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Cite this article: Jarvis GC, Marshall DJ. 2025 Hermaphrodites have lower metabolic rates than gonochores. *Proc. R. Soc. B* **292**: 20252276.
https://doi.org/10.1098/rspb.2025.2276

Received: 3 September 2025
Accepted: 29 October 2025

Subject Category:
Evolution

Subject Areas:
ecology, evolution, physiology

Keywords:
evolutionary ecology, life-history theory, hermaphroditism, metabolic rate, metabolic theory, phylogenetic comparative analyses

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Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.8142787.

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Hermaphrodites have lower metabolic rates than gonochores

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Hermaphroditism, where an individual can reproduce as both male and female, offers some clear reproductive advantages. Simultaneous hermaphroditism guarantees that every mature adult can mate with another—a particular advantage when opportunities to mate are scarce. Despite this potential benefit, hermaphroditism is relatively rare in animals. This paradox has long involved an energetics argument: hermaphrodites require more energy to fuel two reproductive roles instead of only one, which favours the evolution of separate sexes. However, this argument has never been tested. Here, we compare resting metabolic rates between hermaphrodites and gonochores across 536 species of marine invertebrates, spanning 11 phyla. Our analyses, which control for body size, environmental temperature, motility and phylogeny, contradict predictions from classic theory: instead of requiring more energy than gonochores, hermaphrodites require approximately 27% less energy on average. These findings overturn a 150-year-old argument that hermaphroditism is rarer in animals because it is more costly and highlight the need to reconsider the role of energetics in the evolution of sexual systems.

1. Introduction

> The sole motive for the separation of the sexes which occurs to me, is that … the same individual should not have its vital powers taxed … by producing both pollen and seeds.
>
> Darwin [1, p. 344]

Simultaneous hermaphroditism, where individuals reproduce as both male and female, offers some clear reproductive advantages. Hermaphrodites can mate with any mature conspecific they encounter, doubling the effective density of compatible partners relative to gonochores—a particular advantage in low-density populations [2–4]. Some hermaphrodites can self-fertilize when mates are particularly rare [5,6] and many optimize their success by strategically reallocating resources between male and female roles according to circumstance [7]. Consistent with these benefits, most plants (approx. 95%) are hermaphrodites. In contrast, almost all (approx. 94%) animals are gonochores [5]. Darwin, who thought deeply about the evolution of hermaphroditism in both plants and animals, wrestled with this idea and concluded that hermaphroditism was likely to be more energetically costly than gonochorism [1]. The role of energy has remained central to debates about the evolution of hermaphroditism ever since.

It might indeed be more energetically costly to be a hermaphrodite. Hermaphrodites must perform two reproductive roles instead of only one, possibly resulting in higher ‘fixed costs’: the total energy required to both produce and maintain reproductive structures (e.g. gonads and the tissues that store and/or transport gametes [8]). It has been argued, therefore, that hermaphrodites must expend more of their energy on fixed costs, reducing their reproductive output relative to gonochores and perhaps hampering the evolution of combined sexes [8–10]. Under this 'fixed-cost' model, hermaphrodites should have higher energetic demands than gonochores, all else being equal, because hermaphrodites must pay more maintenance costs for more reproductive structures (figure 1).

On the other hand, one might also argue that it could be more energy-efficient to be a hermaphrodite. Because hermaphrodites produce structures that can serve both male and female functions, they might pay the same fixed costs as gonochores [7,11,12]. Under this 'cost-sharing' model, hermaphrodites must expend less energy than gonochores overall because hermaphrodites must expend less energy on mate-finding to ensure cross-fertilizations [7] (figure 1).

Overall then, despite the idea that energy demands set the costs and benefits of hermaphroditism stretching back to Darwin, tests of this idea are lacking. There are also clearly conflicting predictions from more modern theoretical treatments of the evolution of hermaphroditism [10,13–18]. Yet, remarkably, there have been no systematic attempts to test these predictions empirically—there has been no synthesis of how metabolic rates differ between hermaphrodites and gonochores despite 150 years of speculation.

Here, we test the components of Darwin's hypothesis that have been formalized by modern theory: specifically, whether maintenance costs (e.g. metabolic rates) differ between hermaphrodites and gonochores [8–10]. We address this knowledge gap by comparing the resting metabolic rates of hermaphrodites and gonochores across 536 species of marine invertebrates, spanning 11 phyla. Marine invertebrates provide a robust test of the covariance between metabolic rate and reproductive mode because hermaphroditism has independently evolved repeatedly in this group, even within genera on occasion [19]. We analysed the covariance between metabolic rate (joules per hour, J h^{-1}) and reproductive mode, while taking account of body size (grams (g), wet weight), environmental temperature (°C) and phylogenetic relatedness among species. Because some have argued that hermaphroditism in animals may be linked to a sessile lifestyle [2,3,20,21], we also tested whether motility affects the relationship between metabolic rate and reproductive mode. The logic of our comparative approach leverages the assumption that, on average (and after accounting for the other factors), no other differences between hermaphrodites and gonochores exist other than reproductive mode. Hence, any differences in metabolic rate must be associated with the trait of hermaphroditism.

2. Methods

(a) Metabolic rate data

We compiled interspecific data for resting adult metabolic rate, adult size, environmental temperature, reproductive mode and motility for 536 species of marine invertebrates (figure 2 and electronic supplementary material, table S1). The species in our dataset came from previously published meta-analyses on metabolic rate [22,23], supplemented with additional species yielded from our own searches. For our own searches, we collected metabolic data from studies from Google Scholar (https://scholar.google.com/) based on the following search terms: '[Phylum]' or more common clade terms, e.g. 'Sponge', together with terms 'metabol*', 'metabol* rate', 'metabol* scaling', 'respir*' or 'oxygen consum*'. Within those selected studies and the studies compiled in Brey [22] and White *et al.* [23], we only included studies that (i) measured adults (cf. eggs, larvae or juveniles), (ii) reported body size and measurement temperature (if the measurement temperature did not match species' environmental temperature at the time of collection, then the measurement temperature needed to be within the species' annual temperature range, with an acclimation time of at least 1 day per 1°C, for the study to be included *sensu* [22]), and (iii) adhered to basic assumptions of resting/standard metabolic rates (animals were in a quiescent, post-absorptive and non-reproductive state). Within all studies, we also explored relevant citations to identify as many studies on metabolic rate as possible. In many cases, raw data for respiration were extracted from figures using WebPlotDigitizer (https://apps.automeris.io/wpd4/; RRID:SCR_013996) [24].

When data for metabolic rate were reported as oxygen consumption (97% of species in our dataset), carbon/calorie consumption, or watts (each <1% of species in our dataset), we converted them to joules per individual per hour based on known conversion factors [22]. Notably, metabolic measurement type did not differ between reproductive modes: for 98% of gonochores and 96% of hermaphrodites metabolic rates were originally measured as oxygen consumption.

When data for adult size were reported as length, width, diameter, volume or another measure of tissue weight (e.g. carbon weight, ash-free weight), we converted values to grams of whole-organism wet tissue mass based on known conversion factors [25,26]. We used whole-organism wet mass because metabolic rate was originally measured on wet, whole organisms, and because wet mass is a widely accepted size metric for metabolic studies (e.g. [27,28]). However, some exclusively hermaphroditic phyla may also have a relatively high water content (e.g. Ctenophora and Porifera), and some phyla include species with shells, while others do not. In such cases, similarly sized species with higher water/shell content might have lower metabolic rates simply because they have less metabolically active tissue, independent of reproductive mode. We therefore compiled information for the proportion of water/shell content from Brey *et al.* [25] for all of the species in our dataset to assess the role of body composition on our results. Notably, the proportion of water/shell content did not covary with any other predictors of metabolic rate (i.e. hermaphrodites did not differ from gonochores in their body composition) (electronic supplementary material, table S2), and our qualitative results were unchanged after controlling for water/shell content (electronic supplementary material, table S3).

As with any compilation of this kind, our dataset probably shares the same biases as broader physiological datasets (*sensu* [29]). For example, species from coastal regions in the USA, Europe and Australia are over-represented, while those from

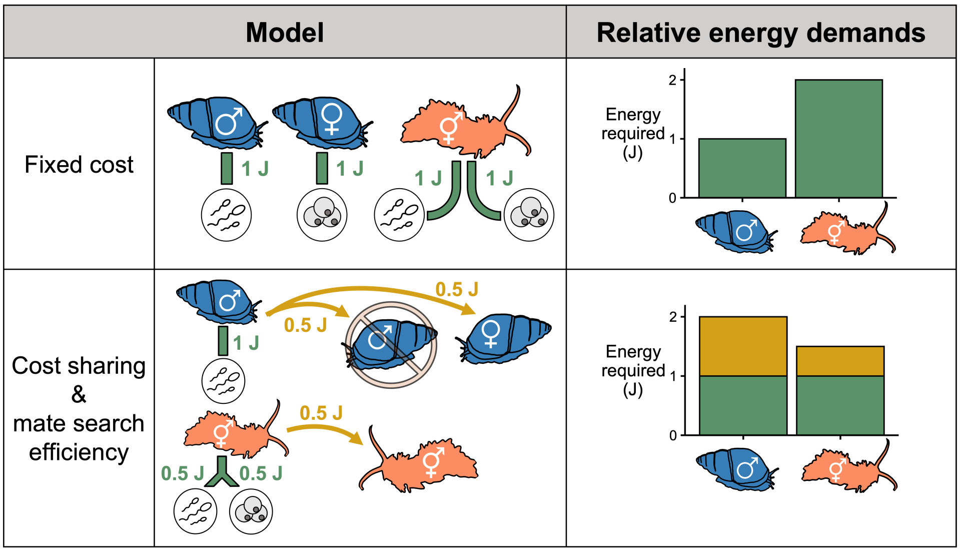

Figure 1. Fixed-cost and cost-sharing models make opposing predictions about the energy requirements of hermaphrodites and gonochores. The model for fixed costs predicts that a hermaphrodite (orange sea slug) should have higher energetic demands than a gonochore (blue snail), because hermaphrodites must pay more to maintain more reproductive machinery (green text and bars). The model for cost-sharing predicts the opposite: hermaphrodites should require less energy than gonochores overall, because hermaphrodites (1) pay the same amount for reproductive machinery as gonochores by sharing common structures for both male and female function, but (2) require only half as much energy for mate search because every encounter can be a mating (yellow text, arrows and bars).

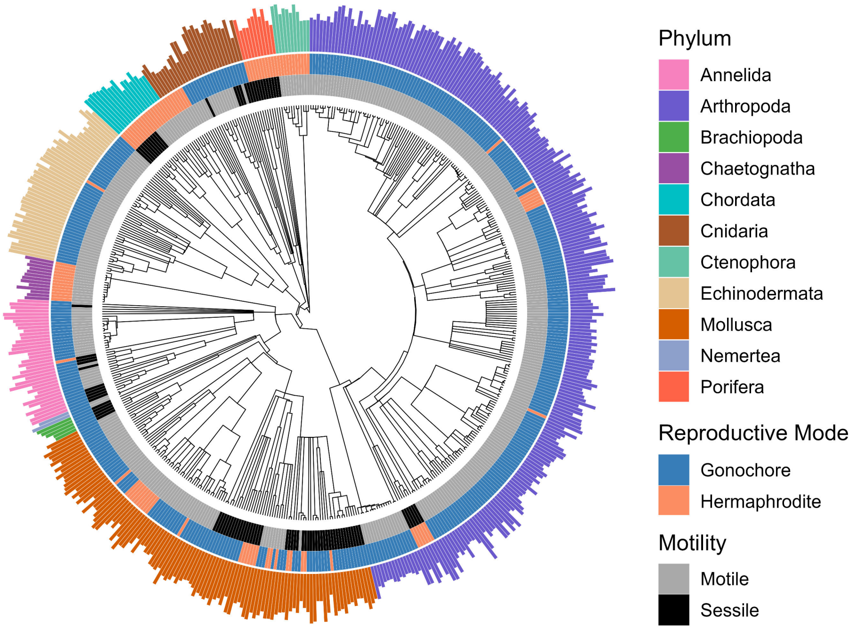

Figure 2. Distribution of species' body size, reproductive mode and motility. Adult body mass (estimated as natural-log-transformed wet weight, in grams; coloured bars by phylum) mapped to the phylogeny of species in our dataset. The inner rings represent whether species are gonochoric (blue) or hermaphroditic (orange), and motile (grey) or sessile (black). Note that in some phyla, hermaphroditism co-occurs with a sessile habit (e.g. Porifera), while in other clades, there is no covariance between hermaphroditism and motility (e.g. Mollusca), such that across all of our dataset, we are able to disentangle the relative contributions of reproductive mode and motility in our analyses.

Africa, South America and Antarctica are under-represented. In addition to geographical biases, there can also be taxonomic bias: to assess this, we compared the proportion of species per phylum in our dataset with those of the *World register of marine species* [30]. In our dataset, arthropods, echinoderms and chaetognaths are over-represented, while molluscs and sponges are under-represented, but most of the phyla deviate by less than ±2% from their known species proportions (electronic supplementary material, figure S1). Furthermore, the species representation in our dataset reflects natural patterns in species richness: more speciose phyla make up a greater proportion of our dataset (electronic supplementary material, figure S1).

(b) Classifying reproductive mode and motility

Once we had compiled the data for metabolic rate, adult size and environmental temperature for each species, we then collected data for their reproductive mode. Most of the information came from book chapters on marine invertebrate reproduction (various taxa [31]; polychaetes [32,33]; prosobranch gastropods [34]), supplemented with species-specific literature searches via Google Scholar: e.g. '[Genus species]' along with the terms, 'hermaph*', 'gonochor*', 'reproduc*', 'male' or 'female'. Unfortunately, the reproductive modes of many of the species in our dataset are not explicitly mentioned in the literature. In such cases, we coded reproductive mode based on expert descriptions of species' reproductive life history [31], or based on clade-specific patterns (e.g. all known species of chaetognaths [35] and ctenophores [36] are hermaphrodites). Reproductive modes inferred at the genus or family level may be less certain than those where the entire order, class or phylum has a known reproductive mode. We therefore reanalysed the data excluding the four species for which reproductive mode was imputed at the genus (n = 3) or family (n = 1) level, and our results were qualitatively unchanged (electronic supplementary material, table S4).

We classified species as hermaphrodites if they are able to reproduce as both male and female in their lifetime, and as gonochores otherwise. Note that for gonochores, we did not differentiate metabolic rate measurements between males and females—sex was unreported for most of the species in our dataset. Whether metabolic rates differ between males, females and hermaphrodites is an important avenue for future research, and we encourage empiricists to report the sex of individuals when measuring metabolic rate [37]. Under our classification scheme, sequential and simultaneous hermaphrodites were collectively coded as hermaphrodites. From an energy perspective, transitioning from one sex to the other as a sequential hermaphrodite may be particularly costly [38]. Therefore, energy requirements might differ not only between sequential hermaphrodites and gonochores but also between sequential and simultaneous hermaphrodites. Unfortunately, we could not test these predictions formally owing to the limited representation of sequential hermaphrodites across a comparable range of body size and temperature [39]. However, our results were qualitatively unchanged when we omitted sequential hermaphrodites from our analyses (electronic supplementary material, table S5). For now, we are inclined to treat our findings with regard to sequential hermaphrodites with caution until additional data on metabolic rate in this group can be assembled for a more representative sample.

Because many phyla in our dataset are represented by only a single reproductive mode (electronic supplementary material, table S1), we ran an additional analysis to assess the role of single-mode phyla in driving our results: excluding the six phyla with only a single mode did not affect our results (electronic supplementary material, table S6).

For motility, we coded as motile any species that are able to move as adults—including those with facultative movement (e.g. scallops, crinoids)—and all others as sessile (e.g. barnacles, sponges, most bivalve molluscs).

(c) Statistical analyses

We characterized the covariance between adult metabolic rate and reproductive mode, while accounting for the effect of motility, body size and environmental temperature. We analysed our data with phylogenetically controlled models to account for species' shared evolutionary history on patterns in metabolic rate. Specifically, our model assessed whether there is an association between metabolic rate and reproductive mode, along with our other traits of interest, while incorporating the covariation among species due to phylogenetic relatedness in the model residuals [40,41].

We fitted phylogenetic generalized least squares (PGLS) models with maximum likelihood with the function 'gls' in the package nlme v. 3.1-168 [42,43]. Our model included natural-log-transformed metabolic rate as the continuous response variable, along with environmental temperature and natural-log-transformed body mass (both continuous), reproductive mode (categorical: hermaphrodite or gonochore) and motility (categorical: motile or sessile) as fixed effects, and a phylogenetic random effect as predictors. We evaluated the significance of model predictors using F-tests, and we estimated the proportion of residual variation in metabolic rate (conditioned on the fixed effects) explained by the random effect of phylogeny as Pagel's λ [44,45]. We tested whether reproductive mode differed between sessile and motile species with a Pearson's χ^2 test.

We extracted phylogenies from the Open Tree of Life [46] with the package rotl v. 3.1.0 [47] and constructed our phylogenetic tree with the package phytools v. 2.4-4 [48]. We used the function 'congruify.phylo' [49] with the PATHd8 scaling method [50] in the package geiger v. 2.0.11 [51,52] to time-calibrate the tree according to time data from the TimeTree of Life [53]. This function maps known species' divergence times from a reference tree (time-calibrated) to a target tree (uncalibrated) sampled from the same lineage. We then randomly resolved all polytomies in the time-calibrated tree with the function 'multi2di' in the package ape v. 5.8-1 [54], after which we rescaled all zero-length branches with the function 'zero.brlen' in the package dispRity v. 1.9 [55].

We tested the fit of Brownian motion (BM; corBrownian), Pagel's λ (PL; corPagel) and Ornstein–Uhlenbeck (OU; corMartins) models of character evolution for metabolic rate (package ape). First, we compared PL and OU models with BM models with likelihood ratio tests: for all models, PL and OU models fitted the data better than BM models (electronic supplementary material, table S7). Next, we compared the PL model with the OU model using the Akaike information criterion (AIC; [56]). In all cases, the PL model was a better fit than the OU model according to the lowest AIC values and ΔAIC > 2 (electronic supplementary material, table S7), so we used models fitted with PL correlation structure for all analyses.

All statistical analyses were completed in RStudio v. 4.5.1 [57]. Figures were created using the packages ggplot2 v. 3.5.2 [58], ggrepel v. 0.9.6 [59], ggtree v. 3.16.3 [60,61] and ggtreeExtra v. 1.18.0 [62]. All data and code required to reproduce our analyses and figures are deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.j3tx95xt4 [63].

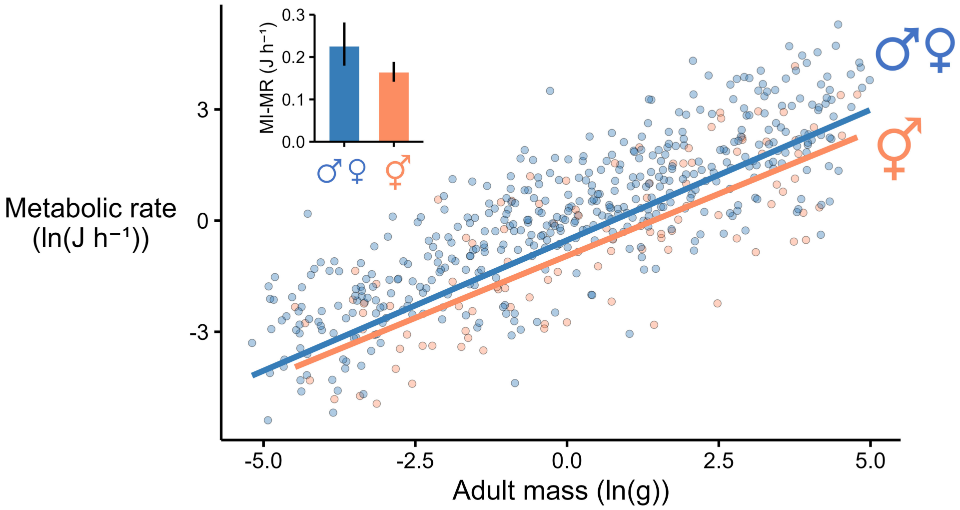

Figure 3. Hermaphrodites have lower metabolic rates than gonochores across body sizes. Relationship between metabolic rate (in natural-log-transformed (ln) joules per hour) and adult mass (natural-log-transformed wet weight in grams) for gonochores (blue) and hermaphrodites (orange). Points represent raw data for each species, and the linear fits represent the relationship from phylogenetically controlled regressions. The inset shows the average (± s.e.) mass-independent metabolic rate (MI-MR, in joules per hour) across all species.

3. Results

(a) Hermaphrodites have lower metabolic rates

After taking account of body size, environmental temperature and phylogeny, metabolic rates do indeed prove to be associated with reproductive mode (figure 3 and electronic supplementary material, table S3): on average, metabolic rates of hermaphrodites are 27% lower than those of gonochores of equivalent size (reproductive mode: $F_{1,531} = 5.02$, $p = 0.03$; figure 3 inset). In other words, for two species of equivalent body mass that differ only in their reproductive mode, the hermaphrodite uses 27% less energy than the gonochore. When we exclude sequential hermaphrodites, the difference is even stronger: all else being equal, simultaneous hermaphrodites use 34% less energy than gonochores (reproductive mode: $F_{1,506} = 4.72$, $p = 0.03$; electronic supplementary material, table S5). Phylogeny explains 43% of the residual variation in metabolic rate (electronic supplementary material, table S3).

(b) Motility has little effect on metabolic rate

In our dataset, reproductive mode and motility are correlated: sessile species are more likely to be hermaphroditic than motile species ($\chi^2 = 35.56$, d.f. = 1, $p < 0.01$; electronic supplementary material, figure S2). However, after accounting for reproductive mode, motility does not affect metabolic rate (motility: $F_{1,531} = 3.35$, $p = 0.07$). The one exception is a specific case, where excluding sequential hermaphrodites from our analysis reveals that sessile species tend to have slightly higher resting metabolic rates than motile species (motility: $F_{1,506} = 4.35$, $p = 0.04$; electronic supplementary material, table S5).

4. Discussion

Here, we test the long-standing idea that hermaphrodites are rarer than gonochores because hermaphroditism is more energetically costly [1,8,9,16–18,64,65]. Instead, we find that, for an equivalent body size, hermaphrodites only use around 75% as much energy as gonochores on average: it is remarkable that such a large difference has remained unrecognized for so long. Metabolic rate is a critical trait, affecting everything from the pace of life to the demography of populations [23,66–69]—our results predict that hermaphrodites should differ from gonochores in every aspect of their life history and ecology in ways that have not been anticipated but can now be tested.

Our results are exactly the opposite of what we expected, and what is assumed by theory: hermaphrodites, with their dual sexual roles, have lower metabolic rates than gonochores. What could explain this difference? Our analysis rules out differences in motility as a driver for two reasons. First, we included motility as a separate factor in our analysis, and it was a relatively weak predictor of metabolic rate. Second, while our findings confirm the long-standing speculation that sessile species are more likely to be hermaphrodites, the covariance between motility and metabolic rate is opposite to what we would expect. Motile species—which are more likely to be gonochores—tend to have lower metabolic rates than sessile species.

We believe there are at least two non-mutually exclusive possible explanations for why hermaphrodites have lower metabolic rates. First, hermaphrodites are expected to expend less energy on securing fertilizations because the effective density of compatible mates is double that of gonochores [2,3,70]. Assuming that lower resting metabolic rates also reflect lower active or field metabolic rates, hermaphrodites may have lower metabolic rates than gonochores overall because hermaphrodites are required to expend less energy to find mates.

Second, the covariance between hermaphroditism and metabolic rate could be the outcome of selection on each trait independently. Hermaphroditism has long been argued to be associated with low population densities. Going back to at least Meyer [71], authors have argued that hermaphroditism might be favoured when the chances of encountering mates are low because it doubles the number of encounters that can result in cross-fertilization [4,17,20]. Low population densities are often found in unproductive, low-resource environments. It could be that the metabolic signal we detect in hermaphrodites is due to hermaphrodites being especially likely to live in low-resource environments. Under this view, lower metabolic rates in hermaphrodites are the outcome of selection on two traits separately, but this leads to a covariance between the two: low-resource environments select for lower metabolic rates and also for hermaphroditism; hence, those species that have lower metabolic rates are also more likely to be hermaphrodites [23]. Exploring whether resource availability differs between hermaphrodites and gonochores is an important next step: studies in molluscs certainly suggest that such differences are possible (e.g. [72]).

Regardless of the factors leading to the difference in metabolic rate between hermaphrodites and gonochores, metabolic theory predicts that—under equivalent resource conditions—these differences will have demographic consequences. Because metabolic rates covary with energy demands and energy use, theory predicts that metabolic rates should be positively correlated with population growth rates and negatively correlated with population-carrying capacities [67,68,73,74]. Thus, for a given amount of resources, our results predict that hermaphroditic populations should grow more slowly but achieve higher densities than gonochoric populations. Mass-independent metabolic rate is also thought to be negatively correlated with generation time and lifespan [75,76]—hermaphrodites should therefore, *ceteris paribus*, live longer than gonochores. These predictions await testing, but, regardless, our results suggest that any given hermaphrodite will have much lower energy demands than a gonochoric species of equivalent size. For example, the gonochoric snail *Gibbula umbilicalis* must consume 0.87 J of energy per hour to meet its metabolic maintenance demands, while the similarly sized hermaphroditic sea slug *Cadlina laevis* requires 77% less energy (0.20 J h^{-1}) [77]. For now, it seems likely that these differences in metabolic rates will affect many different life-history traits and they suggest that hermaphrodites and gonochores will play very different trophic roles in ecosystems. For example, food chains with hermaphrodites should be more efficient (i.e. less energy is lost owing to respiration) than those of gonochores because maintenance metabolic rate will ‘waste’ less energy at each trophic level [78]. Furthermore, higher metabolic rates in gonochores should demand more foraging activity [79], which may entail greater risk of predation, relative to hermaphrodites [80]. All of these predictions require testing, but these marked differences in metabolic rate between reproductive modes strongly suggest that other traits are likely also to differ in predictable ways.

An important next step will be to determine whether the covariance between reproductive mode and metabolic rate extends beyond invertebrates. We focused on marine invertebrates because they are well studied with regard to metabolic rates and show substantial variation in reproductive mode. Both fish and plants also exhibit simultaneous hermaphroditism, but in the former group, hermaphroditism is relatively rare [81], and in the latter group, whole-organism metabolic rate is relatively less well studied [82–84]. We therefore urge more exploration in both groups, focusing on measuring metabolic rate in hermaphroditic fishes specifically and compiling more metabolic data on plants more generally. For now, it seems that Darwin’s famous speculation about the energy dynamics of gonochores and hermaphrodites has been refuted, but we eagerly await data from these other clades.

Our findings challenge a long-standing assumption about the energetic costs of reproductive modes: hermaphrodites have significantly lower resting metabolic rates than gonochores. The finding is robust to possible effects of phylogeny, body size, temperature and motility, and we suspect that it is driven by ecological differences between hermaphrodites and gonochores. Determining how the energy availability of habitats varies between hermaphrodites and gonochores is an important next step towards understanding the relative influence of ecology and reproductive mode on resting metabolic rate. Furthermore, although we focused on whole-organism metabolic rates, future work that quantifies the energetic costs of reproductive structures themselves [85]—and how energy allocated to these structures may differ between hermaphrodites and gonochores—would provide a more complete exploration of Darwin’s hypothesis about the energy dynamics of reproductive modes.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. All data and code required to reproduce our analyses and figures are deposited in the Dryad Digital Repository [63]. Supplementary material is available online [86].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors’ contributions. G.C.J.: conceptualization, data curation, formal analysis, methodology, visualization, writing—original draft, writing—review and editing; D.J.M.: conceptualization, supervision, writing—review and editing.

Both authors gave final approval for publication and agreed to be held accountable for the work performed herein.

Conflict of interests. We declare we have no competing interests.

Funding. G.C.J. was partially funded by a Postgraduate Publication Award from Monash University’s Graduate Research Office.

Acknowledgements. We sincerely thank Thomas Brey, John McNamara, Jeff Drazen, Thomas Kiørboe, Félix Leiva, Levi Lewis, Samuel Faria and Nelly Tremblay for generously sharing their raw data for metabolic rate. We are also very grateful to Deborah Charlesworth and Michael Jennions for reviewing earlier drafts of the manuscript and providing helpful feedback. The manuscript benefited greatly from the constructive comments from two anonymous reviewers. We thank Craig White, Monique van Dorssen, James Farrands, Shiho Ozeki and the members of the Marine Evolutionary Ecology Group for thoughtful discussions, which greatly improved this manuscript. Finally, we thank the interlibrary loan team and library staff at Monash University for helping us access older literature. Open access publishing was facilitated by Monash University, as part of the Wiley–Monash University agreement via the Council of Australian University Librarians.

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