

John L. Ackerman · David R. Bellwood ·  
James H. Brown

## The contribution of small individuals to density-body size relationships: examination of energetic equivalence in reef fishes

Received: 1 September 2003 / Accepted: 17 February 2004 / Published online: 10 March 2004  
© Springer-Verlag 2004

**Abstract** A key relationship in ecology is that between density and body size, with the emphasis placed on energetic rules constraining the abundance of larger organisms below that of smaller organisms. Most studies have focused upon the density-body size relationship at the species level. However, energy is gathered at an individual level. We therefore examined this relationship in a coral reef fish assemblage, focusing on individuals. Using a comprehensive data set, with over 14,000 observations we found that the relationship between local density and adult body size differs from the linear relationship predicted by the ‘energetic equivalence rule’. However, excluding the smallest size classes, the relationship between body size and individual abundance for intermediate to larger fish did not depart from the predicted  $-0.75$ . Unlike plants and intermediate to large reef fishes, the smallest fishes appear to have constraints that may reflect different patterns of resource acquisition.

**Keywords** Acquisition · Capacity · Resource · Species · Utilisation

### Introduction

The relationship between body size and density has received much attention in the last 20 years, with smaller species often found in greater numbers than larger ones (Damuth 1981; 1991; Ackerman and Bellwood 2003). The focus of these studies has often revolved around the substantiation or contravention of the ‘energetic equivalence rule’ (Damuth 1981). Basically this hypothesis states that all species, regardless of size, have a similar total energetic intake: numerous small individuals of a small body size taking the same total energy from the environment as a few larger individuals of a large species. The ‘energetic equivalence rule’ was established based upon the relationship between body size and local density exhibiting a power function with an exponent of  $-0.75$  (Damuth 1981). As metabolic rate increases with increasing body size, resulting in an exponent of  $0.75$ , energetic usage across species of varying body sizes becomes constant. Work of Damuth (1981; 1991) and others (Peters and Wassenberg 1983) have quantified the observation that species of small size generally contain more individuals per unit area, but there are usually more species of a smaller size (May 1986). This raises the question of what unit determines the carrying capacity of an environment as a function of an organism’s body size and resource use.

In a previous study, Ackerman and Bellwood (2003) examined the relationship between body size (mass) and density for a local assemblage of reef fishes. The analysis focused upon the shape of the density-body size relationship. The pattern observed was linear rather than polygonal but at  $-0.41$  the slope differed markedly from the expected  $-0.75$ . However, given that energetic rules should operate at the individual level, rather than the species level (Brown et al. 2004; Savage et al. 2004), the results could not unequivocally reject a role for energetic

---

J. L. Ackerman (✉)  
Marine and Freshwater Systems, Department of Primary  
Industries,  
Queenscliff, Victoria, 3225, Australia  
e-mail: john.ackerman@anu.edu.au  
Tel.: +61-2-61252866  
Fax: +61-3-61255573

J. L. Ackerman · D. R. Bellwood  
Department of Marine Biology, James Cook University,  
Queensland, 4811, Australia

D. R. Bellwood  
Centre for Coral Reef Biodiversity, James Cook University,  
Queensland, 4811, Australia

J. H. Brown  
Department of Biology, University of New Mexico,  
Albuquerque, NM, 87131, USA

*Present address:*  
J. L. Ackerman  
School of Botany and Zoology, The Australian National  
University,  
Canberra, ACT, 0200, Australia

rules in limiting maximum densities. A further problem, especially with fish, is that they have relatively small juvenile stages compared with that of the final adult body size. This creates difficulties in calculating a meaningful average size and density at the species level. Previously, energetic equivalence at the level of the individual has been shown for phytoplankton (Li 2002) and plants (Enquist et al. 1999), while analyses of other taxa that have examined the relationship at the species level (Damuth 1981; Knouft 2002; Russo et al. 2003) have had conflicting results. However, if energetic use is indeed at the same rate across body sizes, individuals (not species) in each size class need to be examined. In the present study therefore, we directly investigate the utility of the energetic equivalence rule in coral reef fishes by examining the total numbers of individuals among multiple size classes in a local assemblage of over 14,000 individuals in 185 species.

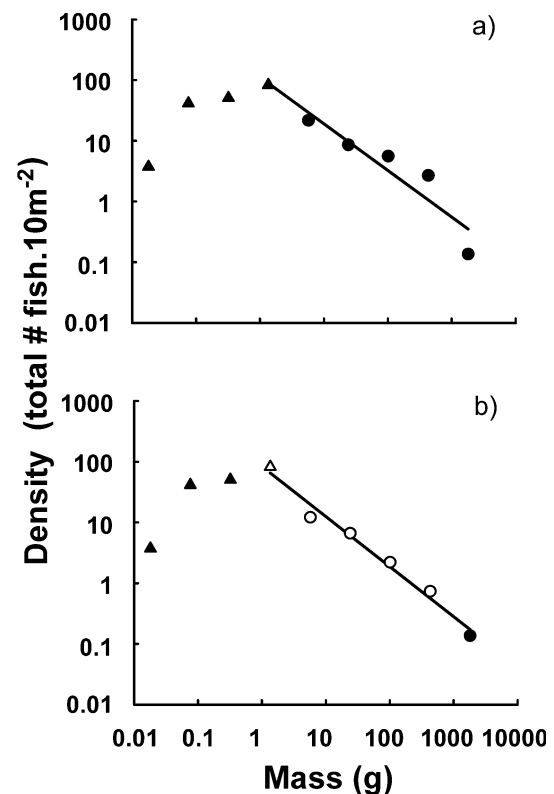
## Materials and methods

Body size and absolute densities of the reef fish assemblage at Orpheus Island (18°35' S, 146°28' E), Great Barrier Reef, were assessed using a combination of the ichthyocide rotenone (in enclosed samples) and visual strip censuses. Over 14,000 specimens from a total of 10 3.5 m<sup>2</sup> rotenone stations and 81 visual censuses were examined (details in Ackerman and Bellwood 2000). Enclosed rotenone stations represent the most effective method available for complete sampling of fish assemblages, sampling both small cryptic individuals and fishes residing within the reef matrix (Ackerman and Bellwood 2000; 2002). Mass of individual fish from the rotenone samples was measured to three decimal places. Mass of individuals identified in visual censuses was estimated through species-specific length-weight regressions from the literature (Kulbicki et al. 1993) or length-weight data from the rotenone collections. Individuals were then assigned to one of nine logged mass categories, and summed [eight mass categories following Ackerman and Bellwood (2003) plus a smaller size class to account for the very small individuals lost in the process of taking mean mass for species]. Values were standardized to number of individuals per 10 m<sup>2</sup>. The larger of the two estimates (rotenone or visual census) in each mass bin was taken to be the most accurate. Rotenone has the properties of collecting all small fishes; however, large individuals may escape from the enclosing net. In contrast, visual censuses may miss some of the smaller more cryptic individuals (Ackerman and Bellwood 2000). The two complementary methods therefore provide a comprehensive sample of the local fauna. As expected, rotenone had the highest estimate in the four smallest mass bins, whilst visual censuses had the highest estimates in the five largest bins. All numbers were log<sub>10</sub>-transformed and relationships between mass bins and total numbers estimated using least-squared regressions (Zar 1999). Mass bins to the left of the mode were subsequently excluded from the regression analysis, as they did not contribute to slope determination. In order to test whether the number of mass categories had any impact upon the resultant slope the above procedure was repeated using 7, 8, 10, 11 and 12 logged mass categories. All slopes are reported with ±95% confidence intervals for the regression coefficients.

## Results

The log density/log mass relationship for individuals differed markedly from that of species, as it was not linear

( $F_{1,7}=5.16$ ,  $P=0.06$ ,  $r^2=0.42$ , slope= $-0.32\pm0.34$ ). Rather, there was a steep incline from the smallest size classes towards the peak at small to intermediate mass, followed by a decline in density in the larger categories (Fig. 1a). However, there was a strong negative linear relationship from the modal size class to the larger size classes with a slope of  $-0.77\pm0.34$  ( $F_{1,4}=39.39$ ,  $P=0.003$ ). Further, examination of the slopes using different numbers of body size categories showed that these relationships were robust. Both the non-linear relationship using all data and the strong linear relationship in the mass bins to the right of the mode remained, regardless of the number of logged mass categories (Table 1). All relationships from the modal size class to the largest size class were significant, with no slope deviating from the predicted theoretical value of  $-0.75$ . The removal of the transient caesionids from the entire assemblage (using nine mass categories) increased the strength of the relationship ( $r^2$ ) from 0.91 to 0.98 and increases the magnitude of the slope from  $-0.77\pm0.34$  to  $-0.82\pm0.16$ . However, the difference between the inclusion and exclusion of the caesionids was not statistically significant ( $t_{0.05,8}=0.41$ ,  $P=0.69$ ). Neither slope differs from the theoretical expectation of  $-0.75$ .



**Fig 1** Relationship between density (total number of fish.10 m<sup>-2</sup>) and body size classes (mass of individuals in grams) in **a** an entire assemblage of reef fishes ( $n=14,664$ ) and **b** with the reef associated caesionids removed ( $n=10,902$ ). Circles represent data collected through visual census techniques; triangles represent data collected through the use of rotenone (see Materials and methods). Solid symbols indicate that no caesionids were removed; open symbols indicate that caesionids were present and removed. The central solid line represents a significant least squares regression with data to the left of the mode excluded

**Table 1** Regression analyses between  $\log_{10}$  density (total number of fish.10 m<sup>-2</sup>) and  $\log_{10}$  body size (mass of individuals in grams) for a varying number of body size categories. Results are shown

No of body size classes	All data					From the mode to the largest size category				
	Slope ( $\pm$ 95% Confidence interval)	$r^2$	$F$	$P$		Slope ( $\pm$ 95% confidence interval)	$R^2$	$F$	$df$	$P$
7	-0.39 ( $\pm$ 0.39)	0.57	6.73	0.049		-0.78 ( $\pm$ 0.46)	0.91	29.76	1, 3	0.012
8	-0.36 ( $\pm$ 0.37)	0.50	5.87	0.52		-0.73 ( $\pm$ 0.32)	0.91	39.74	1, 4	0.003
<b>9</b>	<b>-0.33 (<math>\pm</math>0.34)</b>	<b>0.42</b>	<b>5.16</b>	<b>0.057</b>		<b>-0.77 (<math>\pm</math>0.34)</b>	<b>0.91</b>	<b>39.39</b>	<b>1, 4</b>	<b>0.003</b>
10	-0.32 ( $\pm$ 0.33)	0.38	4.98	0.056		-0.76 ( $\pm$ 0.28)	0.90	47.17	1, 5	0.001
11	-0.35 ( $\pm$ 0.35)	0.37	5.31	0.047		-0.81 ( $\pm$ 0.27)	0.90	53.29	1, 6	<0.001
12	-0.34 ( $\pm$ 0.33)	0.34	5.09	0.048		-0.86 ( $\pm$ 0.29)	0.90	54.16	1, 6	<0.001

## Discussion

The density-body size relationship for individual reef fishes was not linear across all body sizes. This is in contrast to the pattern found when analysing body size and density at the species level (Ackerman and Bellwood 2003). This result suggests that energy use is not equivalent across all body sizes, particularly in smaller individuals. This differs from phytoplankton (Li 2002) and plants (Enquist et al. 1999) where the relationship has been found to remain consistent across all body sizes. However, examining the relationship from the mode to the largest size class of reef fishes reveals a negative linear relationship, with a slope that is not significantly different from the predicted  $-0.75$ . If all species have access to similar energetic resources, which appears to be the case for intermediate to large fishes, then the values fit the theoretical expectation exceptionally well. Nevertheless, this relationship does not apply to the smallest fishes. It appears that these individuals are not accessing the same suite of resources.

The smallest reef fish may not have the highest densities due to physiological, rather than energetic constraints (Munday and Jones 1998). The smallest reef fish are at the structural limits of vertebrate functionality (Harrison 1996; Bellwood and Fisher 2001). Significantly lowered reproductive potential coupled with higher size specific metabolic rates may present physiological constraints on the densities of the smallest fishes (Miller 1996). Energetic requirements may be directed disproportionately to maintenance rather than growth or reproduction in this group and therefore the ability to maintain high densities may be reduced.

Furthermore, there are several lines of evidence to suggest that these smallest of reef fishes may not be accessing the same range of resources as their larger counterparts. Firstly, most of the species in the smallest three bins are below the minimum size reported for vertebrate herbivory, precluding a significant trophic pathway used by larger species (Depczynski and Bellwood 2003). Secondly, as reef fishes have a bipartite life cycle, with a short period in the plankton followed by what is usually a longer period on the reef, most reef fishes access two different ecosystems. Most species in the smaller size classes settle on to the reef at a relatively large size

using all data points and with the removal of mass bins to the left of the mode. Bold type represents data used throughout (see methods). Caesionids are included in all analyses

(especially relative to their adult size), thus a large proportion of the somatic growth in these species is a result of energy collected in a completely different ecosystem (the plankton). Even on the reef, the smallest of reef fishes are in an unusual position as the majority of taxa of a similar size are invertebrates. On coral reefs the vast majority of mobile invertebrates are relatively small, it is only in the larger size classes that fishes dominate most trophic pathways (Choat and Bellwood 1991). In the smallest size classes examined, trophic resources are shared by both fishes and a wide range of invertebrates (primarily crustaceans and gastropods). The low density of the smaller reef fish classes may, to a significant extent, be a reflection of their status as only a small component of the community of that body size that is accessing resources. Finally, unlike phytoplankton and plants, reef fishes are mobile. Small individuals may not be capable of acquiring available resources due to predator avoidance (Lima and Dill 1990; Van Buskirk 2001; Turner and Montgomery 2003). Therefore, acquisition may be the limiting factor rather than utilization (Depczynski and Bellwood 2004). There is a clear need to understand the role of resource acquisition in limiting densities of small reef fishes.

In conclusion, the reef fish assemblage examined does not, in its entirety, support the 'energetic equivalence rule'. However, with the exclusion of the smallest individuals, the intermediate to large individuals appear to fit the predictions exceptionally well. We suggest that for vertebrates, acquisition of resources for the smaller individuals may be the key to understanding deviations from the predicted pattern of abundance.

**Acknowledgements** We thank S. Adams and two reviewers for helpful comments on the manuscript and the staff of Orpheus Island Research Station for field support. This study was supported by the Australian Research Council (DRB). JCU Experimentation Ethics Review Committee Approval #A428. Centre for Coral Reef Biodiversity contribution # 85.

## References

Ackerman JL, Bellwood DR (2000) Reef fish assemblages: a re-evaluation using enclosed rotenone stations. *Mar Ecol Prog Ser* 206:227–237

- Ackerman JL, Bellwood DR (2002) Comparative efficiency of clove oil vs rotenone for sampling tropical reef fish assemblages. *J Fish Biol* 60:893–901
- Ackerman JL, Bellwood DR (2003) The contribution of small individuals to density-body size relationships. *Oecologia* 136:137–140
- Bellwood DR, Fisher R (2001) Relative swimming speeds in reef fish larvae. *Mar Ecol Prog Ser* 211:299–303
- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. *Ecology* (in press)
- Choat JH, Bellwood DR (1991) Reef fishes; their history and evolution. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, New York, pp 39–66
- Damuth J (1981) Population density and body size in mammals. *Nature* 290:699–700
- Damuth J (1991) Of size and abundance. *Nature* 351:268–269
- Depczynski M, Bellwood DR (2003) The role of cryptobenthic reef fishes in coral reef trophodynamics. *Mar Ecol Prog Ser* 256:183–191
- Depczynski M, Bellwood DR (2004) Microhabitat utilization patterns in cryptobenthic reef fish communities. *Mar Biol* (in press)
- Enquist BJ, Brown JH, West GB (1999) Allometric scaling of plant energetics and population density. *Nature* 395:163–165
- Harrison IJ (1996) Interface areas in small fish. In: Miller PJ (ed) *Miniature vertebrates: the implications of small body size*. Zoological Society of London, Oxford, pp 175–195
- Knouft JH (2002) Regional analysis of body size and population density in stream fish assemblages: testing predictions of the energetic equivalence rule. *Can J Fish Aquat Sci* 59:1350–1360
- Kulbicki M, Moutham G, Thollot P, Wantiez L (1993) Length-weight relationships of fish from the lagoon of New Caledonia. *Naga ICLARM Q* 16:26–30
- Li WKW (2002) Macroecological patterns of phytoplankton in the northwestern North Atlantic Ocean. *Nature* 419:154–157
- Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68:619–640
- May RM (1986) The search for patterns in the balance of nature: advances and retreats. *Ecology* 67:1115–1126
- Miller PJ (1996) The functional ecology of small fish: some opportunities and consequences. In: Miller PJ (ed) *Miniature vertebrates: the implications of small body size*. Zoological Society of London, Oxford, pp 175–195
- Munday PL, Jones GP (1998) The ecological implications of small body size among coral-reef fishes. *Oceanogr Mar Biol Annu Rev* 36:373–411
- Peters RH, Wassenberg K (1983) The effect of body size on animal abundance. *Oecologia* 60:89–96
- Russo SE, Robinson SK, Terborgh J (2003) Size-abundance relationships in an Amazonian bird community: implications for the energetic equivalence rule. *Am Nat* 161:267–283
- Savage VM, Gillooly JF, Brown JH, West GB, Charnov EL (2004) Effects of body size and temperature on population growth. *Am Nat* (in press)
- Turner AM, Montgomery SL (2003) Spatial and temporal scales of predator avoidance: experiments with fish and snails. *Ecology* 84:616–622
- Van Buskirk (2001) Specific induced responses to different predator species in anuran larvae. *J Evol Biol* 14:482–489
- Zar JH (1999) *Biostatistical analysis*, 4th edn. Prentice Hall, Upper Saddle River, N.J.