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Rapid declines in metabolism explain extended coral larval longevity

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Abstract

Lecithotrophic, or non-feeding, marine invertebrate larvae generally have shorter pelagic larval durations (PLDs) than planktotrophic larvae. However, non-feeding larvae of scleractinian corals have PLDs far exceeding those of feeding larvae of other organisms and predictions based on energy reserves and metabolic rates, raising questions about how such longevity is achieved. Here, we measured temporal changes in metabolic rates and total lipid content of non-feeding larvae of four species of reef corals to determine whether changes in energy utilization through time contribute to extended larval durations. The temporal dynamics of both metabolic rates and lipid content were highly consistent among species. Prior to fertilization, metabolic rates were low (2.73-8.63 nmol O_2 n^{-1} hr^{-1}) before rapidly increasing to a peak during embryogenesis and early development 1-2 days after spawning. Metabolic rates remained high until shortly after larvae first became competent to metamorphose, then declined by up to two orders of magnitude to levels at or below rates seen in unfertilized eggs over the following week. Larvae remained in this state of low metabolic activity for up to two months. Consistent with temporal patterns in metabolic rates, depletion of lipids was extremely rapid during early development, and then slowed dramatically from one week onwards. Despite the very low metabolic rates in these species, larvae continued to swim and retained competence for at least two months. The capacity of non-feeding coral larvae to enter a state low metabolism soon after becoming competent to metamorphose significantly extends dispersal potential, thereby accruing advantages typically associated with planktotrophy. In particular, extended larval durations have important implications for potential range expansion of corals in response to ongoing environmental change.

Key words: connectivity, coral reefs, dispersal, larvae, lipid, metabolism

Introduction

Marine invertebrate larvae can be broadly classified into two categories, lecithotrophs or planktotrophs, depending on their source of nutrition during development. Planktotrophic larvae require external food sources to complete development, whereas lecithotrophic larvae are capable of completing development based solely on maternal provisions (Thorson 1950). The potential to feed should enable planktotrophic larvae to survive longer in the plankton (Scheltema 1986), and there are numerous examples of planktotrophic larvae that spend more time in the plankton than closely related species with lecithotrophic development (e.g., Emlet et al. 1987; Kempf and Todd 1989; Shanks et al. 2003). The longer PLDs of planktotrophic larvae are thought to confer greater dispersal potential for species with such larvae, enabling higher levels of gene flow over larger areas and potentially larger geographic ranges compared to species with non-feeding larvae (Jablonski and Lutz 1983; Pechenik 1999). Relationships between PLD, genetic population structure and range size have been documented for echinoids (Hunt 1993; Emlet 1995), gastropods (Hoskin 1997; Collin 2003; Paulay and Meyer 2006), and various other invertebrates (Foggo et al. 2007; Selkoe and Toonen 2011). However, the role of PLDs in driving such relationships is not always clear (Weersing and Toonen 2009), because population connectivity depends on many factors, including post-settlement processes (Marshall et al. 2010) and barriers to dispersal (Keith et al 2011), that may obscure the role of larval duration alone.

In reef-building scleractinian corals, larval development mode is generally a good predictor of patterns of dispersal and connectivity. Populations of brooding species, whose larvae are ready to settle on release, typically have higher genetic structure than broadcast spawning species, whose larvae have an obligate planktonic period of 2-4 days (e.g., Hellberg 1996; Nishikawa et al. 2003). Corals, along with some high-latitude echinoderm taxa, are the only groups with non-feeding larvae for which extremely long PLDs have been documented (Birkeland et al. 1971; Hartnoll 1975; Sebens 1983; Bosch and Pearse 1990; Bryan 2004, Hizi-Degany et al. 2007; Graham et al. 2008; Connolly and Baird 2010). For example, coral larvae can survive up to 200 days (Graham et al. 2008), and can

complete metamorphosis up to at least 100 days after spawning (Hizi-Degany et al. 2007; Connolly and Baird 2010). These examples indicate that species with lecithotrophic larvae, including many coral species, have developed strategies to extend larval duration, and thus accrue the advantages of dispersal traditionally associated with planktotrophy.

If lecithotrophic larvae are to survive long periods in the plankton, they must possess a large supply of stored energy, have low metabolic rates, or be able to supplement their endogenous reserves. Large initial energy stores, slow development rates, and low rates of metabolism in Antarctic echinoderms imply that these larvae can persist for up to five years in the plankton (Shilling and Manahan 1994). For scleractinian corals, a few species equip their propagules with photosynthetic symbionts (zooxanthellae), which may provide energy to larvae during dispersal and support PLDs over 100 days (Richmond 1987; Harii et al. 2010). However, most (>75%) coral species have larvae that lack such symbionts (Baird et al. 2009), yet even larvae of these species have exceedingly long PLDs. In *Acropora tenuis* larvae, initial energy content and metabolic rates observed during the first few weeks after fertilization imply larval longevities of only ~30 days (Richmond 1987, Graham et al. 2008). This estimate is less than half the 69 days observed for this species (Nishikawa et al. 2003), and many months less than larval longevities reported for other *Acropora* species (Graham et al. 2008, Connolly and Baird 2010). Similar discrepancies between energy reserves, metabolic rates, and observed larval durations have been found in echinoderms (Bryan 2004). This suggests that corals and at least some other lecithotrophic larvae must either reduce their metabolic rates substantially as they age, take up additional energy (e.g., by absorption of dissolved organic matter (DOM)), or combine elements of both of these strategies. Although there is some evidence for uptake of DOM in soft coral larvae (Ben-David-Zaslow and Y. Benayahu 2000), this has not been documented in scleractinian coral larvae. Similarly, knowledge of metabolic rates for coral larvae is limited. Temporal changes in lipids over the first month after fertilization suggest that lipids are depleted rapidly in the first week, after which the rate of depletion slows and then picks up again in the fourth week (Harii et al. 2007; Figueiredo et al 2012). Consistent with these patterns of lipid depletion, respiration rates of *Acropora intermedia* larvae declined to about one-third of peak values one week after

spawning (Okubo et al. 2008). These studies indicate that metabolic rates can decrease as coral larvae age, although these changes do not appear to be of sufficient magnitude to account for the extended PLDs documented in coral larvae.

Determining whether long PLDs are widespread among coral species with lecithotrophic larvae, and understanding how these PLDs are attained, is critical to estimating the dispersal potential of this dominant group of reef builders. Such knowledge has important implications for understanding the ecology, evolution, and biogeography of corals and for anticipating how dispersal potential and population connectivity may be impacted by changing ocean conditions that have implications for metabolic rate, particularly increased seawater temperature. Therefore, we investigated physiological mechanisms underpinning extended PLDs in scleractinian corals with non-zooxanthellate, lecithotrophic larvae, by quantifying respiration rates and energy use over larval lifespans. We found strong evidence in both respiration rates and lipid levels for a rapid decline in rates of energy use within approximately one week of spawning, even though larvae are still capable of metamorphosis. We conclude that low metabolic rates (i.e, hypometabolism) allow non-feeding coral larvae to extend larval life by minimising depletion of their energy reserves.

Materials and methods

Study site and larval cultures

The study took place at Orpheus Island, Australia, in December 2008, and November and December 2009. Gametes from a total of four broadcast spawning scleractinian species whose larvae lack zooxanthellae (*Goniastrea aspera*, *Acropora tenuis*, *A. nasuta*, and *A. spathulata*), were collected and cultured using established methods (Willis et al. 1997). Four to six adult colonies of each species were collected immediately prior to anticipated spawning dates and brought onshore. For each species, gametes were collected within an hour of release and combined. Once fertilized, developing embryos were transferred to 500 L fibreglass aquaria with flow through 0.2 µm filtered seawater (FSW) and continuous aeration, one tank per species. The aquaria were maintained in

temperature controlled rooms at near-ambient temperature (27 +/- 1°C) and a 12 h light:dark cycle.

Sampling design

At regular sampling intervals, subsamples of eggs, embryos, or larvae (hereafter "propagules") were randomly selected, for each species, and used for respiration measurements and lipid analysis. The first sample was taken from newly released gametes, prior to fertilization. For respiration measurements, five replicates of 50 propagules were used. For lipid analysis of each *Acropora* species, the same 50 propagules used to measure respiration rates were subsequently frozen and used for lipid analysis. However, for lipid analysis of *G. aspera* propagules, due to their smaller size, three replicates of 600 propagules were used. Sampling took place every 12 h for the first 36-48 h to capture larval development through embryogenesis to a swimming larva, followed by daily sampling until the majority of larvae were competent to settle at 5 days after spawning (DAS). From 5 DAS, sampling was further reduced to every three days, unless low numbers of surviving larvae forced a further reduction to weekly sampling. Survival experiments and settlement assays, described in detail below, were conducted at each sampling point after larvae began swimming to determine whether patterns in energy use affected larval mortality rates or the larvae's capability to metamorphose.

Respirometry

To measure egg, embryo, and larval respiration rates, a temperature compensated, fiber-optic oxygen meter called the Fibox was used (PreSens GmbH). Respiration chambers were custom made, with each chamber consisting of a 1.5 ml glass vial integrated with a 5 mm diameter oxygen sensitive sensor foil spot on the inside of the chamber. Prior to each experiment, the respirometer was calibrated using sodium dithionite ($Na_2S_2O_4$) and air-saturated FSW for a two-point (0, 100%) calibration following the manufacturer's instructions. A sterilized miniature magnet was placed inside each chamber and magnetically stirred to ensure adequate mixing. For each of the five replicates of each species, 50 propagules were counted into the chamber and topped with fresh 0.2 µm FSW. The change in oxygen concentration in the chamber was measured for 5 min. Following each

replicate, the chamber was flushed and refilled with fresh FSW, and oxygen measurements were taken of the individual-free seawater for an additional 5 min to serve as a control. Oxygen consumption was calculated as the slope of oxygen concentration over the 5 min measuring period, and then converted into nmol O_2 $larva^{-1}$ hr^{-1}.

There is no a priori theory that predicts a particular functional form to describe how oxygen consumption should change with DAS. Moreover, initial plots of oxygen consumption rate as a function of DAS suggested a complex nonlinear relationship between the two variables. A log transformation of the observed values improved the homogeneity of variances, but the underlying relationship remained highly nonlinear. Therefore, to analyse the change in oxygen consumption rate, a nonparametric generalized additive model (GAM) was fitted to the log-transformed data. GAM uses a locally-weighted smoothing function to characterize arbitrary nonlinear relationships between the response (respiration rate) and predictor (DAS) variables (Zuur et al. 2009). GAM was implemented using the mgcv package in R (Wood 1994).

Lipid analysis

To measure the total amount of lipid in each sample, a TLC-FID detection system was used (Iatroscan MK-5). Lipids were extracted using a modified Bligh-Dyer chloroform:methanol method, with an internal standard added to provide an estimate of lipid recovery (Sewell 2005). Two developments were used to separate the lipid sample into the following classes: aliphatic hydrocarbons, wax esters (WE), triacylglycerides (TG), free fatty acids, free aliphatic alcohols, cholesterols (ST), and phospholipids (PL) (Parrish 1999). The lipid classes were then divided into two groups -- energetic lipids (WE and TG) and structural lipids (ST and PL) -- and analysed separately. Since energetic lipids are most likely to be available for maintenance of metabolism during the larval phase, we present the energetic lipids in the results. However, we also assess the extent to which qualitative trends in total lipids reflect those of energetic lipids.

Like the respiration data, there is no a priori reason for favouring a particular mathematical function to describe lipid depletion over time. Moreover, visual inspection of lipid data revealed a complex nonlinear relationship with time. Therefore, after applying a square-root transformation to the lipid data (to

homogenize variances), a GAM was used to characterize the nonlinearity in the change in lipid levels over time. Our approach was similar to that described above for respiration. However, because coral larvae are non-feeding and lack zooxanthellae, a monotonicity constraint was applied to the GAM (i.e., we constrained fitted lipid levels to decrease over time, as per Wood 1994). This helped to avoid over-fitting of the model, and yielded narrower confidence intervals than an unconstrained fit. We obtained 95% confidence intervals for this constrained GAM fit by bootstrapping residuals (Efron and Tibshirani 1993).

Survival

To determine if larval survival was affected by energy use, once swimming larvae had developed, five replicate 70 ml specimen jars were set up containing 0.2 µm FSW and 100 larvae each. At each sampling time, the number of surviving larvae was recorded and larvae were transferred into new specimen jars. Because coral larvae typically lyse within 24 hours of death, there was no need to distinguish between live and dead larvae, i.e., the larvae remaining at each interval were assumed alive (Baird et al. 2006). A Kaplan-Meier product-limit analysis was used to obtain nonparametric estimates of the median survival time and 95% confidence intervals around this estimate for each species.

Settlement assays

To determine the onset of competence and whether this capability was maintained throughout larval duration, at each sampling point following the onset of swimming, a subsample of 120 larvae was placed into a 6-well plate. Twenty larvae were introduced into each well containing 0.2 µm FSW and a small piece of crustose coralline algae, a known settlement inducer for *Acropora* species (Morse et al. 1996). After 24 h, the number of larvae that had successfully metamorphosed was recorded. Metamorphosis was defined as the deposition of a basal plate following Baird and Babcock (2000).

Results

Respirometry

Qualitative patterns in respiration rates through time were highly consistent among all four study species (Fig. 1). Oxygen consumption increased from very low levels in unfertilized eggs to a peak 1-2 DAS. Peak oxygen consumption coincided with the onset of larval motility (Fig. 1, vertical dashed lines). Respiration rates had all declined significantly from the peak prior to the first larvae becoming competent (Fig. 1, vertical dotted lines). After a week, oxygen consumption had fallen substantially, reaching levels similar to those of unfertilized eggs, and remained low until the conclusion of the experiments (up to 60 days later). Of the four species, *Acropora tenuis* exhibited the most pronounced peak in oxygen consumption; respiration rates fell by approximately two orders of magnitude over the week following peak respiration (Fig. 1b). In contrast, *A. spathulata* exhibited the smallest change, with an approximately two-fold decline from peak levels over approximately two weeks (Fig. 1d). Unique among the four species, there was a delay until approximately 12 h after fertilization before larval respiration rates of *A. nasuta* began to increase, but otherwise its overall pattern of oxygen consumption was very similar to those of the other species (Fig. 1c).

Lipid

Total lipids consisted overwhelmingly of energy lipids, and these two quantities exhibited quantitatively very similar temporal dynamics (see Electronic Supplemental Material), so only energetic lipids were used in the analysis. Consistent with the trends for respiration rates, larvae of all four species exhibited qualitatively similar patterns of energy lipid depletion (Fig. 2). Initial lipid levels declined rapidly through embryogenesis and development until approximately the time at which larvae became competent (i.e, capable of metamorphosis) (Fig. 2, vertical dotted line). Subsequently, energy lipid levels declined very slowly throughout the remainder of the experiment. In contrast to the three other species, lipid levels in *A. nasuta* larvae remained high for the first 12-24 h after fertilization, before declining rapidly (Fig. 2c), consistent with the delayed

increase in metabolic rates observed for this species (Fig. 1c). Of the *Acropora*, *A. tenuis* larvae had the greatest initial decline in energy lipid levels, with an approximately three-fold reduction occurring in the first week (Fig. 2b), consistent with its higher metabolic rates prior to the acquisition of competence (Fig. 1b). In contrast, *A. spathulata* exhibited the smallest decline in lipid levels, decreasing only two-fold in the first week (Fig. 2d), consistent with a smaller decline in metabolic rates (Fig. 1d). Once competence was acquired, larvae from all species remained capable of settlement at every sampling point over the remainder of the experiment (Fig. 1, Fig. 2, shaded areas).

Survival

Survival times varied among species, with estimated median lifetimes ranging from 4 d for *A. spathulata*, 14 d for *A. nasuta*, and 57 d for *A. tenuis* (Fig. 3). A median lifetime for *G. aspera* was not estimable, due to the very high survival in this species (>98% after 35 d; Fig. 3a). Mortality rates also varied, but in most cases, increased mortality did not occur until after larvae were competent to settle (slope of the lines in Fig. 3, shaded areas). The exception was *A. spathulata*, whose survival decreased the most between the onset of swimming and the acquisition of competence (vertical dashed and dotted lines, Fig. 3d). For each species, some larvae were alive at the conclusion of the experiment.

Settlement

Once competence was acquired, larvae from all species maintained competence to settle for the duration of the study (Fig. 4). The overall proportion of competent larvae was highest for *A. nasuta* and *A. spathulata*, with the majority of the larvae of these two species acquiring competence 8-14 DAS (Fig. 4c, d). Forty percent of *A. tenuis* larvae were competent by day 5 and this proportion competent remained high for another 10 d before declining (Fig. 4b). *Goniastrea aspera* larvae, on the other hand, were unusual with only a small proportion of larvae competent from day two until 24 DAS, with a peak in competence only reached after 28 days. The proportion of *G. aspera* and *A. tenuis* larvae that acquired competence never

reached more than 50%, but a relatively large proportion of larvae was capable of settlement at the conclusion of the experiment (Fig. 4a, b).

Discussion

Temporal patterns in the metabolic rates and lipid levels of lecithotrophic, non-zooxanthellate larvae for four broadcast spawning species of corals were strikingly similar in the first three weeks after spawning. Although the specific values of oxygen consumption varied among species, in all cases, respiration rates were relatively low for eggs, followed by a rapid increase through embryogenesis to a peak, the timing of which varied among species from 12-48 h after fertilization. This spike in respiration rates is short-lived, and rates quickly fall back to initial levels within 3-6 days, where they remain for up to eight weeks. Consistent with these observations, lipids are depleted rapidly during development, until a few days after larvae become competent to metamorphose, at which time the rate of lipid utilization slows dramatically. The high concordance between these two measures of energy use strongly support the hypothesis that an extended period of reduced larval metabolism explains, at least partly, the long PLDs observed in many coral species with non-feeding larvae. Moreover, the capacity of larvae to maintain competence throughout this extended period of reduced energy use implies the capacity to settle over a broad range of dispersal distances.

Although embryogenesis and larval development are the most energetically demanding periods in the larval life of many marine invertebrates (e.g., Shilling and Manahan 1994; Anger 1996; Hoegh-Guldberg and Emlet 1997; Bryan 2004), the magnitude of the declines observed in some species suggests that lecithotrophic larvae have the capacity to achieve much lower levels of energy use than have previously been documented. High rates of respiration correspond firstly with high rates of cell division during embryogenesis (approximately 12-36 h post-fertilization) and secondly with the development of specialised cells, such as spirocysts, that are associated with attachment and metamorphosis (36-96 h post fertilization) (Hayashibara et al. 2000; Okubo and Motokawa 2007). Once these energetically demanding processes are complete, larvae enter a state of substantially reduced metabolism. The magnitude of

decrease in respiration varied from ~2.5-fold in *A. spathulata*, to about 100-fold in *A. tenuis*. Temporal changes in respiration have been examined previously in only one species, *A. intermedia* (Okubo et al. 2008), and were found to decrease by ~3-fold, which is within, but towards the low end of the range of declines in our species.

The pattern of rapid decline in lipid content during the first week of embryogenesis and larval development, followed by a period when further lipid depletion was minimal, is consistent with the observed trends in respiration rate. Overall, larvae lost between half (*A. spathulata*) to ~75% (*A. tenuis*) of their initial lipids during the first week. This is similar to, but larger than, the ~30-40% depletion of lipids observed over a similar period in the one previous study that reports comparable data (Harii et al. 2007). For at least three of the four study species, lipid levels were stable after this period. The exception was *G. aspera*, which exhibited a secondary decline over the final (fifth) week. However, this decline must be treated with some caution, because it was driven entirely by samples on the final sampling date, and lipid levels were very stable over the preceding three weeks. For the three *Acropora* species, the rates of lipid depletion apparent at the end of the study are consistent with very long PLDs observed in other *Acropora* coral species, such as *A. valida*, which has been observed to successfully metamorphose at ~110 d (Connolly and Baird 2010). On the final sampling date (63, 26, and 22 DAS for *A. tenuis*, *A. nasuta*, and *A. spathulata*, respectively), the observed rates of lipid depletion in larvae of these species (the slopes of the fitted lipid line in Fig. 2) varied from ~0.11 µg d^{-1} to <<0.01 µg d^{-1} (Table 1). At these rates, after a further 100 days in the plankton, *A. tenuis* and *A. nasuta* larvae would have used approximately 6% and 16% of remaining energetic lipids, respectively (Fig. 2b,c), suggesting that energy reserves are consistent with the very long (100+ days) PLDs that have been documented for corals (Hizi-Degany et al. 2007; Connolly and Baird 2010). *Acropora spathulata* had sufficient lipid for an additional 77 d at the rate of consumption at the end of the study, with a total estimated PLD for this species of 99 d (Table 1).

In contrast to estimates based on rates of energy lipid decline, estimates of PLDs based on respiration rates prevailing at the end of the experiment still fall short of empirically observed PLDs in the literature (Table 2). One possible explanation for this apparent discrepancy between metabolic rates and rates of

energy lipid depletion is that the larvae are supplementing their endogenous reserves by absorbing dissolved organic matter (Ben-David-Zaslow and Benayahu 2000), which would have been present both in the filtered seawater being supplied to them, and as a consequence of the lysing of dead coral larvae. Alternatively, the handling necessary to place larvae in respirometry vials for measurement of oxygen consumption may have stimulated a temporary elevation in metabolic rates for these sampled larvae, causing respirometry measures to be biased upwards, relative to average levels prevailing for larvae remaining in the tanks.

Even though metabolic rates measured in vials may be high relative to rates for larvae in tanks, the rates are still substantially lower than those predicted from metabolic scaling theory. This strongly suggests that metabolic rates are indeed unusually low after competence is achieved. Whole-organism metabolic rate is known to exhibit power-scaling with body mass. In particular, for temperatures between 8-27°C, mass-normalized resting metabolic rates of multicellular invertebrates typically lie between 0.002 and 0.135 W $g^{-3/4}$, where W is metabolic rate in Watts (joules per second) (Gillooly et al. 2001). Using egg dry weights for *G. aspera* of 0.000012 g and for *A. nasuta* of 0.000031 g (Graham 2007), and assuming *A. tenuis* and *A. spathulata* have comparable egg dry weights as similar-sized eggs of *A. digitifiera* (0.000043 g) and *A. divaricata* (0.000027 g) respectively (Graham 2007), we calculated mass-normalized metabolic rates for larvae in this study at 27°C (Fig. 5). These estimates are much lower than expected even though the larvae were actively swimming (i.e., not resting) (Fig. 5).

The consistency in the overall patterns of reduced oxygen consumption and lipid depletion for all four study species is striking, and implies that the energetic cost of delaying metamorphosis may be much smaller than is commonly assumed for lecithotrophic larvae. These findings help to explain large discrepancies between energetic estimates of larval duration based on metabolic rates measured early in larval life (Richmond 1987) and the much greater durations measured empirically (Graham et al. 2008, Connolly and Baird 2010). This suggests that very low basal metabolic rates underpin the extended competence periods and larval durations of scleractinian corals, which are on par with or greater than those of most planktotrophs (Shanks et al. 2003, Shanks 2009). While there are undoubtedly costs associated with increased time in the

plankton, our results suggest that some of the hypothesized post-settlement costs, such as increased mortality and decreased growth (Pechenik 2006), may be less severe for scleractinian coral larvae than might be expected based on the metabolic rates prevailing early in larval life, or typical of similar-sized invertebrates. Few studies of the temporal dynamics of metabolism in other lecithotrophic larvae have lasted more than two weeks (e.g., Okubo et al. 2008; Hoegh-Guldberg and Emlet 1997; Moran and Manahan 2003). This raises the possibility that other invertebrate lecithotrophs may extend larval durations in a similar fashion. If reduced larval metabolism leading to extended larval duration is a common early life history trait underpinning current coral population structures, then ocean warming, which should elevate these basal metabolic rates, is likely to have significant consequences for dispersal potential and hence population connectivity, not only for the majority of reef-building corals but for other marine invertebrates as well.

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Figure Legends

Fig. 1 Rates of oxygen consumption through time in four scleractinian coral species. Each open circle represents one replicate measurement. Solid lines represent fitted mean respiration rates from the GAM. Dashed lines show upper and lower 95% confidence intervals on the fitted GAM values. Fitted values and confidence intervals were obtained on the log-scale (on which the analysis was conducted), and have been back-transformed to the arithmetic scale for plotting. Two vertical lines show developmental stage; a dashed line for time to swim and a dotted line for the time larvae first become competent to settle. Shaded areas indicate sampling times when settlement was observed (i.e, larvae were competent).

Fig. 2 Depletion of energy lipids through time in four scleractinian coral species. Each open circle represents one replicate measurement. Solid lines represent mean respiration rates, and dashed lines show upper and lower 95% confidence intervals. Means and confidence intervals were obtained from the GAM fits by back-transforming from the log-scale (on which fits were made) to the arithmetic scale (for plotting). Two vertical lines show developmental stage: a dashed line for time to swim, and a dotted line for the time larvae first become competent to settle. Shaded areas indicate sampling times when settlement was observed (i.e, larvae were competent).

Fig. 3 Kaplan-Meier survival estimates for four scleractinian coral species. Solid lines represent median estimates; dashed lines show upper and lower 95% confidence intervals. Vertical dashed lines indicate when larvae began swimming; vertical dotted lines when larvae acquired competence to settle, and gray shaded areas indicate when settlement was observed. Note the different scales on the y-axes.

Fig. 4 Proportion of larvae that are competent to settle for four species of scleractinian corals. Each open circle represents a settlement assay. Error bars represent one standard error.

Fig. 5 Mass-normalized resting respiration rates for multicellular invertebrates (recreated from Gillooly et al. 2001), in comparison to mass-normalized respiration rates of the four scleractinian corals maintained at 27°C in this study. *An* = *Acropora nasuta*; *Ga* = *Goniastrea aspera*; *At* = *Acropora tenuis*; *As* = *Acropora spathulata.*

Electronic Supplemental Material: Analysis of lipid depletion

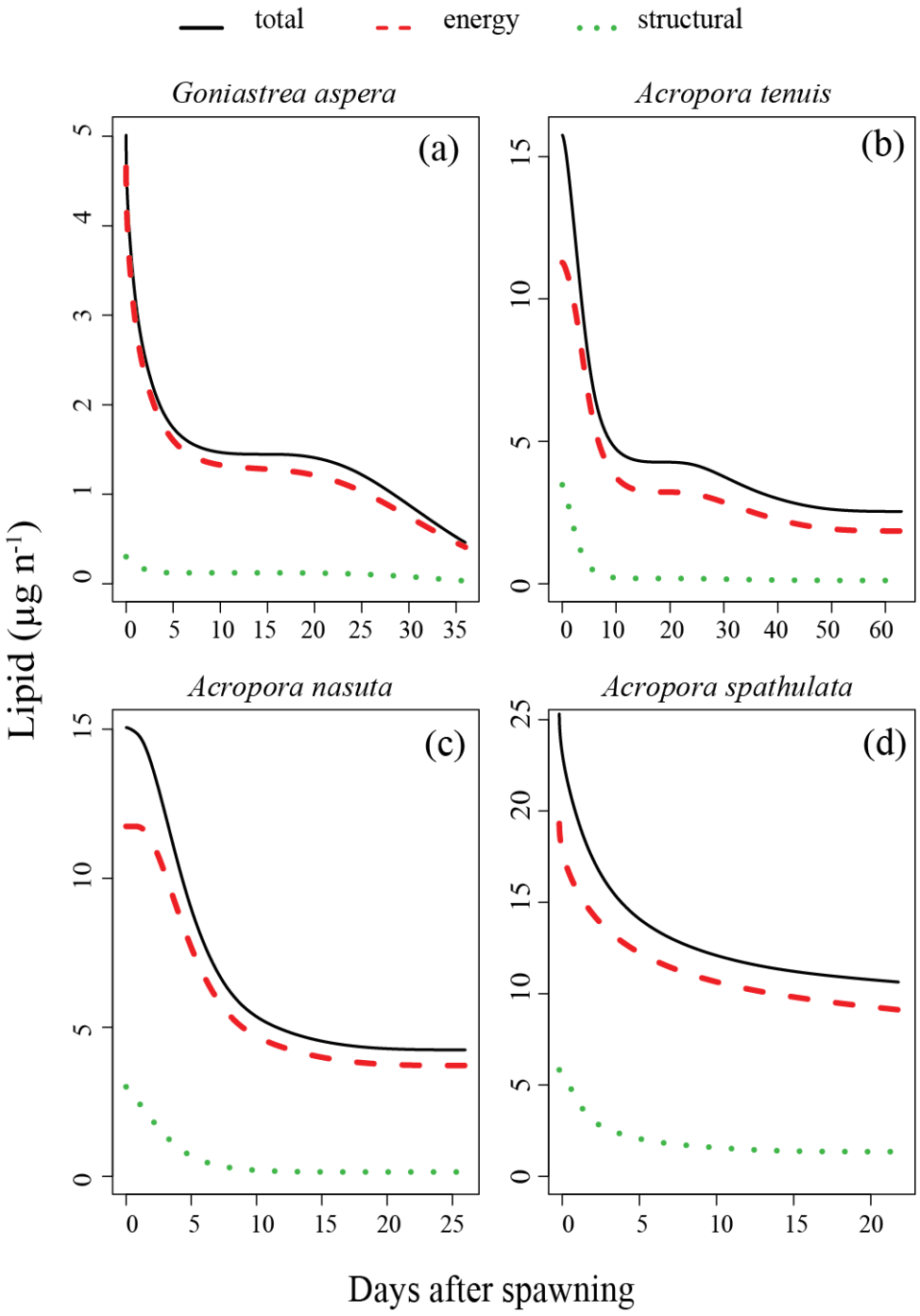


Fig. ESM1 Depletion of different lipid classes through time in four scleractinian coral species. Solid lines represent the total lipid (i.e., all lipid classes combined), dashed lines represent energetic lipids (WE and TG), and dotted lines represents structural lipids (ST and PL). The lines are fitted values from the GAM fits to measured lipid data, and have been back-transformed from the log-scale (on which fitting was done) to the arithmetic scale.

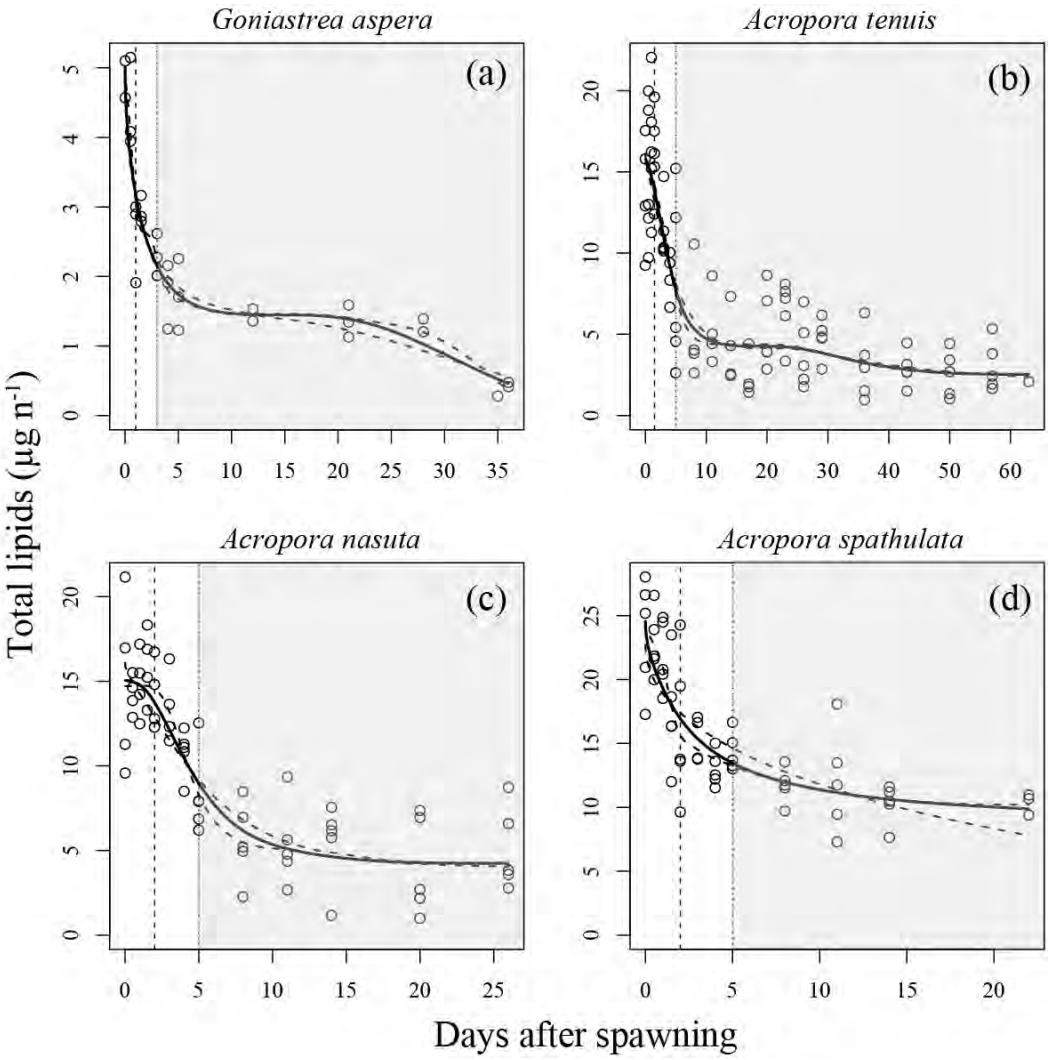
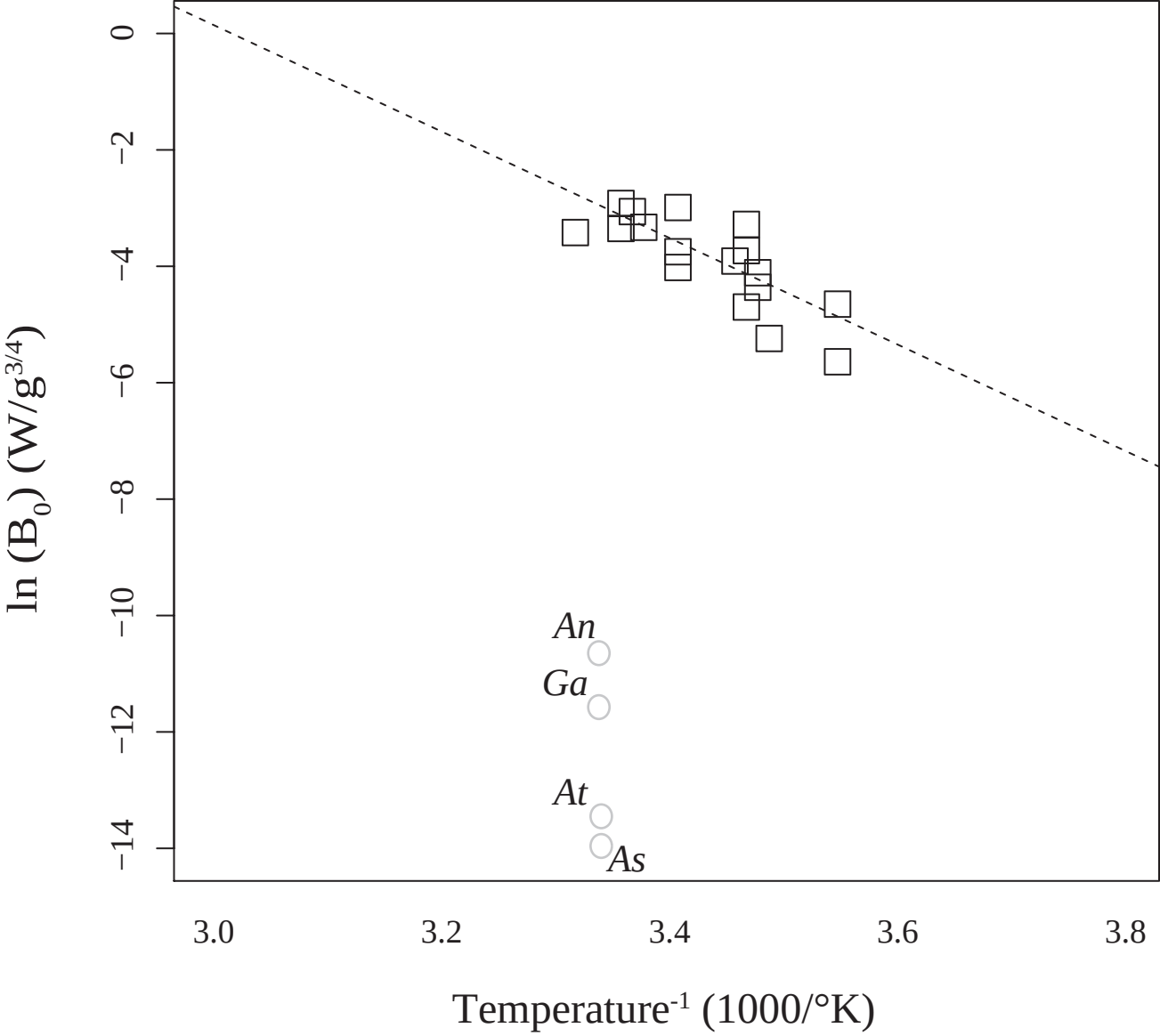
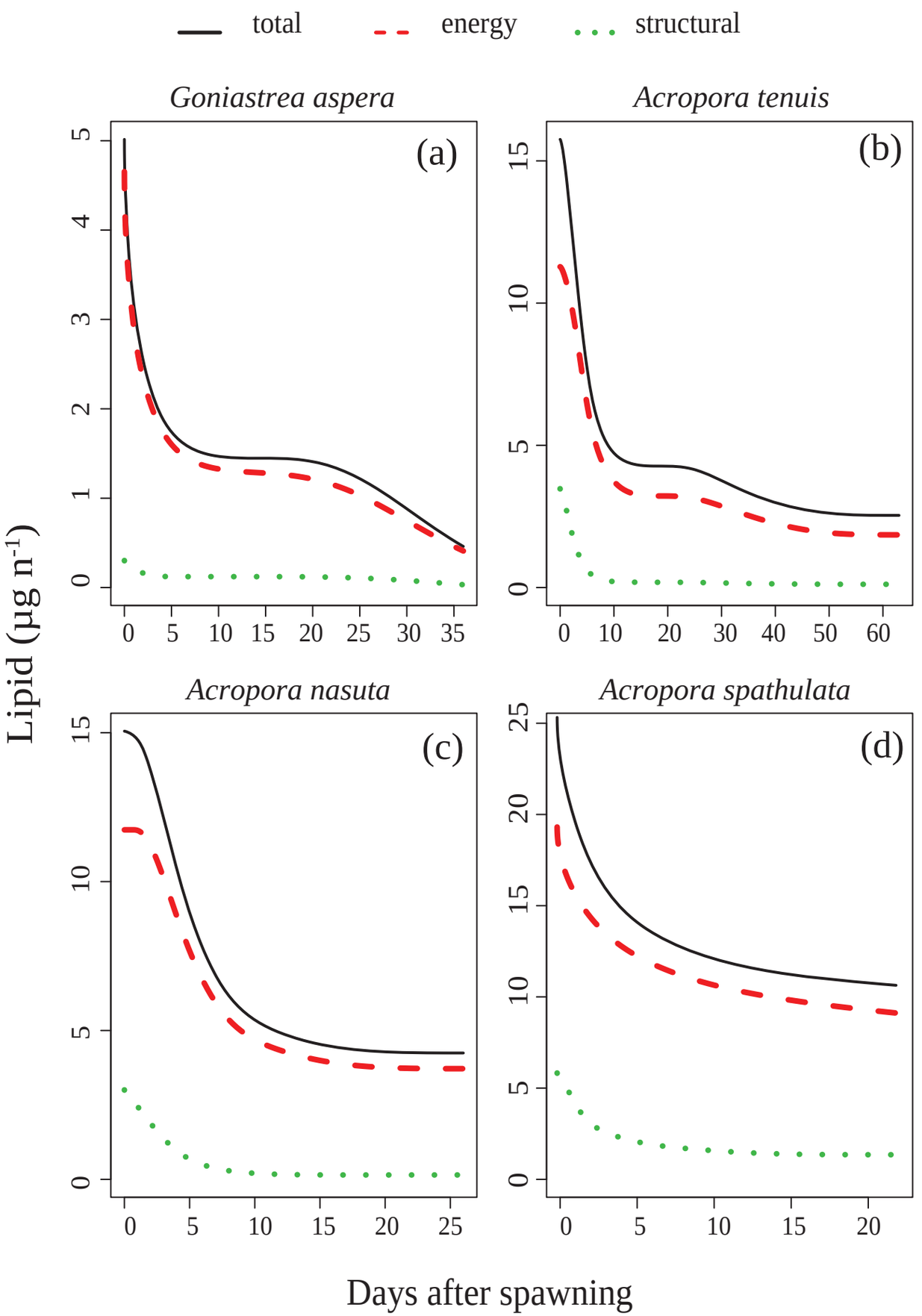
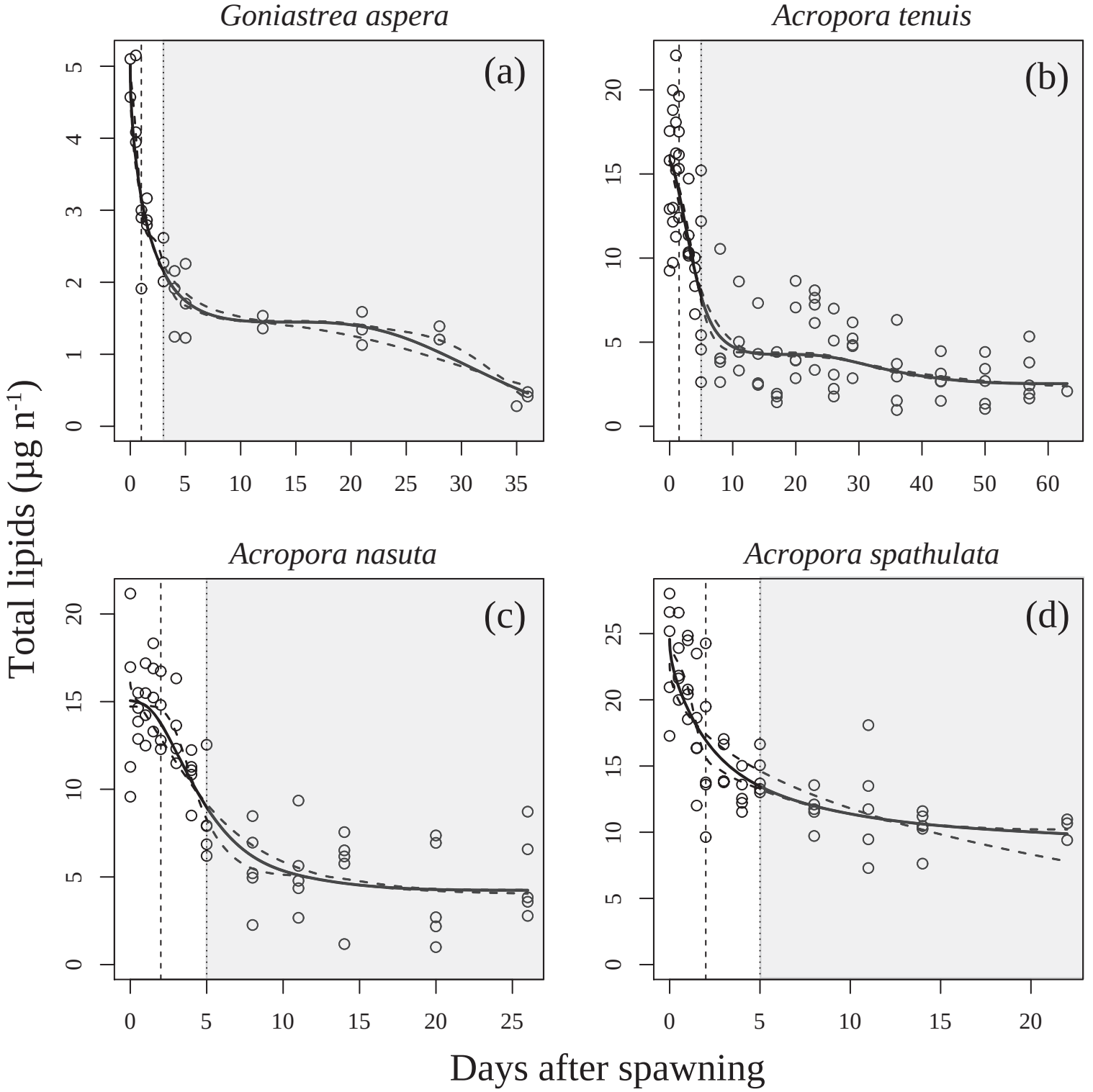
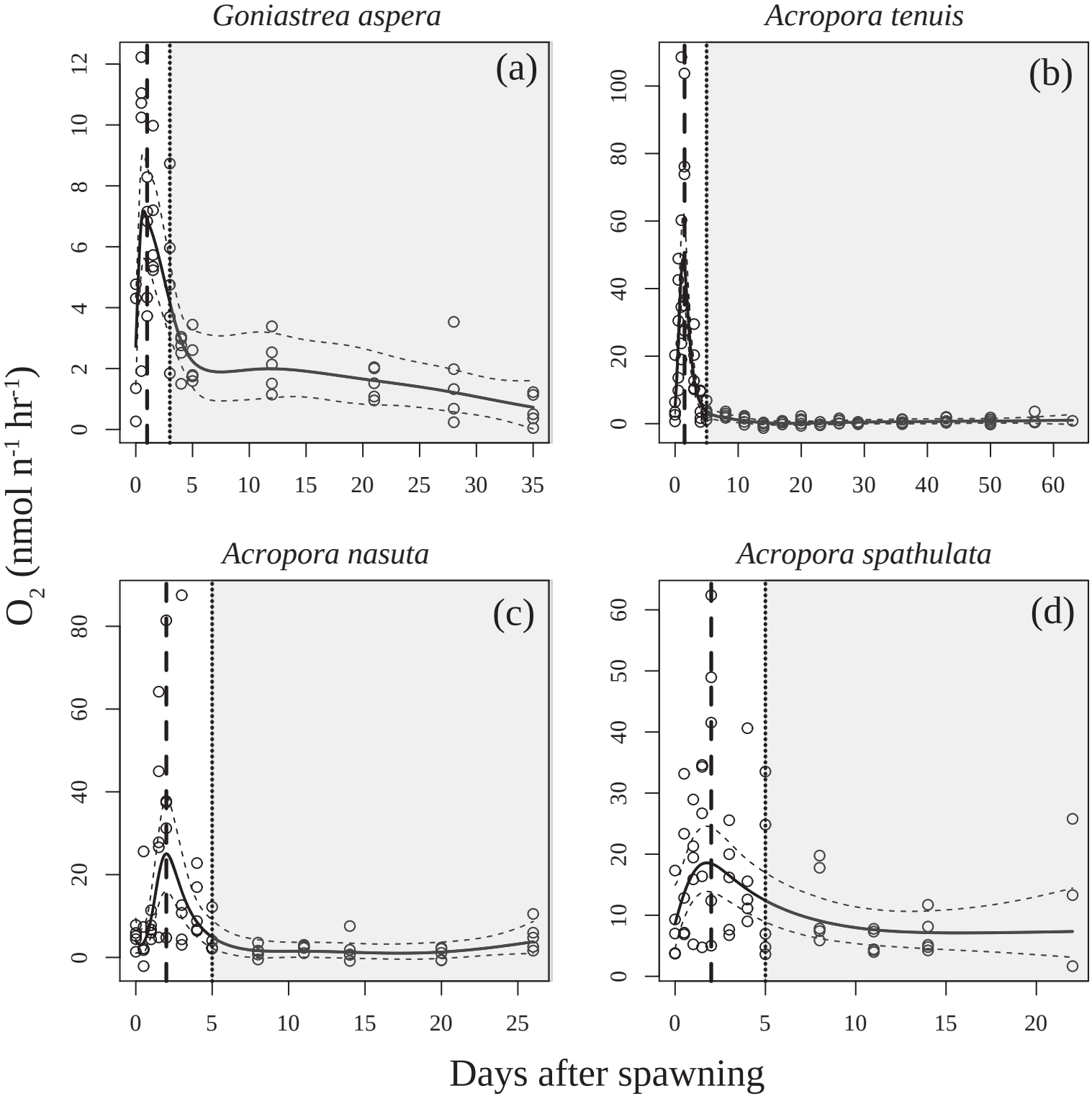


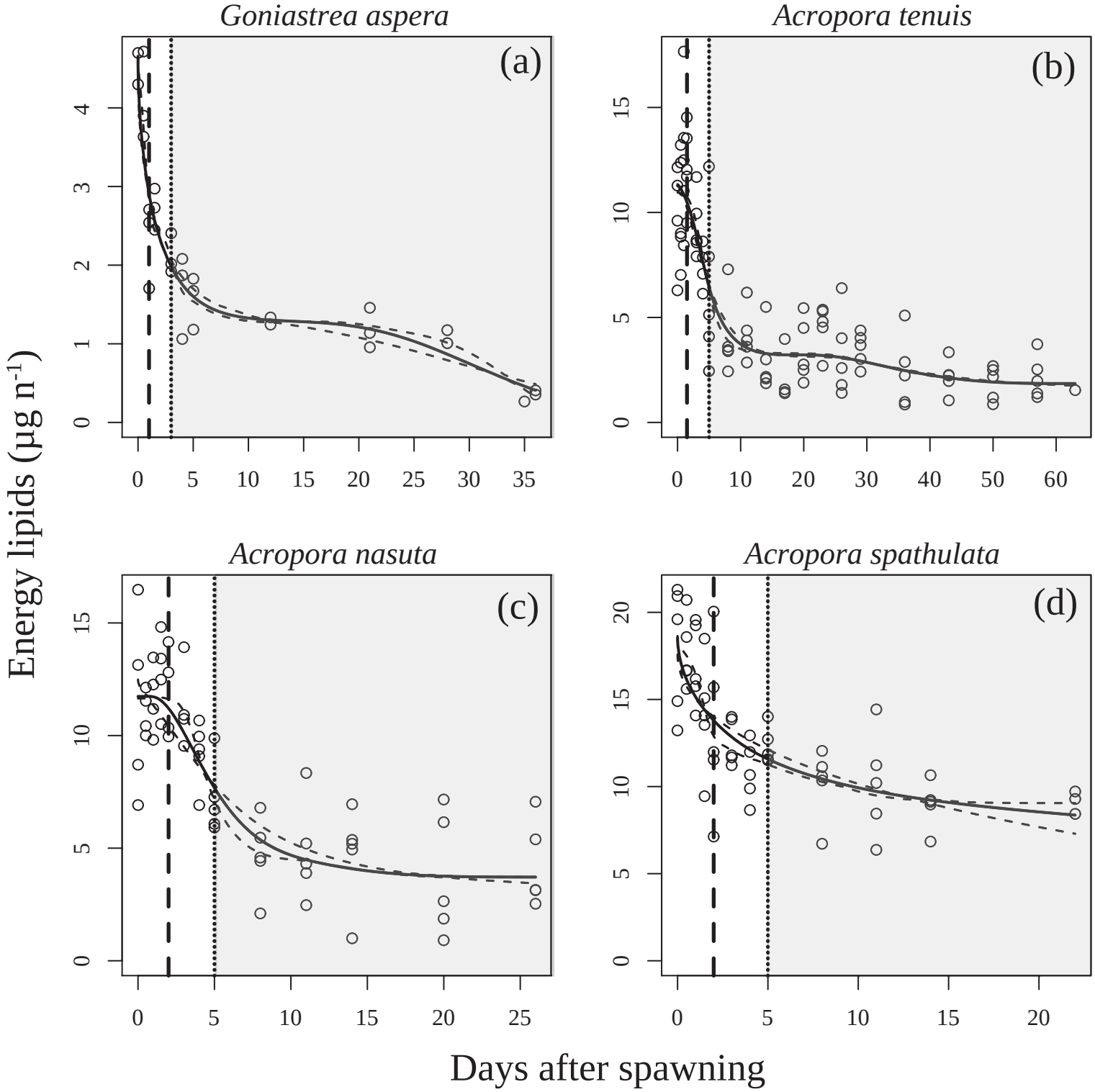
Fig. ESM2 Depletion of total lipids through time in four scleractinian coral species. Each open circle represents one replicate measurement. Solid lines represent mean respiration rates, and dashed lines show upper and lower 95% confidence intervals. Means and confidence intervals were obtained from the GAM fits by back-transforming from the log-scale (on which fits were made) to the arithmetic scale (for plotting). Two vertical lines show developmental stage: a dashed line for time to swim, and a dotted line for the time larvae first become competent to settle. Shaded areas indicate sampling times when settlement was observed (i.e, larvae were competent).

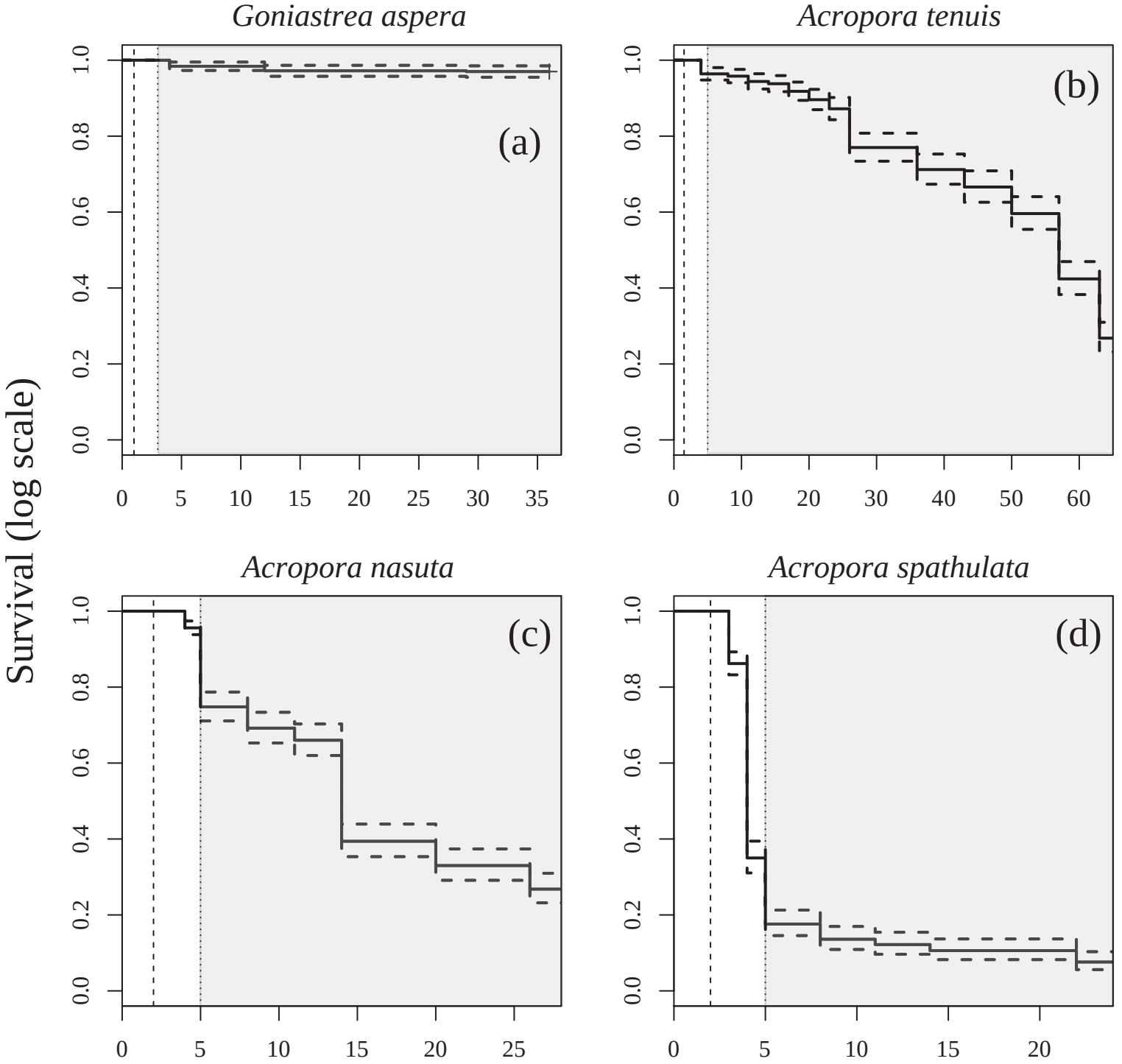

ln (B0) (W/g3/4)
0
−2
−4
−6
−8
−10
−12
−14
An
Ga
At
As
3.0
3.2
3.4
3.6
3.8
Temperature-1 (1000/°K)

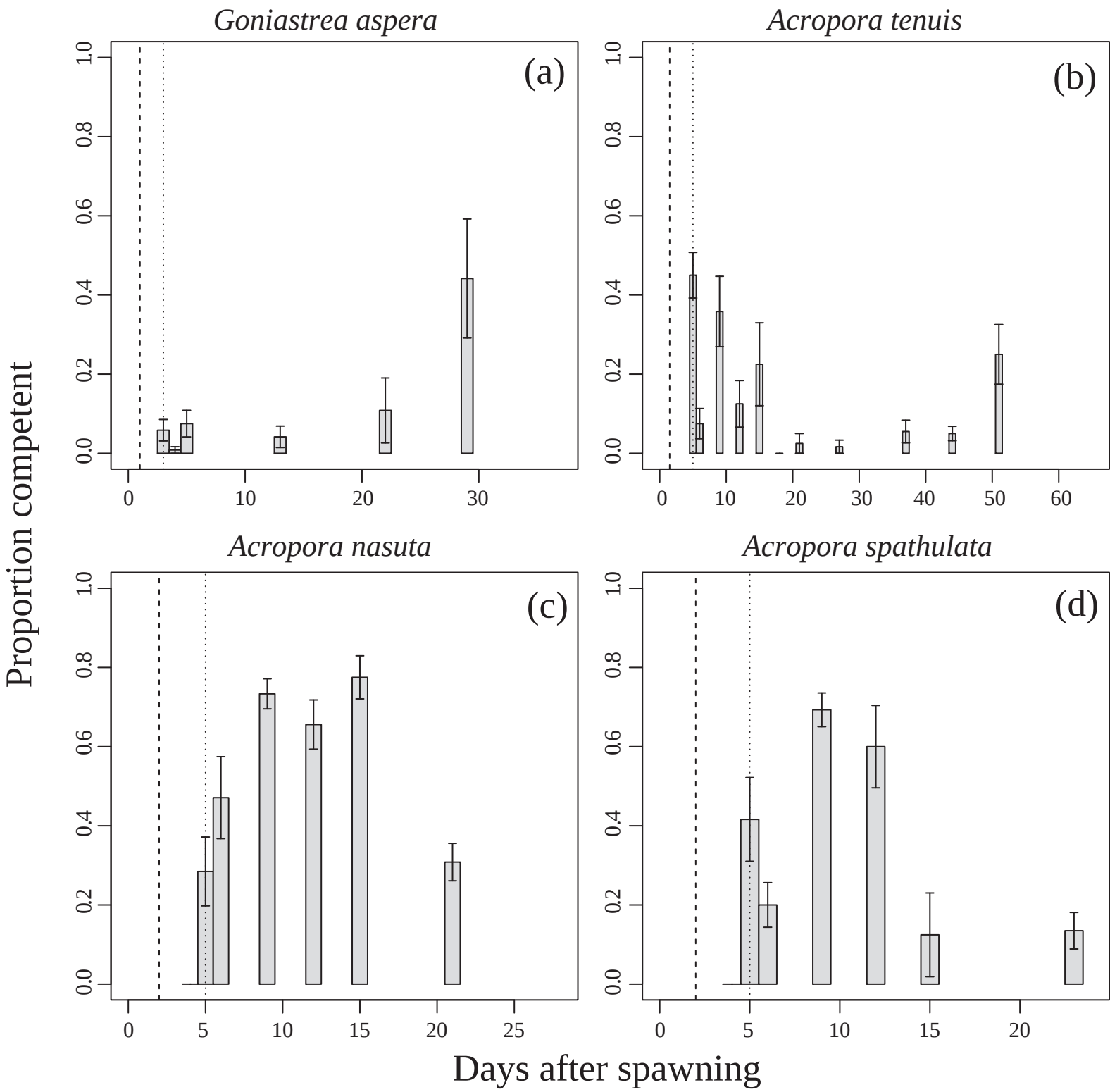

total
energy
structural
Goniastrea aspera
(a)
Acropora tenuis
(b)
Acropora nasuta
(c)
Acropora spathulata
(d)
Lipid (µg n-1)
Days after spawning

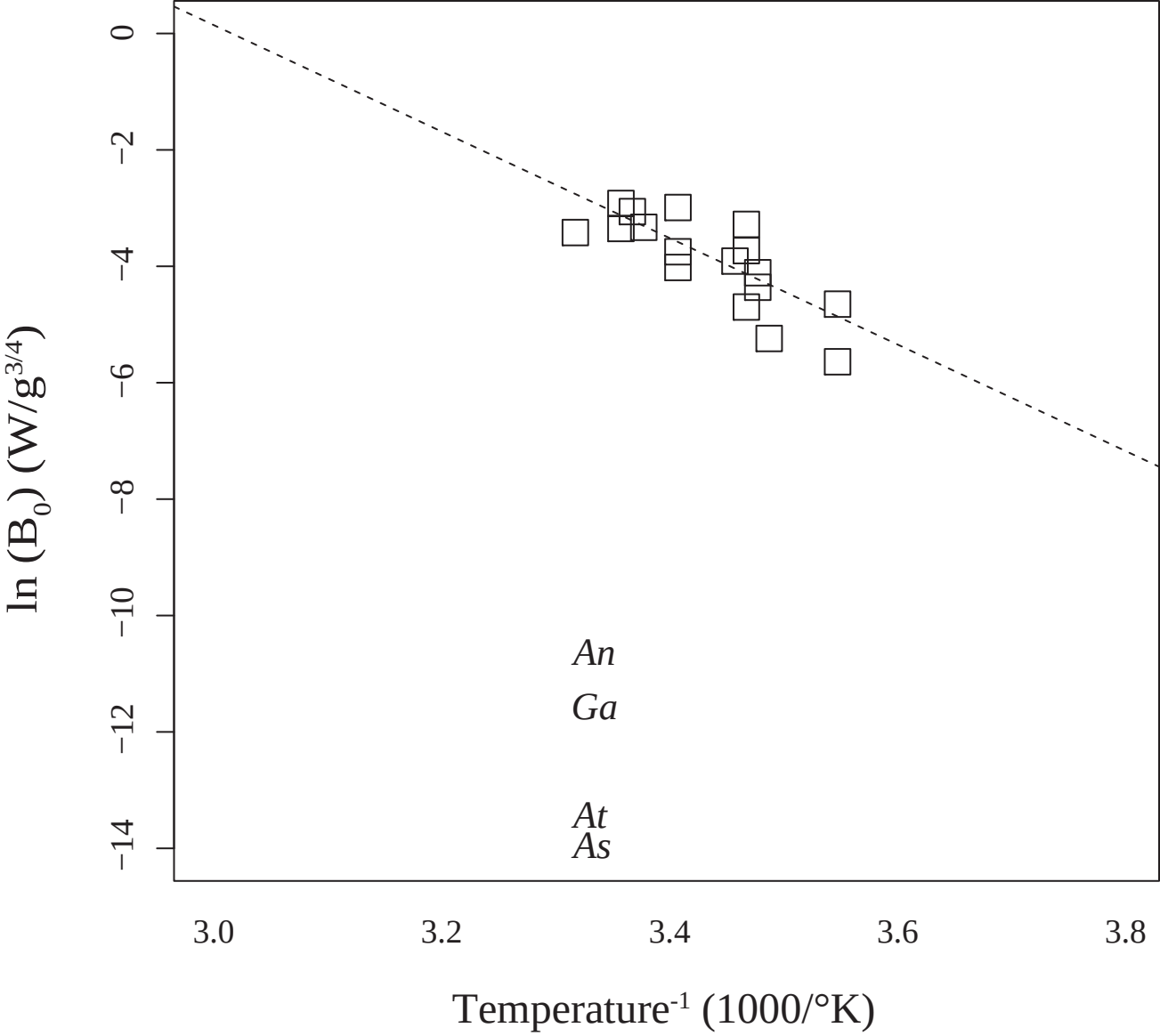

Goniastrea aspera
(a)
Acropora tenuis
(b)
Acropora nasuta
(c)
Acropora spathulata
(d)
Total lipids (µg n-1)
Days after spawning


Goniastrea aspera
(a)
Acropora tenuis
(b)
Acropora nasuta
(c)
Acropora spathulata
(d)
O2 (nmol n-1 hr-1)
Days after spawning


Goniastrea aspera
(a)
Acropora tenuis
(b)
Acropora nasuta
(c)
Acropora spathulata
(d)
Energy lipids (µg n-1)
Days after spawning


Goniastrea aspera
(a)
Acropora tenuis
(b)
Acropora nasuta
(c)
Acropora spathulata
(d)
Survival (log scale)
0.0
0.2
0.4
0.6
0.8
1.0
0
5
10
15
20
25
30
35
40
50
60


Goniastrea aspera
(a)
Acropora tenuis
(b)
Acropora nasuta
(c)
Acropora spathulata
(d)
Proportion competent
Days after spawning
0.0
0.2
0.4
0.6
0.8
1.0
0
10
20
30
40
50
60
5
15
25


0
−2
−4
−6
−8
−10
−12
−14
ln (B0) (W/g3/4)
An
Ga
At
As
3.0
3.2
3.4
3.6
3.8
Temperature-1 (1000/°K)