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Do invasive species live faster? Mass-specific metabolic rate depends on growth form and invasion status

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Abstract

1. Invasive organisms often share characteristics that make them successful. Traits such as rapid growth and short generation times are classic "weed" phenotypes, such that invasive species often have r-selected rather than k-selected life histories. Given that invasive species often display "fast" life histories, invasive species may have relatively higher metabolic rates but systematic tests across taxa are lacking.

2. We compared metabolic rate across 14 sessile invasive and native marine invertebrates. We also investigated the influence of growth form (erect vs. flat species) on the metabolic rate of these species, since growth form can also affect metabolic rate.

3. For species with an erect growth form, we found an effect of invasive status on mass-specific metabolic rate. Invasive species had much higher mass-specific metabolic rates than native species and this was particularly pronounced for organisms with smaller body masses.

4. Given that smaller-bodied invasive organisms are typically early-successional, "fugitive" species, a higher metabolic rate may allow a faster pace of life, enhancing their capacity to invade and reproduce in newly created disturbed habitats.

KEYWORDS
artificial structures, energy consumption, invasion ecology, life history, metabolic scaling, pace of life, sessile organisms

1 | INTRODUCTION

The probability of biological invasions is influenced by the characteristics of the potentially invaded habitat, the traits of the invasive species, and the interaction between these two factors (Andow, Kareiva, Levin, & Okubo, 1990; Arim, Abades, Neill, Lima, & Marquet, 2006; van Kleunen, Dawson, Schlaepfer, Jeschke, & Fischer, 2010; van Kleunen, Weber, & Fischer, 2010; Zhao & Feng, 2015). Invasive organisms often share common characteristics that make them successful invaders: relative to native species, they generally have more rapid growth, reproduce sooner and therefore have shorter generation times (Ehrlich, 1986; Lejeusne, Latchere, Petit, Rico, & Green, 2014; Lodge, 1993; Matzek, 2012; van Kleunen, Dawson, et al., 2010). Together, these

traits make for the classic "weed" phenotype, whereby invasive species are thought to have r-selected rather than k-selected life histories (Ehrlich, 1986; McMahon, 2002; Sakai et al., 2001). That invasive species tend to have faster life histories than noninvasive species has long been recognised, but the underlying physiological drivers of faster, more-invasive life histories are poorly understood. Measures of metabolic rate integrate the costs associated with a range of organismal functions, including the maintenance of homeostasis, feeding and digestion, growth, and reproduction. Metabolic rate is therefore a likely driver of differences in life history among invasive and native species.

Several lines of evidence suggest that systematic differences in the metabolic rates of native and invasive species are likely. Generally, metabolic rate is thought to covary with key life-history

traits, which together determine the pace of the life history (Burton, Killen, Armstrong, & Metcalfe, 2011). For example, according to the "increased intake" hypothesis, higher metabolic rates are correlated with faster growth and greater movement (Boratynski & Koteja, 2010; Burton et al., 2011). Similarly, early theories about the "rate of living" assumed a negative relationship between life span and metabolic rate (Pearl, 1928; Schmidt-Nielsen, 1984). A more recent study showed that individuals with higher metabolic rates grow faster but reproduce and died sooner in the field (Pettersen, White, & Marshall, 2016). We might therefore expect invasive species to have higher metabolic rates than natives. On the other hand, the "compensation hypothesis" predicts that lower metabolic rates allow for the reallocation of more energy to growth and reproduction, and increasing both may also facilitate invasion (Burton et al., 2011; Nilsson, 2002). In support of the compensation hypothesis, lower metabolic rates were associated with higher growth rates in fishes in the field (Alvarez & Nicieza, 2005; Norin & Malte, 2011). Thus, general theory makes conflicting predictions about the association between metabolic rate, the pace of the life history and invasion (Burton et al., 2011).

Despite the ambivalence of general theory regarding invasion and metabolism, a higher metabolic rate has repeatedly been invoked as a key trait for successful invaders (Maazouzi, Piscart, Legier, & Hervant, 2011). For example, is has been suggested that invasive freshwater clams are successful invaders in part because they have higher metabolic rates than native species occupying the same niche, allowing them to burrow and filter food more rapidly (McMahon, 2002). Nevertheless, others have argued that invasive organisms have lower metabolic rates than their native congeners (Gonzalez-Ortegon, Cuesta, Pascual, & Drake, 2010; Lejeusne et al., 2014). Thus, there are conflicting accounts about how metabolic rate varies systematically between native and invasive species. Most studies have been restricted to only one or two species, hampering our ability to generalise about whether metabolic rate is related to invasion success.

To better understand the relationship between metabolic rates and invasion success, systematic comparisons of the metabolic rates of native and invasive species from the same system are necessary, ideally involving species within the same trophic guild but across wide taxonomic ranges. Here, we tested how metabolic rate differs between invasive and native species. We estimated the rate of oxygen consumption in 14 species of marine sessile invertebrate from a range of taxa that varied in whether they were native or invasive. Because metabolic rate scales strongly with body mass, we measured metabolic rates across a range of body masses.

In addition to examining the effect of invasion status on metabolic rate, we also examined growth form because there is a link between the growth form and the oxygen requirements of sessile marine invertebrates (Ferguson, White, & Marshall, 2013). Species with a flatter, two-dimensional growth form (e.g. sponges, encrusting bryozoans and many colonial ascidians) can cope with lower oxygen levels than species with an erect, three-dimensional growth form (e.g. tubeworms, solitary ascidians, arborescent bryozoans; Ferguson et al., 2013). Presumably these differences in tolerance to low oxygen conditions reflect the fact that flat species live entirely within the oxygen depleted

boundary layer while erect species may project out of it (Ferguson et al., 2013). It is unclear whether metabolic rates also covary with growth form, though theory predicts that there should be systematic differences in the relationship between body mass and metabolic rate for two- and three-dimensional organisms (White, Kearney, Matthews, Kooijman, & Marshall, 2011).

2 | MATERIALS AND METHODS

2.1 | Organism collection and maintenance

Animals were collected from sites within Port Phillip Bay, Victoria Australia: Altona Pier (37°52′23″S; 144°49′49″E), Blairgowrie Yacht Squadron (38°21′23″S; 144°46′22″E), Portarlington pier (38°6′40″S; 144°39′9″E), Royal Brighton Yacht Club (37°54′23″S; 144°58′53″E) and Royal Melbourne Yacht Squadron (St Kilda) (31°51′45″S; 144°57′51″E). Larger species (e.g. solitary ascidians), were collected by scraping organism from the floating pontoons, and smaller species (e.g. bryozoans and colonial ascidians) were cut from pre-roughened acetate sheets collected from the field. Acetate sheets had been deployed for 2 years on PVC panels, hanging from floating pontoons at 1.5 m depth. The organisms were transported to the laboratory in insulated aquaria with aerated seawater to be acclimatised to laboratory conditions for 2 days in the dark at 19°C. Organisms were then classified according to their invasive-native status. All of these invasive species are thought to have originated from outside of Australia. The list of species used in this study is provided in Table 1 and for more information on native origin, distribution and invasion status in Australia see WoRMS (www.marinespecies.org) and Atlas of living Australia (www.ala.org.au) respectively. Species were also classified according to their growth form; species with a body thickness lower than 5 mm high were considered as flat organisms, while more than 5 mm were classified as erect.

2.2 | Measurement of metabolic rate

Rate of oxygen consumption, a widely used proxy for metabolic rate, was measured using two different closed respirometry systems based on the size of the species (Ferguson et al., 2013; Pettersen, White, & Marshall, 2015). Larger organisms were measured using hermetic 1.8 L chambers with circulating water connected to a 4-channel Firesting O_2 fiber optic oxygen meter (Pyro Sciences, Aachen, Germany). Each experimental run of 12 chambers included four chambers containing water but no animals to act as controls for background rates of oxygen consumption. For smaller organisms, sections of the acetate bearing whole organisms and placed in 25 ml vials were mounted on a 24-channel sensor dish reader (Sensor Dish Reader SDR; PreSens, Aachen, Germany). Each experimental run of 24 vials included 4 vials containing only water and acetate as controls. The experimental chambers were filled with previously micro-filtered (0.2 μm) and pasteurized seawater that had been kept at 19°C with constant aeration for at least 24 hr prior to experiments to allow water temperature to stabilize. Measurements were conducted in darkness for a period of 1

TABLE 1 Sessile species used and the sample size (*n*). Species are classified according to their status (invasive or native), growth form (erect or flat), organization (solitary or colonial), and taxonomic groups

Species	Phylum	Class	Order	Shape	Status	Organization	*n*
Styela plicata	Chordate	Ascidiacea	Stolidobranchia	Erect	Invasive	Solitary	11
Styela clava	Chordate	Ascidiacea	Stolidobranchia	Erect	Invasive	Solitary	18
Ciona intestinalis	Chordate	Ascidiacea	Phlebobranchia	Erect	Invasive	Solitary	9
Pyura dalbyi	Chordate	Ascidiacea	Stolidobranchia	Erect	Native	Solitary	9
Pyura doppelgangera	Chordate	Ascidiacea	Stolidobranchia	Erect	Native	Solitary	9
Herdmania grandis	Chordate	Ascidiacea	Stolidobranchia	Erect	Native	Solitary	16
Botrylloides magnicoecum	Chordate	Ascidiacea	Stolidobranchia	Erect	Native	Colonial	19
Bugula dentata	Bryozoa	Gymnolaemata	Cheilostormatida	Erect	Native	Colonial	17
Bugula neretina	Bryozoa	Gymnolaemata	Cheilostormatida	Erect	Invasive	Colonial	15
Bugula flabellata	Bryozoa	Gymnolaemata	Cheilostormatida	Erect	Invasive	Colonial	13
Watersipora subtorquata	Bryozoa	Gymnolaemata	Cheilostormatida	Flat	Invasive	Colonial	14
Didemnum sp.	Chordate	Ascidiacea	Aplousobranchia	Flat	Invasive	Colonial	13
Diplosoma sp.	Chordate	Ascidiacea	Aplousobranchia	Flat	Invasive	Colonial	11
Celleporaria sp.	Bryozoa	Gymnolaemata	Cheilostormatida	Flat	Native	Colonial	11

to 10 hr; the duration of measurement depended on the rate of oxygen consumption of each species.

Rate of oxygen consumption (VO_2, ml/hr) was calculated from the slope of the line relating oxygen saturation and time for the vials containing organisms (m_a, % air saturation hr^{-1}), the equivalent slope for the control vials (m_c, % air saturation hr^{-1}), the oxygen capacitance of air-saturated seawater (βO_2, 5.3 ml/L at 19.0°C; Cameron, 1986) and the volume of the vial, minus the volume of the organism and acetate (when relevant) using the following equation (Ferguson et al., 2013; Pettersen et al. 2015; White et al., 2011):

$$VO_2 = -\left[(m_a - m_c)/100\right] \times V \times \beta O_2. \tag{1}$$

After the oxygen measurements, the organisms were placed in an oven for 1 week at 60°C to obtain dry body mass. The species used were classified according to their status (i.e. native or invasive; Table 1) and their growth form (i.e. erect or flat; Table 1).

2.3 | Data analysis

All oxygen consumption (VO_2, ml/hr) and body mass (*M*, g) data were log–log transformed. A mixed effects partly nested analysis was used to determine how growth form and invasions status affected mass-specific metabolic rate (ml g^{-1} hr^{-1}) (where invasion status and growth form were fixed effects and species nested within each was a random effect). We also included a size category factor for two reasons. First size affects mass specific metabolic rate. Second, due to logistical constraints, we used moving water respirometry for larger organisms (>4 g mass) and still water respirometry for smaller organisms (<4 g). Thus, we wanted to explore the effects of invasion status and growth form while explicitly accounting for different body sizes and experimental approaches. Because there was not sufficient replication at the level of species, we could not test for a mass × growth form × invasion status three-way interaction, instead, we could only test for

mass × growth form and mass × status. Therefore, we tested the effects of growth form across all species, then invasion status for erect species only as this was the group for which we had sufficient species in both categories.

We also explored variation in metabolic across body masses within species. How metabolic rate scales with body mass is usually mathematically described by the power function $Y = aM^b$, where *Y* is the VO_2, *a* is the scaling factor, *M* is the body mass of the organism and *b* is the scaling exponent (Pettersen et al. 2015; White & Seymour 2011). We used linear regression to calculate coefficient and scaling exponent values for log$_{10}$-transformed data for each species according to the equation:

$$\log_{10} VO_2 = b \times \log_{10} M + \log_{10} a. \tag{2}$$

Wald tests were done to test whether the scaling exponent different significantly from 0, and from 1. All analyses were done using the statistical software Systat ver.13. (Systat, Cranes Software International, Bengaluru, India).

3 | RESULTS

Across species, mass-specific metabolic rate varied according to growth form and invasion status (Table 2). Species with erect growth forms had higher metabolic rates than species with encrusting, flat growth forms (Figures 1 and 2b). Invasive species had higher metabolic rates than native species and these differences were particularly pronounced for species with smaller body sizes (Table 3, Figures 1 and 2c). There was still significant variation in respiration rates within each classification however. For example, relative to other species, higher respiration rates were found in *Styela plicata*, with values around up to two-fold higher than *Bugula neritina*—the species that showed lowest oxygen consumption (Table 3, Figure 2a)—even though both species are invasive and both species have an erect growth form.

TABLE 2 Partly-nested mixed model of the effect of (a) growth form on mass specific oxygen consumption in sessile marine invertebrates and (b) invasion status and body size on mass specific oxygen consumption in sessile marine invertebrates with an erect growth form only. The effect of invasion status was tested over the appropriate denominator of species (status) as species is the appropriate unit of replication

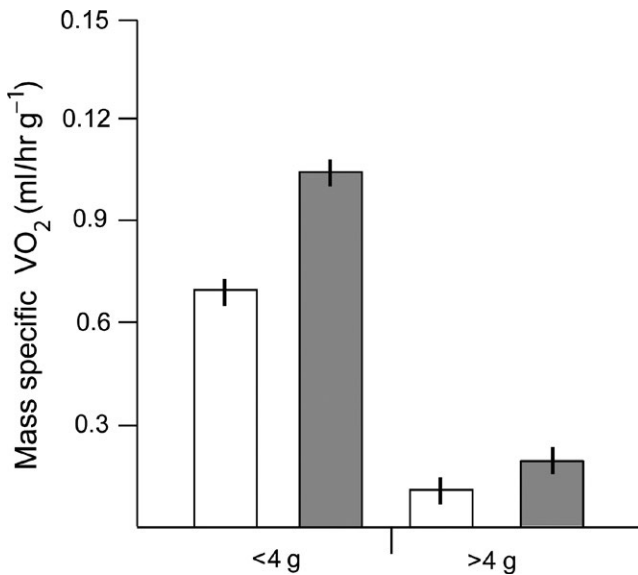| Test	Source	df	F	p
(a) Growth form	Growth form	1, 12	20.98	.001
	Size	1, 173	98.5	<.001
(b) Invasion status	Status	1, 7	23.65	.002
	Size	1, 126	327.72	<.001
	Size × Status	1, 126	9.75	.002

FIGURE 1 Mean mass-specific oxygen consumption of native and invasive species across size categories ("big" >4 g body mass, "small" <4 g body mass) and invasion status. Note that standard errors are generated from partly nested mixed model as is appropriate (see Quinn & Keough, 2002 for details). Invasive species shown in shaded bars, native species in open bars

Within species, due to the high variation in VO_2 within species, we found significant relationships between mass and VO_2 in only five of the 14 measured species (Table 3, Figure 2).

FIGURE 2 Linear regressions for the relationship between log_{10} dry body mass (g) and log_{10} oxygen consumption (VO_2, ml/hr). (a) For all the species measured. Invasive-Erect species (black continue lines): (1) *Bugula flabellata*, (2) *Bugula neritina*, (3) *Ciona intestinalis*, (4) *Styela clava*, (5) *Styela plicata*. Native-Erect species (blue continue lines): (1) *Botrylloides magnicoecum*, (2) *Bugula dentata*, (3) *Herdmania grandis*, (4) *Pyura dalbyi*, (5) *Pyura doppelgangera*. Invasive-flat species (black dashed lines): (6) *Didemnun* sp., (7) *Diplosoma* sp., (8) *Watersipora subtorquata*. Native-flat species (blue dashed line: 6) *Celleporaria* sp. (b) For each growth form (erect and flat). (c) For invasion status (Invasive and native)
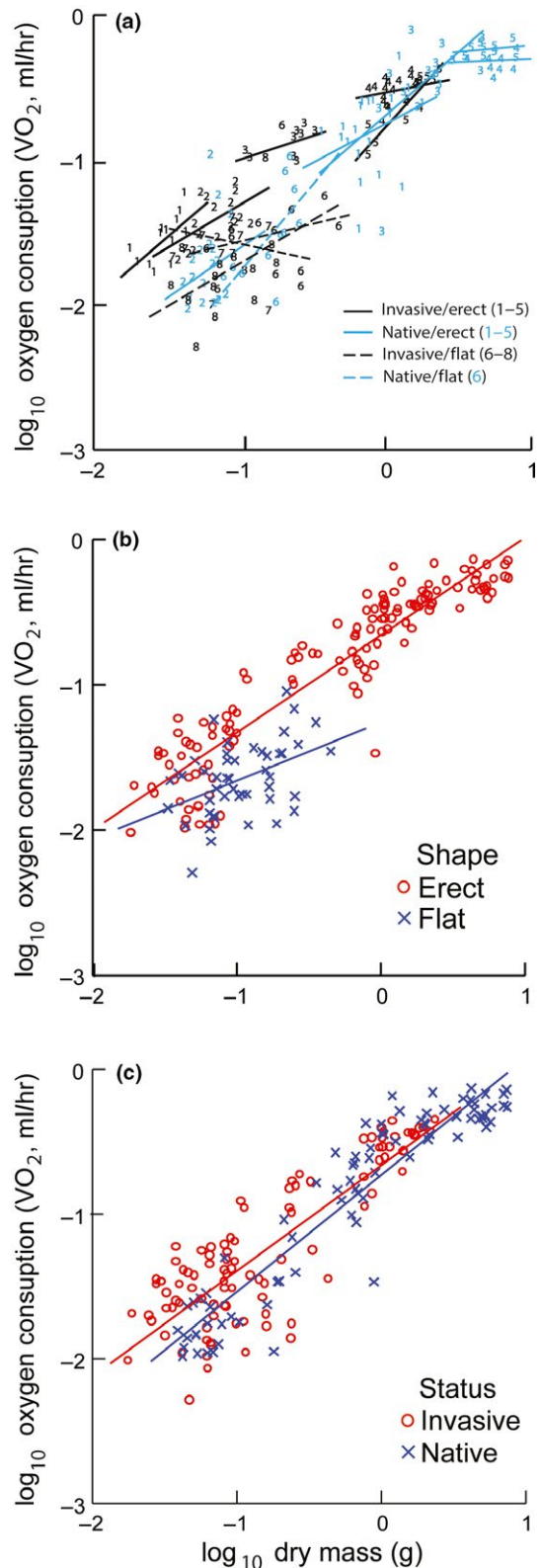
4 | DISCUSSION

Mass specific metabolic rate depends on both growth form and invasion status in the sessile marine invertebrates we studied. Species with a flat growth form tended to show a shallower scaling relationship than

species with an erect growth form. The scaling exponent for the relationship between mass and metabolic rate was higher in native species than invasive species, but invasive species had an overall higher metabolic rate (higher intercept) than natives (Figure 2). Overall, mass specific metabolic rates of invasive species with erect growth forms were much higher than those of native species, particularly for lower body masses.

We found a clear association of invasion status with mass-specific metabolic rate—our study joins a growing list finding such an association (Alvarez & Nicieza, 2005; Bruijs, Kelleher, van der Velde, & de Vaate, 2001; Marras et al., 2015; Norin & Malte, 2011). It is unclear whether invaders are successful because they have a higher metabolic rate or species that are invasive evolve to have a high metabolic rate. Certainly some traits that are known to affect invasion seem to covary positively with higher metabolisms (McMahon, 2002). For example, high metabolic rates are sometimes associated with faster growth and earlier onset of reproduction (Pettersen et al., 2016). Such "r-selected" or "weed" phenotypes can be especially important for species living in communities where the sessile style of life is dominant. When animals are sessile and small, susceptibility to predation and being out-competed is often high (Buss, 1980; Jackson, 1979; Paine, 1974). The characteristics associated with erect organisms allow them to quickly reach a size refuge in order to avoid predation and being out-competed, while allowing for fast regeneration of lost body parts. Smaller invasive individuals clearly have higher metabolic rates than their native counterparts, at least under our experimental conditions. It is likely that the relatively higher metabolic rate of small invasive organisms is one of the causes of their invasibility. Nevertheless, it is unlikely that small invasive species can compete against adults or larger-sized natives, especially in communities that are reaching equilibrium (MacArthur, 1970; Shea & Chesson, 2002). However, as early successional species they can quickly reproduce after settlement and can be highly successful at colonising disturbed habitats or environments with vacant patches (Ghermandi, Guthmann, & Bran, 2004; Sakai et al., 2001).

Growth form affects the scaling relationship between body mass and metabolic rate in ways anticipated by theory. So far, several models have attempted to estimate the differences in energy expenditure between two- and three-dimensional organisms. The "fractal geometry model" predicts a scaling exponent of 2/3 for two-dimensional organisms and 3/4 for three-dimensional organisms (West, Brown, & Enquist, 1999), however recent modifications of fractal geometry predict wider ranges of scaling exponents (Enquist et al., 2007; Kolokotrones, Savage, Deeds, & Fontana, 2010). Previous studies have shown the dynamic energy budget theory (DEB) proved to be a good predictor of metabolic scaling, as empirical data fits with the predictions of a scaling exponent of 0.5 for two-dimensional species (White et al., 2011). We found that the scaling exponent of flat and erect sessile species to be significantly different with "b" equal to 0.40 and 0.67 for flat and erect species respectively. As the coefficient "a" is lower in flat-shaped species, their overall metabolic rate is lower than in erect organisms for any measured size. The difference between both groups increases considerably at bigger body masses. Interestingly, studies of pelagic invertebrates also show changes across larger body masses: Hirst, Lilley, Glazier, and Atkinson (2017) find that the exponent "b" changes from an almost isometric value to sublinear allometry ($b < 1$) as body surface area increases. Changes in the degree of body flattening or elongation during ontogeny affects the ratio between delivery and waste of resources between the external environment and mitochondria. This trade-off may affect the allocation of energy used for structural growth, somatic storage, reproduction, and other vital activities (Glazier, Hirst, & Atkinson, 2015; Hirst, Glazier, & Atkinson, 2014; Hirst et al., 2017). Whether such constraints also drive the patterns in our system remains unclear.

A potential explanation of the relatively higher metabolism of erect-shaped species over flat-shaped species, could be that oxygen limitation occurs in flat species more than in erect species due to higher amounts of self-shading. Dynamic energy budget theory predicts that in flat colonies metabolic rates of the edges are higher than in the centre (White et al., 2011). While the edges must fulfil the metabolic cost

TABLE 3 Summary of scaling exponents (b) ($\pm SE$) and coefficients for metabolic rate and mass (a) of invasive and native sessile species, using a log–log transformed linear relationship, where: $\log_{10} VO_2 = b \times \log_{10}$ dry mass $+ a$. Data are in groups of individual species, growth form, invasive-native status and the interaction shape-status (erect-flat, invasive-native), for which significant relationships were found

Species	n	Coefficient (a)	Scaling exponent (b)	p-value b ≠ 0	p-value b ≠ 1	R²
Styela plicata	11	0.185	1.100 (±0.132)	<.01	.47	.885
Herdmania grandis	16	0.228	0.877 (±0.340)	.02	.72	.322
Bugula neritina	16	0.198	0.593 (±0.246)	.03	.13	.294
Bugula flabelata	13	0.679	0.886 (±0.342)	.02	.75	.378
Celleporaria sp.	11	0.307	1.219 (±0.461)	.02	.64	.437
Erect organisms	137	0.229	0.676 (±0.024)	<.01	<.01	.849
Flat organisms	51	0.071	0.445 (±0.154)	.01	<.01	.147
Invasive organisms	107	0.222	0.715 (±0.046)	<.01	<.01	.702
Native organisms	81	0.187	0.819 (±0.035)	<.01	<.01	.871
Erect-Invasive organisms	67	0.267	0.637 (±0.025)	<.01	<.01	.91
Erect-Native organisms	70	0.193	0.795 (±0.036)	<.01	<.01	.875

of maintenance and colony growth, the zooids in the centre only require energy for maintenance (White et al., 2011). The growth pattern of the two-dimensional flat organisms may enable lower energetic demands than erect shaped organisms, which grow three-dimensionally and have less self-shading. In solitary, erect organisms such as large ascidians, the use of a muscular system in order to move the water through the body and extract oxygen incurs a higher energetic cost, however oxygen intake is more efficient (Kumpp, 1984). Recently, it was suggested that the lower energetic costs associated with increased size in colonial organisms explains their competitive advantage over solitary organisms (Barneche, White, & Marshall, 2017).

Alternatively, the differences in oxygen consumption that we observed across different masses may be driven by methodology. Recall that we used a still water approach for smaller species and a re-circulating approach for larger species. It seems likely that self-shading and oxygen limitation at a very small scale is more likely in a still water system relative to a re-circulating system. We found that mass specific metabolic rates between invasive and native species were most different for small-bodied species—but these species were also studied in still water. It is possible that the apparent difference in metabolic rate between invasive and native species arises because invasive species are better able to maintain higher metabolic rates under local oxygen limitation than native species. Indeed, in a separate study we found that invasive species are better able to tolerate low oxygen conditions than native species (Lagos, Barneche, White, & Marshall, 2017). The methodological differences we used between larger and smaller body sizes were unavoidable due to practical constraints so it is unfortunate we cannot disentangle the relative roles of different methods and body size. Regardless of this limitation our primary observation that metabolic rates differ among native and invasive species remains unaffected (status still affected metabolic rate in species with larger body sizes), it is the status × mass interaction that may be driven by the methodological differences.

Our results indicate that body shape affects the relationship between metabolic rate and body mass of sessile species. At least in erect shaped species, the comparative metabolic advantage of the small invasive species may provide an advantage over their native counterparts. However, it still remains to be seen how metabolic rate changes through different ontogenetic stages and how it could be linked with the ecology of invasion.

AUTHORS' CONTRIBUTIONS

M.E.L.: data collection, data analysis and writing. C.R.W.: writing, experimental design and conception of the idea. D.J.M.: writing, data analysis, experimental design and conception of the idea. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

All data are available in the Figshare repository (https://figshare.com). https://doi.org/10.6084/m9.figshare.4989593.

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