third, our comparison between field and laboratory studies indicated that, in the natural environment, factors such as predation and environmental stress make an additional contribution to mortality, particularly for younger individuals.

In the field, allometric exponents of mortality–weight relationships were similar among species, and we estimated a common exponent of -0.40 , which falls in the range of observed intra-specific allometric exponents obtained in previous studies on marine organisms (-0.26 to -0.46 ; McGurk 1986, 1996; Lorenzen 1996, 2000; Bevacqua et al. 2011). In laboratory conditions, allometric exponents were also similar among species and the estimated common slope was -0.21 , which falls in the range of exponents

obtained for fish species in culture conditions (Lorenzen 1996). These consistent relationships confirm previous observations that juvenile abalones suffer higher mortality rates than adult individuals (Hines and Pearse 1982; Leaf et al. 2007). Laboratory data thus suggest that, besides predation, other sources of mortality are likely to be size-dependent. Intra-specific competition for food resources in the laboratory experiments analyzed in the present study seems unlikely as food was given ad libitum. Similarly, competition for space was also unlikely as abalones covered on average less than 20% of available space in all the laboratory experiments considered. As inter-specific ecological interactions—i.e. predation and inter-specific competition—are likely to be absent, higher mortality rates of smaller individuals with respect to larger adults may be due to ontogenetic development of the immune system, differences in abilities to handle environmental stressors, or variation in available energy reserves (Ellis 1988; Post and Evans 1989; Kalinin et al. 1993). Studies on energy allocation in abalones (Peck et al. 1987) show that the fraction of the energy budget used for somatic growth decreases with increasing body mass, whereas energy allocated to mucus production, which is important for locomotion, protection and signal transmission (Davies and Williams 1998; Hutchinson et al. 2007), increases with increasing body mass (Peck et al. 1987). Such energetic trade-offs between growth rates and maintenance could be partially responsible for higher mortality rates of young, fast-growing individuals with respect to adult individuals (Mangel and Stamps 2001; Hou et al. 2008). The degree by which the amount of energy allocation to maintenance could be a direct predictor of mortality rates, however, requires further investigation.

In our study, allometric exponents were remarkably similar among the different species of *Haliotis* spp. Mortality rates at unit weight, on the contrary, were markedly different among abalone species, especially in the field. Interestingly, previous studies on the scaling of mortality versus body size among species also found more variability in mortality at unit weight than in allometric exponents (Lorenzen 1996, 2000). Abalone populations considered in these analyses have different geographic distributions spanning from America to Japan to Australia (Table S1), different water depth ranges, i.e. intertidal for *H. fulgens* and *H. rubra* and subtidal for *H. corrugata*, *H. discus hannai*, *H. laevigata*, *H. rufescens* and *H. tuberculata* (Guzmán del Prío 1992; Tegner et al. 1992; James et al. 2007), and different maximum adult sizes, from 8 to 30 cm shell length (Day and Fleming 1992). However, the apparent variability in overall mortality rates could not be attributed to a latitudinal effect, i.e. to the different temperature ranges experienced by the various abalone species. Additionally, species with large maximum adult sizes did

not appear to have lower mortality rates than smaller species: for example, *H. tuberculata*, the smallest species of abalones considered in the analysis, tended to experience lower level of mortality rates both in the field and in the laboratory than *H. rufescens*, which has the greatest adult size (Fig. 2). However, the different habitat ranges occupied by the abalone species could entail different levels of overall predation, food availability and/or exposure to environmental stress that could explain the dissimilarity in mortality at unit weight within the genus *Haliotis*.

Comparison of allometric relationships between field and laboratory studies showed that mortality rates are significantly greater in the field than in controlled laboratory conditions. This is consistent with the expectation that in the natural environment mortality may be higher because organisms are exposed to temperature extremes, storms, disease, starvation, and to ecological interactions, e.g., predation and competition, which may all cause an increase in abalone mortality (Shepherd and Breen 1992). The steeper allometric scaling in field populations compared to laboratory studies suggests that natural causes of mortality present in the field may be more severe for juveniles than for adults. In particular, natural predation is thought to be strongly size dependent for abalone as juveniles are more vulnerable to predators than adults given their thinner shell (Prince et al. 1988; Shepherd and Breen 1992). In our study, all species are represented both in natural and in culture conditions, thus avoiding possible confounding factors due to variability in allometric exponents among species. In addition, the differences in allometric scaling between laboratory and wild populations remained consistent when including only the laboratory studies with the same body mass range as the field studies, making us confident in the robustness of our analysis. The only previous comparison of allometric scaling of mortality rates in wild and cultured fish populations at the intra-specific level (Lorenzen 1996) found that mortality rates were lower overall in the laboratory, as in our study, but that allometric scaling was more negative in the laboratory than in natural populations, the opposite of our results for abalone. One possible reason for such discrepancy is that juvenile fish mortality in cultured conditions could increase due to cannibalism, which has been observed in several fish species but is highly unlikely for grazing mollusks such as abalones. Further comparisons of allometric scaling between field and laboratory studies could contribute to a better understanding of the size-dependent differences in mortality.

Temperature had little effect on the size scaling of mortality rates within a single species. This could be due to the small temperature ranges experienced by some species in the field and laboratory studies (Table 1) and/or to the effect of local adaptation that may obscure the temperature

dependence of vital rates within a species (Yamahira and Conover 2002; Tilman et al. 2004). Indeed, several laboratory experiments suggest that the ability of abalone to acclimate to water temperature is strongly related to the biogeographical distribution of the species (Dalhoff and Somero 1993) and that thermal tolerance is relatively constant over the temperature range experienced by a species in its natural environment (Diaz et al. 2000, 2006). However, among species, the temperature effect on mortality rates was significant and consistent with previous studies conducted at the inter-specific level (McCoy and Gillooly 2008), suggesting that mortality is generally higher at high temperatures. Estimated activation energy (0.62 eV) falls in the presumed range of 0.2–1.2 eV (Gillooly et al. 2001; Downs et al. 2008) and was similar to the values of E found at the inter-specific level (0.57 eV; McCoy and Gillooly 2008).

Other factors are likely to influence mortality rates in abalone besides body mass. In our study, the residual variability in mortality could be attributed to different diets, local environmental or density conditions both in the field and in the laboratory, as well as random variation among studies. In addition, chronic diseases, e.g., the withering syndrome, can tremendously increase mortality rates leading to precipitous population declines (such as the mass mortality events observed in California for the black abalone *H. cracherodii*; Raimondi et al. 2002). Understanding the circumstances under which mortality is likely to increase is fundamental to guide management and restoration efforts.

Abalones are representative of a suite of marine invertebrates including mollusks and echinoderms that share similar life history and characteristics, such as size refuges from predation associated with the development of shells, tests, and spines, and benthic, sedentary juveniles and adults. Thus, we hypothesize that our results could be broadly applicable to other taxa.

Acknowledgments We thank Stefano Leonardi, Luca Bolzoni and Simone Vincenzi for helpful comments on statistical analysis and presentation of results and Marc Mangel and Ashley Greenley for editorial advice. We are also grateful to three anonymous referees for useful comments on the manuscript draft. This work was supported through funds from the Walton Family Foundation and from the Italian Ministry of Research (PRIN project 2008 and Interlink project # II04CE49G8).

References

- Berg CJ, Alatalo P (1985) Biology of the tropical bivalve *Asaphis deflorata* (Linne, 1758). *Bull Mar Sci* 37:827–838
- Bevacqua D, Melià P, De Leo GA, Gatto M (2011) Intra-specific scaling of natural mortality in fish: the paradigmatic case of European eel. *Oecologia* 165:333–339
- Blueweiss L, Fox H, Kudzma V, Nakashima D, Peters R, Sams S (1978) Relationships between body size and some life history parameters. *Oecologia* 37:257–272
- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. *Ecology* 85:1771–1789
- Byström P, Andersson J, Kiessling A, Eriksson LO (2006) Size and temperature dependent foraging capacities and metabolism: consequences for winter starvation mortality in fish. *Oikos* 115:43–52
- Calder WA (1983) Body size, mortality and longevity. *J Theor Biol* 102:135–144
- Charnov EL (1993) Life history invariants: some explorations of symmetry in evolutionary ecology. Oxford University Press, Oxford
- Dalhoff E, Somero GN (1993) Effects of temperature on mitochondria from abalone (genus *Haliotis*): adaptive plasticity and its limits. *J Exp Biol* 185:151–168
- Davies MS, Williams GA (1998) Mucus in marine molluscs. *Adv Mar Biol* 34:1–71
- Day RW, Fleming AE (1992) The determinants and measurement of abalone growth. In: Shepherd SA, Tegner MJ, Guzmán del Prío SA (eds) Abalone of the World: biology, fisheries and culture. Fishing News, Oxford, pp 141–168
- Diaz F, Rio-Portilla MA, Sierra E, Aguilar M, Re-Araujo AD (2000) Preferred temperature and critical thermal maxima of red abalone *Haliotis rufescens*. *J Therm Biol* 25:257–261
- Diaz F, Re AD, Medina Z, Re G, Valdez G, Valenzuela F (2006) Thermal preference and tolerance of green abalone *Haliotis fulgens* (Philippi, 1845) and pink abalone *Haliotis corrugata* (Gray, 1828). *Aquac Res* 37:877–884
- Dickie LM, Kerr SR, Boudreau PR (1987) Size-dependent processes underlying regularities in ecosystem processes. *Ecol Monogr* 57:233–250
- Downs CJ, Hayes JP, Tracy CR (2008) Scaling metabolic rate with body mass and inverse body temperature: a test of the Arrhenius fractal supply model. *Funct Ecol* 22:239–244
- Ellis AE (1988) Ontogeny of the immune system in teleost fish. In: Ellis AE (ed) Fish vaccination. Academic, London, pp 20–31
- Gillooly JF, Brown JH, West JB, Savage VM, Charnov EL (2001) Effects of size and temperature on metabolic rate. *Science* 293:2248–2251
- Gosselin LA, Qian PY (1997) Juvenile mortality in benthic marine invertebrates. *Mar Ecol Prog Ser* 146:265–282
- Gulland JA (1987) Natural mortality and size. *Mar Ecol Prog Ser* 39:197–199
- Guzmán del Prío SA (1992) A review of the biology of abalone and its fishery in Mexico. In: Shepherd SA, Tegner MJ, Guzmán del Prío SA (eds) Abalone of the World: biology fisheries and culture. Blackwell, Oxford, pp 341–360
- Hines AH, Pearse JS (1982) Abalones, shells and sea otters: dynamics of prey populations in central California. *Ecology* 63:1547–1560
- Hou C, Zuo W, Moses ME, Woodruff WH, Brown JH, West GB (2008) Energy uptake and allocation during ontogeny. *Science* 322:736–739
- Hutchinson N, Davies MS, Ng JSS, Williams GA (2007) Trail following behaviour in relation to pedal mucus production in the intertidal gastropod *Monodonta labio* (Linnaeus). *J Exp Mar Biol Ecol* 349:313–322
- James DS, Day RW, Shepherd SA (2007) Experimental abalone ranching on artificial reef on Port Phillip Bay, Victoria. *J Shellfish Res* 26:687–695
- Kalinin AL, Tadeu-Rantin F, Lesner-Glass M (1993) Dependence on body size of respiratory function in *Hoplias malabaricus* (Teleostei, Erythrinidae) during graded hypoxia. *Fish Physiol Biochem* 12:47–51

- Kozłowski J, Weiner J (1997) Interspecific allometries are by-products of body size optimization. *Am Nat* 147:101–114
- Leaf RT, Rogers-Bennett L, Haaker PL (2007) Spatial, temporal and size specific variation in mortality estimates of red abalone, *Haliotis rufescens* from mark-recapture data in California. *Fish Res* 83:341–350
- Lorenzen K (1996) The relationship between body weight and natural mortality in juvenile and adult fish: a comparison of natural ecosystems and aquaculture. *J Fish Biol* 49:627–647
- Lorenzen K (2000) Allometry of natural mortality as a basis for assessing optimal release size in fish-stocking programmes. *Can J Fish Aquat Sci* 57:2374–2381
- Mangel M, Stamps J (2001) Trade-offs between growth and mortality and the maintenance of individual variation in growth. *Evol Ecol Res* 3:583–593
- Marbà N, Duarte CM, Agustí S (2007) Allometric scaling of plant life history. *Proc Nat Acad Sci USA* 104:15777–15780
- McCoy MW, Gillooly JF (2008) Predicting natural mortality rates of plants and animals. *Ecol Lett* 11:710–716
- McGurk JD (1986) Natural mortality of marine pelagic fish eggs and larvae: role of spatial patchiness. *Mar Ecol Prog Ser* 34:227–242
- McGurk MD (1996) Allometry of marine mortality of Pacific salmon. *Fish Bull* 94:77–88
- Moses ME, Hou C, Woodruff WH, West GB, Nekola JC, Zuo W, Brown JH (2008) Revisiting a model of ontogenic growth: estimating model parameters from theory and data. *Am Nat* 171:632–645
- Peck LS, Culley MB, Helm MM (1987) A laboratory energy budget for the ormer *Haliotis tuberculata* L. *J Exp Mar Biol Ecol* 106:103–123
- Peterson I, Wroblewski JS (1984) Mortality rate of fishes in the pelagic ecosystem. *Can J Fish Aquat Sci* 41:1117–1120
- Post JR, Evans DO (1989) Size-dependent overwinter mortality of young-of-the year yellow perch (*Perca flavescens*): laboratory, in situ enclosure, and field experiments. *Can J Fish Aquat Sci* 46:1968–1985
- Prince JD, Sellers TL, Ford WB, Talbot SR (1988) Recruitment, growth, mortality and population structure in a southern Australian population of *Haliotis rubra* (Mollusca: Gastropoda). *Mar Biol* 100:75–82
- Raimondi PT, Wilson CM, Ambrose RF, Engle JM, Michinton TE (2002) Continued declines of black abalone along the coast of California: are mass mortalities related to El Niño events? *Mar Ecol Prog Ser* 242:143–152
- Savage VM, Gillooly JF, Brown JH, West GB, Charnov EL (2004) Effects of body size and temperature on population growth. *Am Nat* 163:429–441
- Seager JR (1982) Population dynamics of the Antarctic opisthobranch *Philine gibba* Strebel. *J Exp Mar Biol Ecol* 60:163–179
- Shepherd SA, Breen PA (1992) Mortality in abalone: its estimation, variability, and causes. In: Shepherd SA, Tegner MJ, Guzmán del Próo SA (eds) *Abalone of the world: biology fisheries, and culture*. Fishing News, Oxford, pp 276–304
- Sogard SM (1997) Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bull Mar Sci* 60:1129–1157
- Taborsky B, Dieckmann U, Heino M (2003) Unexpected discontinuities in life-history evolution under size-dependent mortality. *Proc R Soc Lond B* 270:713–721
- Tegner MJ, Butler RA (1985) The survival and mortality of seeded and native red abalones *Haliotis rufescens*, on the Palos Verdes Peninsula. *Calif Dep Fish Game* 71:150–163
- Tegner MJ, DeMartini JD, Karpov KA (1992) The California red abalone fishery: a case study in complexity. In: Shepherd SA, Tegner MJ, Guzmán del Próo SA (eds) *Abalone of the World: biology, fisheries, and culture*. Fishing News, Oxford, pp 370–383
- Tilman D, HilleRisLambers J, Harpole S, Dybzinski R, Fargione J, Clark C, Lehman C (2004) Does metabolic theory apply to community ecology? It's a matter of scale. *Ecology* 85:1797–1799
- West GB, Brown JH, Enquist BJ (1997) A general model for the origin of allometric scaling laws in biology. *Science* 276:122–126
- West GB, Brown JH, Enquist BJ (2001) A general model for ontogenic growth. *Nature* 413:628–631
- Yamahira K, Conover DO (2002) Intra- versus interspecific latitudinal variation in growth: adaptation to temperature or seasonality? *Ecology* 83:1252–1262