



Disturbance duration governs mortality risk while cumulative energetic deficit shapes reproduction in Mediterranean mussels

Gianluca Sarà^{a,b,*}

^a Laboratory of Ecology, Department of Earth and Marine Sciences (DiSTeM), University of Palermo, Italy

^b National Biodiversity Future Center (NBFC), Palermo, Italy

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ABSTRACT

Marine mussels are foundation species and ecosystem engineers increasingly exposed to marine heatwaves, hypoxic episodes and food limitation, yet apparently similar events can generate sharply different outcomes among populations. Here I test whether this variation can be explained by the interaction between disturbance duration, cumulative energetic deficit and internal energetic state. Using a Dynamic Energy Budget model for the native Mediterranean mussel *Mytilus galloprovincialis* and the invasive *Brachidontes pharaonis* across four environmental forcing scenarios, I decompose reproductive performance into the probability of reaching maturity and reproductive investment conditional on maturation. At equal cumulative energetic deficit, the uninterrupted duration of feeding suppression governs mortality risk and overall reproductive performance, whereas accumulated deficit governs how much surviving individuals invest in reproduction. Survival declines nonlinearly across a narrow duration range whose position is ordered by the reserve margin maintained under undisturbed conditions. Vulnerability therefore depends on the coincidence between event duration and energetic state, which varies with local food conditions, season and life stage. The native species, operating closer to its starvation boundary, is consistently more vulnerable than the invader, which maintains a larger reserve buffer. These results identify reserve margin as a measurable candidate predictor of recruitment failure and mortality risk. More broadly, they show why cumulative exposure metrics alone may miss the temporal continuity that drives survival loss. This individual-level mechanism provides a testable explanation for why apparently comparable coastal disturbances can generate uneven recruitment failure and contribute to spatially heterogeneous mass mortality in mussel populations.

1. Introduction

Disturbance regimes in coastal marine systems are conventionally described by the frequency, intensity and duration of stressful events and a substantial body of theory has organised how ecological systems respond to them. The distinction between press and pulse perturbations (Bender et al., 1984; Glasby and Underwood, 1996) has structured much of this work, and recent theory has formalised how populations respond to each (Jentsch and White, 2019; Jaggi et al., 2026). In plain terms, a press is a pressure that persists, so the organism lives inside it; a pulse is an event: it begins, it ends and the organism carries what it lost. The same stressor can act as either, depending on how long it lasts relative to the life of the organism experiencing it. This literature operates largely at the level of the community or the structured population, where the disturbance event is represented as an instantaneous change in

demographic rates. Whether a given cumulative amount of disturbance is delivered in a few long events or many short ones is rarely resolved and where it has been addressed it is the trade-off between frequency and intensity that has been examined, not the duration of the individual event (Miller et al., 2011). Yet the duration of a stressful event, relative to the physiological timescales of the affected organism, is expected on energetic grounds to be decisive. Field observations point in the same direction. During Mediterranean mass-mortality events associated with the 2003 and 2022 heatwaves, mortality was linked to how long anomalous thermal conditions persisted, not only to their intensity (Garrahou et al., 2009, 2022), and responses to California Current heatwaves likewise depended on event duration across taxa (Chen et al., 2024).

Why the internal structure of this response matters is an applied question as much as a theoretical one. Coastal disturbance is not

* Laboratory of Ecology, Department of Earth and Marine Sciences (DiSTeM), University of Palermo, Italy

E-mail address: gianluca.sara@unipa.it.

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stationary: climate change is lengthening and intensifying the very events that interrupt an organism's energy supply, from marine heatwaves to hypoxic episodes and pulses of food limitation, so it is increasingly the duration of individual events and not only their frequency that is changing (Montalto et al., 2016; Oliver et al., 2018; Skirving et al., 2020). Mussels are foundation species on temperate and Mediterranean shores. They build biogenic habitat, filter and couple the water column to the benthos and support the biodiversity that depends on the beds they form (Gutiérrez et al., 2003). The persistence of their populations therefore propagates to whole associated assemblages. That persistence turns on two demographic hinges that an energy-budget decomposition resolves directly: whether individuals survive to reproduce, which renews the population and how much those survivors invest in gametes, which sets its reproductive capacity. Where a native and an invasive species differ in how these hinges respond to intensifying disturbance, the disturbance regime itself becomes an agent of community reorganisation and of invasion under warming (Sarà et al., 2013a, 2014, 2018). Anticipating such shifts calls for a mechanistic, trait-level account of which populations are most vulnerable and why, rather than a description tied to a single site or endpoint.

An organism meets a shortfall in energy supply by drawing on its reserve; whether it survives an interruption and whether it can still reproduce afterwards, depends on how long the reserve can sustain the deficit before a physiological limit is crossed. Dynamic Energy Budget (DEB) theory provides the framework, describing how assimilated energy is stored in a reserve and allocated, under a fixed partitioning rule, between somatic maintenance and growth on one side and maturity and reproduction on the other (Kooijman, 2010). Environmental stressors enter such a model as modifications of bioenergetic parameters and for mussels sublethal stress acts principally on the feeding flux and the somatic maintenance cost (Muller et al. 2010a, 2010b). The consequences of a time-varying exposure for an energy budget have been formalised in DEB-based toxicokinetic-toxicodynamic approaches (Jager et al., 2022) and trait-based bioenergetic models have been developed for Mediterranean bivalves (Sarà et al. 2011, 2013b, 2014; Montalto et al., 2014).

A reproductive response assembled from an energy budget need not be of a single kind, because reproduction over the life course is the product of two conditional events: reaching maturity and having matured, investing in gametes. A disturbance can act on either, and as I show, different features of a regime act preferentially on each. It can reduce the energy channelled to reproduction in an individual that matures, producing a graded loss or it can prevent an individual from reaching maturity, by driving its reserve low enough, for long enough, to trigger mortality before first reproduction. An endpoint that records only the final reproductive output conflates them. Distinguishing them and identifying which feature of a regime governs each, is the aim of this study.

I use a DEB model, parameterised for a native and an invasive Mediterranean mussel across four environmental forcing scenarios derived from three coastal settings, to resolve a factorial space of feeding-interruption regimes and to decompose the reproductive response. Throughout the paper an interruption is a continuous interval during which feeding is reduced. Its uninterrupted duration is the length of that unbroken interval. Two regimes can remove the same total amount of energy while differing in this duration: one long interruption or several short ones. I address three hypotheses: (H1) at equal total energetic deficit, the uninterrupted duration of the interruption - not the amount of energy removed - governs the probability of reaching maturity and the overall reproductive outcome, whereas the total deficit sets how much a survivor invests; (H2) the probability of reaching maturity is a nonlinear function of interruption duration, distinct in form from the graded decline of conditional investment; (H3) the critical interruption duration (D50) is ordered by the reserve margin maintained in the undisturbed state and depends on ontogenetic stage independently of seasonal timing.

2. Materials and methods

2.1. Relationship to a companion analysis

I analysed a DEB ensemble at the level of the individual. It is shared with a companion manuscript (Sarà, unpublished manuscript) addressing a different question with a different currency; the two use different blocks of the ensemble and share no response variable or figure. All analyses below use the deterministic block, a fixed, evenly spaced sequence of feeding interruptions.

2.2. The DEB model and the survival submodel

I used a standard DEB model (Kooijman, 2010) with four state variables: structural volume V , reserve energy E , maturity E_H , and a reproduction buffer E_R . A fraction κ of the mobilised reserve flux covers somatic maintenance $p_M \cdot V$ first, the remainder to growth; the fraction $(1-\kappa)$ covers maturity maintenance first, the remainder to maturation (if $E_H < E_{Hp}$) or the reproduction buffer. Assimilation follows a type II functional response, $p_A = p_{Am} \cdot f \cdot V^{2/3}$ with $f = X/(X + K)$. Rates are temperature-corrected by a five-parameter Arrhenius function (all parameters in Supplementary Table S1). Survival $S(t)$ is the product of hourly survival probabilities $\exp(-(h_{starv} + h_{age}))$. The starvation hazard, in the baseline formulation, is a piecewise-linear activation rule, $h_{starv} = h_{max} \cdot (e_{thr} - e)/e_{thr}$ for scaled reserve density e below e_{thr} and zero above; it is continuous but not differentiable at e_{thr} . Its robustness is examined in Section 3.4. The threshold was set at $e_{thr} = 0.05$ for both species (Table S1), below the mean control reserve density of every species-forcing combination (0.079 to 0.347; Table S3), so the undisturbed controls sit above the activation threshold and starvation mortality in the ensemble follows the imposed interruptions.

The reproductive response is decomposed as $E(R) = P_M \cdot Q_M$, where $P_M = S(t_M)$ is the survival probability to the age of maturity, a continuous quantity per trajectory and $Q_M = \sum_{t \geq t_M} r(t) \cdot S(t)/S(t_M)$ is the post-maturity investment weighted by conditional survival $S(t)/S(t_M)$, avoiding double-counting of pre-maturity survival. Here $r(t)$ is the hourly flux allocated to the reproduction buffer, not the DEB specific growth rate, and t_M is the age at maturity. I use $1 - P_M$ as the primary survival response, a continuous probability, rather than a binary classification of regimes. Every trajectory that did not reach maturity within the four-year horizon had in fact died (no trajectory remained alive but immature at the horizon; Section 3.2), so $1 - P_M$ measures pre-maturity mortality and not delayed maturation. Q_M is undefined for trajectories that do not mature and these are excluded from the conditional analysis. The conditional response is reported only over the range of durations in which at least three of the ten regimes per species still reached maturity (the common-support range).

2.3. Species, sites and initial state

The model was parameterised for the native *Mytilus galloprovincialis* and the invader *Brachidontes pharaonis* (Sarà et al., 2013b, 2014 for the invader; Matzelle et al., 2015; Sarà et al., 2011 for the native; the native functional response after Montalto et al., 2017). Four environmental forcing scenarios, derived from three Mediterranean coastal settings, supplied hourly temperature and food data over four years: Trieste in the northern Adriatic Sea; Palermo open and Palermo coastal, which share the same temperature series but differ in food supply (mean food density 0.19 versus 0.49; Table S2) and the Stagnone di Marsala lagoon on the western coast of Sicily. The four hourly forcing series are shown in Fig. S1. The native was represented under the Trieste and Palermo coastal forcing scenarios and the invader under all four. Under the Palermo open forcing, the modelled native phenotype did not reach reproduction in the undisturbed control, so that combination was excluded, yielding six species-forcing combinations. The interspecific comparison and the H1 regressions use the two shared forcing scenarios.

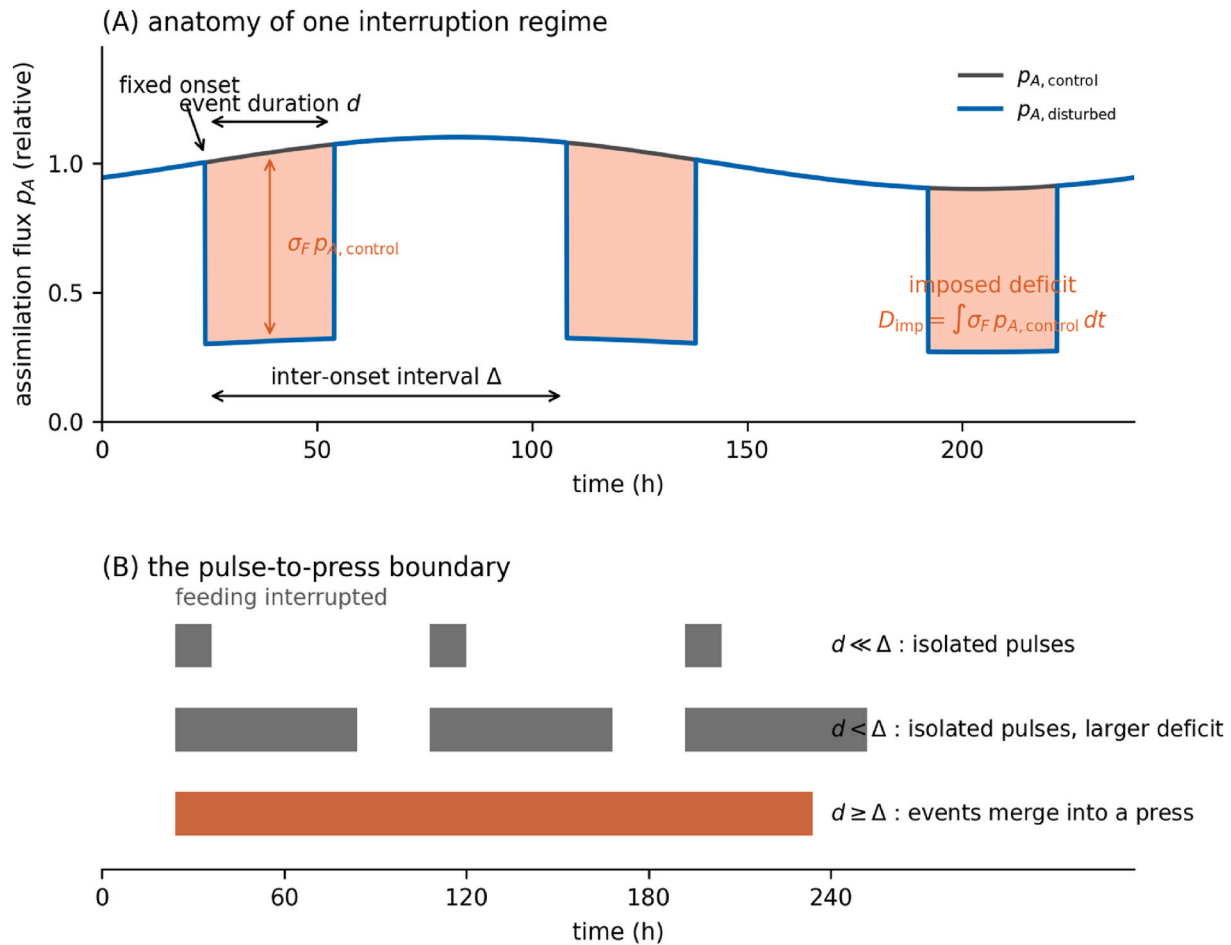


Fig. 1. Disturbance design. (A) One interruption regime: events start at a fixed onset, repeat at the inter-onset interval Δ and last d hours; during an event the assimilation flux is reduced by the fraction σ_F and the shaded area is the imposed deficit D_{imp} . (B) The pulse-to-press boundary: while each event ends before the next begins the regime delivers isolated pulses; when d reaches Δ the events merge into a continuous press.

For the ontogenetic analysis three ontogenetic initial states (settler, intermediate, near-maturity) were generated by undisturbed growth to fixed maturity fractions, then reinitialised at a common calendar hour (1 January) and subjected to the identical forcing sequence, crossed with two seasonal onsets (winter and summer), so that stage and season are separated (Supplementary Table S4).

2.4. Disturbance design, energetic deficit and the pulse-to-press boundary

Disturbance was a regular train of feeding interruptions (Fig. 1). Each simulated year contained a set number of events (1 to 52). Every event started at the same point of its cycle - the fixed onset - and the time between the starts of two successive events is the inter-onset interval. Each event reduced the assimilation flux p_A , the rate at which assimilated energy enters the reserve, by the fraction σ_F : during an event $p_{A, disturbed} = (1 - \sigma_F) p_{A, control}$, outside it the two coincide. When an event lasts longer than the inter-onset interval, successive events fuse into one continuous interruption: the regime stops delivering pulses and becomes a press. The reduction is set, not summed, so overlapping events do not deepen it. I therefore separated an isolated-pulse domain, in which every event ends before the next begins, from a press domain and conducted the principal analyses in the former. Two measures of the energy withheld were computed. The imposed deficit $D_{imp} = \int \sigma_F p_{A, control} dt$ over events, evaluated on the control trajectory, is exogenous: it measures what the regime takes as designed. The realised deficit $D_{real} = \int (p_{A, control} - p_{A, disturbed}) dt$ measures what the disturbed individual actually failed to assimilate. I used D_{imp} for the primary within-

ensemble test of H1 and D_{real} as a robustness check. A separate exploratory stress axis increased the somatic maintenance cost during events by 0-100% of its baseline value ($\sigma_M = 0-1$, from no increase to a doubling of maintenance). Because the feeding and maintenance axes are not on a common energetic scale, this axis was analysed separately as a model exploration (Section 3.6).

2.5. Statistical analysis

Each response component ($1 - P_M$, Q_M relative to control, and overall $E(R)$ relative to control) was regressed on $\log_2$ event duration and log imposed deficit over the isolated-pulse domain of the two common sites ($n = 228$ individual design cells per species, pooled across the two shared forcing scenarios and not averaged across them). Cells with $D_{imp} = 0$ are the undisturbed references and are excluded from the log-deficit term. I report the partial variance explained by each predictor, computed as the reduction in residual sum of squares on adding the term, rather than significance tests, because the ensemble is deterministic and its cells are not an independent sample from a natural population. For the same reason I characterise the conditional response by the reduction in residual sum of squares and the difference in the Akaike information criterion (AIC) between a linear and a segmented fit, and the breakpoint location, rather than by a p-value. The survival transition width was quantified as $D_{90} - D_{10}$, the durations giving 90% and 10% of maximum mortality, obtained by linear interpolation of $1 - P_M$ on log duration. I define the critical duration as D_{50} , the event duration at which pre-maturity mortality reaches 50% of its maximum, the

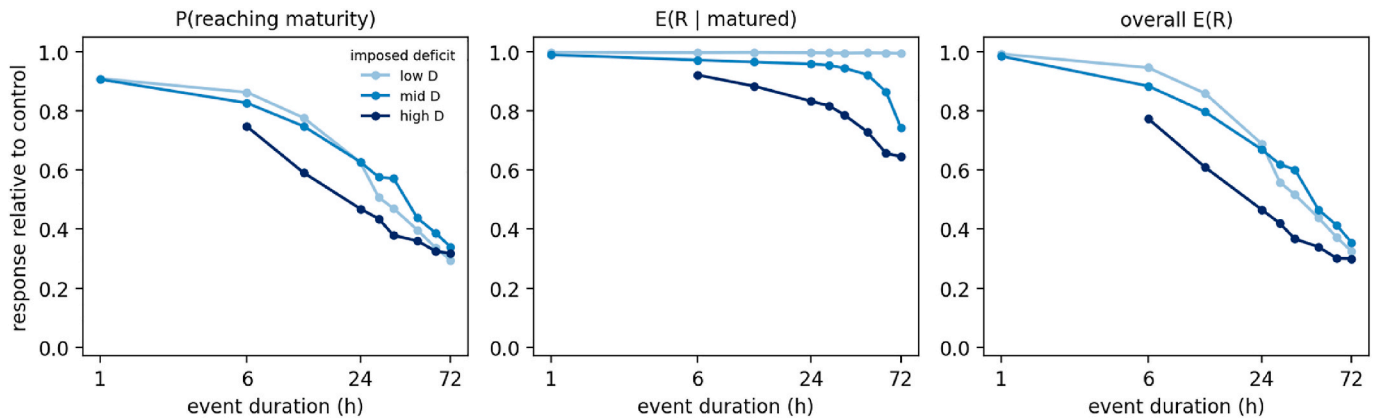


Fig. 2. Response components against event duration within three bands of imposed energetic deficit, at the two shared forcing scenarios. Left: probability of reaching maturity P_M falls steeply with duration and the deficit bands nearly coincide. Centre: conditional investment $E(R | \text{matured})$ separates by deficit band at controlled duration (shown over the common-support range). Right: overall $E(R)$ follows the survival component. Duration governs survival, the cumulative deficit governs conditional investment. All three panels are restricted to the common-support range of durations (to 72 h) over which the three deficit bands are comparably represented by maturing individuals, so the composition change at longer durations does not distort the comparison. Both species pooled across the two shared forcing scenarios; each point is the ensemble mean at that duration and deficit band, expressed relative to the matched undisturbed control.

midpoint of the transition, obtained by the same interpolation; throughout, D_{50} denotes the position of the survival transition and $D_{90} - D_{10}$ its width, while the phenomenon itself is termed the nonlinear survival transition. The critical duration D_{50} was compared with the control reserve margin $m_e = e_{\text{control}} - e_{\text{thr}}$ across the six combinations; with six combinations and right-censored D_{50} values I report this as a descriptive ordering rather than a correlation coefficient. I use D_{50} and $D_{90} - D_{10}$ as the objective position and width metrics of the survival transition rather than defining a separate steepest-slope breakpoint. Because reserve density varies through time, e_{control} in the reserve-margin comparison is the mean scaled reserve density over the four-year undisturbed control trajectory for each species-forcing combination.

2.6. Verification and robustness

The implementation was verified by reproducing the undisturbed control of every combination to the reported precision (Supplementary

Table S3); this was a code verification, not a biological validation. The survival transition was recomputed under three alternatives to the baseline hazard - a steep logistic, a smooth exponential and a broad piecewise-linear rule acting over twice the reserve range - and under a three-by-three variation of the two starvation parameters. Its dependence on initial ontogenetic stage was examined with the season-controlled design of Section 2.3.

3. Results

3.1. Duration and cumulative energetic deficit

Both species enter this analysis, each at the two shared forcing scenarios. At equal cumulative energetic deficit, duration and the imposed deficit governed different components of the response (Fig. 2; Table S5). Regressing each component jointly on log duration and log imposed deficit, duration dominated the probability of reaching maturity (partial variance explained 0.45 in the native, 0.19 in the invader) and overall

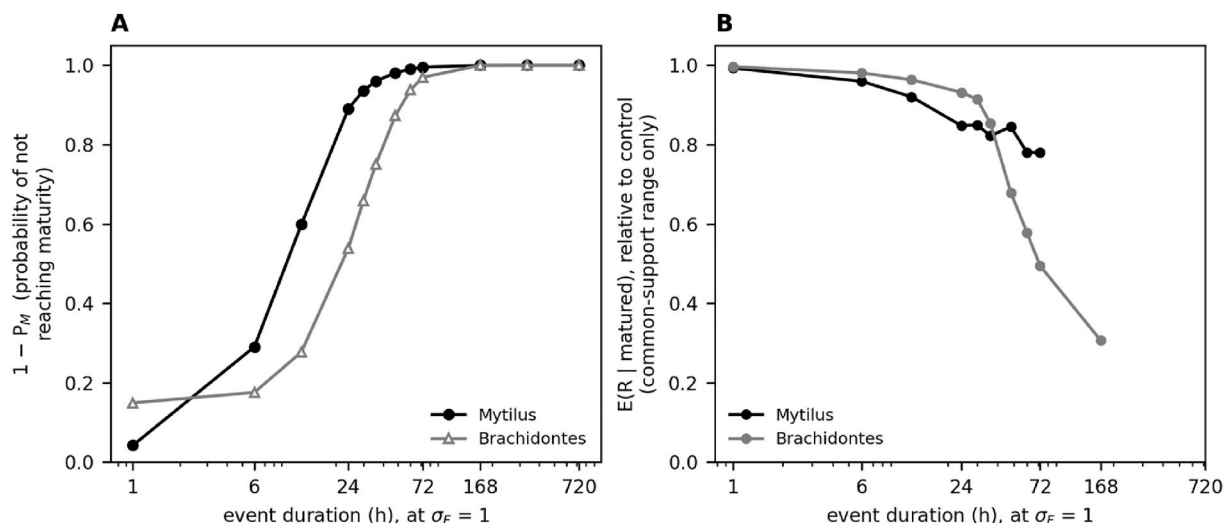


Fig. 3. (A) Probability of not reaching maturity, $1 - P_M$, a continuous per-trajectory quantity, against event duration at maximal feeding stress: a nonlinear transition accelerating through an intermediate range. (B) Conditional reproductive investment of individuals that mature, relative to control, over the common-support range only. Black: the native *Mytilus galloprovincialis*; grey: the invasive *Brachidontes pharaonis*. The survival transition is quantified by D_{50} and $D_{90} - D_{10}$ rather than by a separate steepest-slope criterion; the conditional breakpoint lies near 12 to 18 h (Section 3.2). Major x-axis labels are 1, 6, 12, 24, 72, 168, 336 and 720 h on a log scale; intermediate design durations (30, 36, 48 and 60 h) are plotted but not labelled.

Table 1

Decomposition of the reproductive loss at maximal feeding stress, averaged over the two shared forcing scenarios in the isolated-pulse domain. The decomposition is computed cell by cell and then averaged over the two common sites, not formed from the product of the averaged components. The three terms sum to the total loss $L = 1 - P_M Q_M$.

Duration	Species	survival effect ($1 - P_M$)	reproduction effect ($1 - Q_M$)	interaction
30 h	Mytilus	+0.93	+0.15	-0.14
30 h	Brachidontes	+0.60	+0.09	-0.05
72 h	Mytilus	+0.99	+0.22	-0.22
72 h	Brachidontes	+0.96	+0.51	-0.49

performance (0.48 and 0.26), the imposed deficit adding little (below 0.03). For conditional investment - the reproductive investment of an individual given that it reaches maturity - the ordering reversed: the imposed deficit carried the larger partial variance (0.28 in the native) and duration the smaller (0.05). Holding the imposed deficit within a narrow band, the probability of reaching maturity still fell sharply with duration - from 0.91 at 6 h to 0.38 at 72 h in the mid-deficit band - while at controlled duration conditional investment separated by deficit band. The temporal continuity of the deficit therefore governs survival to maturity and overall performance, whereas the cumulative magnitude of the deficit shapes the investment of those that mature: the two features act at different points of the life course. The result was unchanged when the endogenous realised deficit replaced the imposed deficit (duration coefficient -0.175 versus -0.175 in the native) and duration and deficit were weakly collinear ($|r| < 0.3$). In biological terms, a brief interruption is survivable and costs mainly some reproductive investment, whereas the same energy shortfall delivered as one long uninterrupted spell is what carries an individual past the point of no return before it can breed: whether a mussel dies is set by how long the deficit lasts without relief, how much a survivor reproduces by how much energy it lost in total.

3.2. Decomposition of the reproductive response

Every trajectory that failed to reach maturity within the horizon had reached the numerical extinction criterion before maturity: of 480 cells, 401 matured and 79 died before maturity and none remained alive but immature at the horizon. The quantity $1 - P_M$ is therefore pre-maturity

mortality and the survival transition is not delayed maturation. The two response components differed in form (Fig. 3). The probability of not reaching maturity increased nonlinearly with duration rather than stepping at a single threshold; expressed as the interval spanning 10% to 90% of maximum mortality, the transition width was 23 h in the native and 46 h in the invader. Conditional investment among individuals that matured declined with duration over the common-support range; a segmented fit improved on a linear one (reduction in residual sum of squares, lower AIC) with an early breakpoint near 12 to 18 h, well before the survival transition. Beyond the common-support range the conditional mean is not interpretable, because only the more favourable regimes still reach maturity (Section 3.7), and it is not shown. The failures counted here are deaths before first reproduction and not merely slower development, so they remove individuals from the population. Because survival does not erode smoothly but collapses over a narrow band of durations, a population can look tolerant up to a tipping duration and then lose most of its recruits over a small further increase in event length.

Decomposing the total reproductive loss $L = 1 - P_M Q_M$ as $(1 - P_M) + (1 - Q_M) - (1 - P_M)(1 - Q_M)$, the survival term dominates beyond the transition. At 30 h at maximal feeding stress, averaged over the two shared forcing scenarios in the isolated-pulse domain, the native gave a survival effect of +0.93, a conditional-reproduction effect of +0.15 and an interaction of -0.14 (Table 1). Because the two effects share a substantial negative interaction they are not additively separable and the survival component is the larger contributor to the loss at the durations at which mortality occurs. The practical implication is that, once events are long enough to kill, most of the reproduction lost is lost because individuals never mature rather than because survivors breed less.

3.3. Reserve margin and critical duration (D50)

Across the six species-forcing combinations, the critical interruption duration D50 was ordered by the control reserve margin: all combinations with smaller reserve margins crossed the transition at shorter or equal durations. The native maintains a reserve density of roughly 0.08 to 0.11 across its forcing scenarios and the invader 0.12 to 0.35. With six non-independent combinations, in which predictor and response derive from the same model, I present this as a descriptive ordering rather than a validated predictor. The ordering identifies resting reserve margin as a candidate state variable for predicting vulnerability across a broader

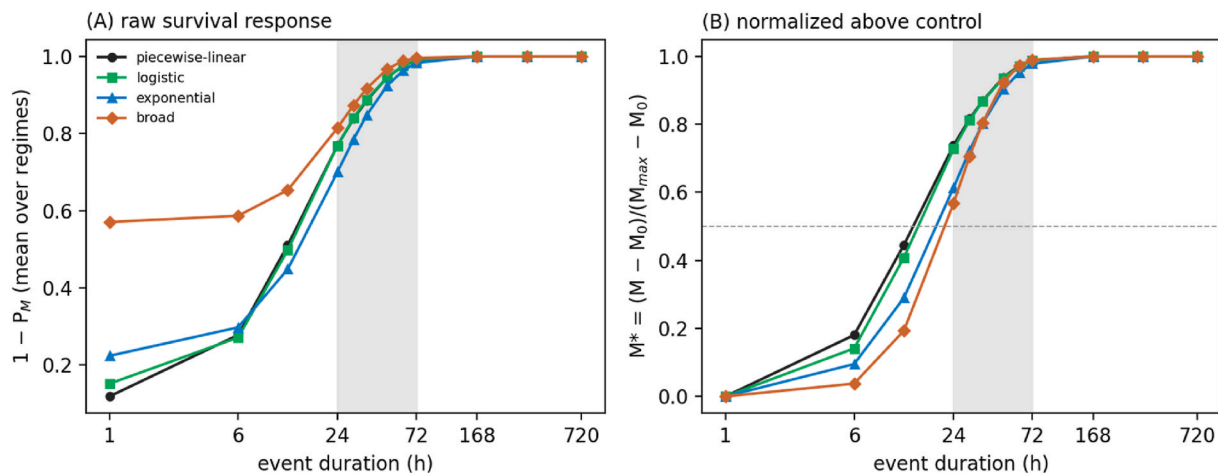


Fig. 4. Survival response under four starvation-hazard formulations; the shaded band marks the 24 to 72 h transition window - piecewise-linear baseline, logistic, exponential and a broad piecewise-linear rule. (A) Mean pre-maturity mortality ($1 - P_M$) against event duration at maximal feeding stress: the broad rule raises the baseline level ($M_0 = 0.57$), because its risk reaches the resting reserve density of the lower-margin combinations, whereas the other three start near zero. (B) The same response normalised above each formulation's own control, $M^* = (M - M_0)/(M_{max} - M_0)$. After baseline normalisation, the four formulations show similar transition positions and broadly overlapping widths, with D50 values of 14, 15, 19 and 21 h. The broad rule therefore preserves the relative position and shape of the transition rather than merely increasing mortality above a high baseline.

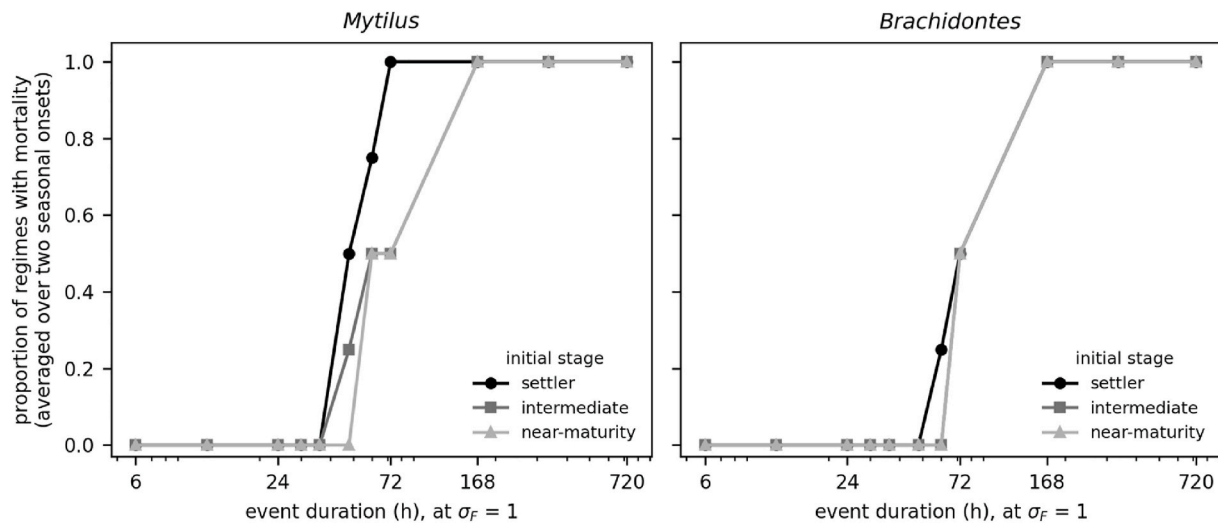


Fig. 5. Proportion of regimes producing mortality against event duration for three initial ontogenetic stages, averaged over two seasonal onsets so that stage and season are separated. D50 increases modestly with stage. The proportion of regimes is a secondary discretised summary; the continuous per-trajectory survival probability is used for the D50 estimates reported in Sections 3.2 to 3.4. Exact D50 estimates by species, site, stage and seasonal onset can be reproduced from the archived model code and analysis scripts described in [Supplementary Section S7](#).

range of life histories and is robust to the starvation parameters (Supplementary Material) and hazard formulation (Section 3.4). Biologically, the spare reserve a mussel carries when undisturbed sets how long an interruption it can absorb. Inferentially, populations living closer to their energetic edge reach the lethal threshold sooner, which makes the resting reserve margin a trait that could be measured before a disturbance to flag the most exposed populations. The corresponding control reserve densities are reported in [Supplementary Table S3](#) and the baseline D50 values in the 0.05/0.05 column of [Supplementary Table S6](#).

3.4. Sensitivity to the hazard formulation

The baseline starvation hazard (the piecewise-linear rule of Section 2.2) is a rule with a non-differentiable point at e_{thr} , so the nonlinear survival transition could in principle be imposed by that rule. Recomputing under a steep logistic, a smooth exponential and a broad piecewise-linear rule acting over twice the reserve range, the transition persisted in every case (Fig. 4). The broad rule raised the baseline mortality, because its risk reaches the resting reserve density of the lower-margin combinations, but the transition with duration remained, and the ordering of combinations by reserve margin was preserved or strengthened under all formulations (the reserve-margin ordering was at least as strong under the broad rule as under the baseline). Because the broad rule elevates the baseline mortality of the lower-margin combinations, its transition was quantified on the mortality increment above its own control, $M^* = (M - M_0)/(M_{max} - M_0)$; on this normalised scale the four formulations show similar transition positions and broadly overlapping widths, with normalised D50 within 14 to 21 h (Fig. 4B), confirming that the broad rule preserves the shape and relative position of the transition and does not merely grow above a high floor. The robust result is the nonlinear transition generated by reserve depletion and its ordering by reserve margin; the precise D50 depends on the hazard form. The abruptness of the survival collapse is thereby a property of reserve depletion itself and not an artefact of how mortality was modelled; what is less certain is the exact duration at which it occurs, not the fact that it occurs and that lower-reserve combinations reach it first.

3.5. Dependence on ontogenetic stage, separated from season

With the three ontogenetic initial states reinitialised at a common

calendar hour and crossed with two seasonal onsets, D50 increased with ontogenetic stage at fixed onset in three of the four shared species-forcing combinations and was flat, not decreasing, in the fourth (Fig. 5). The effect is consistent but modest - one to two duration levels between the newly settled and the near-mature state - and considerably smaller than a naive comparison confounded with seasonal timing would suggest. D50 is therefore a joint property of the reserve margin and the individual's distance from maturity, but the ontogenetic component is a modulation rather than the dominant term. The time of year in which the disturbance falls matters more than the developmental state of the individual it strikes. Tolerance is set mainly by how much reserve a mussel holds and only secondarily by its life stage. Across the transition region, mortality appeared at shorter durations in the native than in the invader at every initial state (Fig. 5).

3.6. Feeding and maintenance stress

Reduction of the feeding flux drove the survival transition; elevation of the maintenance cost produced graded reductions of reproduction but, over the range explored, rarely produced pre-maturity mortality. Because the two axes are not on a common energetic scale, this is a model exploration and an energetically equivalent comparison is left to future work.

3.7. Interspecific comparison and cell selection at long durations

Restricting the comparison to the two shared forcing scenarios, the native carried the larger pre-maturity mortality at every duration at which mortality occurred, converging to the invader only at the longest durations where both approach complete loss. The conditional-investment reduction was mixed between the species. At long durations the set of regimes still reaching maturity shrinks - from ten to one or two per species beyond 168 h - so the conditional mean over surviving regimes is a selected subset and any apparent recovery at extreme durations reflects the changing composition of that subset, not physiological recovery. I therefore restrict the conditional analysis to the common-support range and do not interpret the tail.

3.8. Structural response

Structural length declined gradually with duration, less steeply than

reproduction: among individuals that matured, the native lost about half of its conditional reproductive investment but only about a fifth of its shell length at the longest common-support durations. Final structural length is reported for every design cell in the archived factorial output, and the full trajectories can be reproduced from the model code described in [Supplementary Section S7](#).

4. Discussion

4.1. A dissociation along the life course

Do the results support the hypotheses? H1, yes: at equal imposed deficit, one long interruption kills where several short ones do not, while the size of the deficit sets how much a survivor invests. H2, yes: survival does not erode smoothly but collapses over a narrow band of durations, while the investment of survivors declines gradually. H3, yes for the reserve margin, which orders the critical duration across the six species-forcing combinations; for ontogenetic stage the dependence is present but weaker than the seasonal timing of the event - the calendar position of a disturbance matters more than the developmental state of the individual it strikes.

The central result is a separation of roles. How long a deficit runs without a break decides whether an individual lives to reproduce. How much energy it removes in total decides how much a survivor invests once it gets there. These are two different properties of the same disturbance regime; they act on two different parts of the life course and neither alone describes the response. The result refines, rather than contradicts, a duration-centred reading of disturbance ([Ratajczak et al., 2017](#); [Harris et al., 2018](#); [Chen et al., 2024](#)): duration is decisive for survival and for the bottom line, but the cumulative deficit is not irrelevant - it is where it acts, on conditional investment, that had been obscured by endpoints recording only final output.

4.2. The survival response as an accelerating transition

The probability of not reaching maturity rises nonlinearly with interruption duration, steepening through an intermediate range rather than at a fixed threshold. Read as a continuous per-trajectory probability rather than a binary classification of regimes, the response is an accelerating transition, not a step; describing it as a sharp threshold would overstate its abruptness. Its position is generated by reserve depletion ([Sokolova et al., 2012](#)) - a long interruption holds the reserve below its starvation margin continuously - and it survives continuous, differentiable and broad formulations of the starvation hazard, so it is not an artefact of the submodel's functional form. The precise D50, however, depends on parameterisation and is not a general constant. The contrast with the maintenance-cost exploration supports this mechanism: increasing maintenance produced mainly graded reproductive losses and little pre-maturity mortality, whereas suppressing feeding depleted reserve until the starvation boundary was crossed (Section 3.6).

4.3. Reserve margin and ontogenetic stage

The reserve margin maintained under undisturbed conditions orders D50 across the modelled combinations, and, once seasonal timing is controlled, D50 increases modestly with proximity to maturity. Vulnerability is thus a joint property of the reserve margin a species maintains and the individual's distance from maturation, with the reserve margin the dominant term and ontogenetic stage a modulation. With six non-independent combinations the reserve-margin ordering is heuristic. The native and the invasive species examined differ principally in the survival component, the native sitting closer to its starvation boundary. I frame this as a property of the two species and their reserve margins, not a general consequence of native or invasive status.

4.4. Implications for disturbance indicators

Indicators that accumulate stress over a window, such as the Degree Heating Week ([Skirving et al., 2020](#)), treat a given accumulated exposure as equivalent regardless of its temporal structure. Recent efforts to refine the metric have concentrated on the length of the accumulation window, the anomaly cutoff and regional calibration of the bleaching threshold ([Whitaker and DeCarlo, 2024](#)), not on the temporal structure of the accumulated exposure. For the survival component this equivalence fails: what matters is the maximum uninterrupted duration of the deficit, not the integrated exposure. For the conditional-investment component, by contrast, the cumulative measure is the more relevant one. An indicator intended to anticipate reproductive impact would therefore need to preserve both the continuity of events, for survival and their accumulated magnitude, for conditional investment. A mechanistic analysis of the same two species across the Mediterranean has shown warming impacts to be nonlinear and heterogeneous among species and sites, undetectable by methods focused only on lethal limits ([Montalto et al., 2016](#)). The structural response reinforces this point: shell length declined less than conditional reproductive investment, so a size-based monitoring endpoint may underestimate sublethal reproductive impact (Section 3.8; [Muller et al., 2010b](#)).

4.5. Coincidence, energetic context and heterogeneous mass mortality

If vulnerability is jointly set by the duration of an interruption and the reserve state of the individual it strikes, the outcome of a disturbance cannot be inferred from the physical event alone. The same interruption may be lethal to an individual close to its starvation boundary but survivable for one carrying a larger reserve margin, and that margin varies with recent food conditions, season and ontogenetic stage. This provides a testable individual-level energetic hypothesis for part of the spatial and temporal heterogeneity observed during mass-mortality events ([Garrabou et al., 2009, 2022](#)). Under this hypothesis, apparently similar heatwaves or hypoxic episodes can produce different outcomes because they encounter populations in different energetic states. Forecasts based only on event magnitude or return time may therefore be incomplete; they should combine the temporal continuity of exposure with an indicator of physiological state, for which resting reserve margin is a candidate proxy. Population-level validation will require linking measured reserve state and event continuity to recruitment failure and mortality in the field.

Which of the two species is at higher risk? The native. Wherever a duration was lethal at all, *Mytilus galloprovincialis* carried the larger pre-maturity mortality, converging with *Brachidontes pharaonis* only at the longest events, where both approach complete loss (Section 3.7). The reading the model offers is energetic. The native runs closer to its starvation boundary under undisturbed conditions, so a shorter unbroken interruption suffices to push it across; the invader keeps a larger reserve buffer and needs a longer one. If coastal disturbance keeps lengthening, this asymmetry should progressively favour the invader, with consequences for the relative distribution of the two species on Mediterranean shores. The apparent recovery of conditional reproduction at extreme durations is not resilience but a consequence of cell selection: beyond 168 h only one or two regimes per species still reach maturity, so the conditional mean represents the few most favourable trajectories (Section 3.7).

The larger reserve margin of *Brachidontes pharaonis* identifies an additional comparative hypothesis. Whether this difference reflects evolutionary adaptation to a more variable native environment remains unknown, and the present two-species comparison cannot explain invasion success. A broader test should ask whether reserve margin covaries with environmental variability across species' native ranges and whether it predicts tolerance to prolonged energetic interruption. If supported, reserve margin could provide a mechanistic trait linking evolutionary history to disturbance response. Here, however, it is

Table 2

Literature-based mapping of six coastal stressors onto the two model fluxes. Qualitative, not calibrated. Hypoxia is a limiting case in which the maintenance perturbation changes sign within an event; ocean acidification is a chronic baseline shift.

Stressor	Feeding flux	Maintenance	Physiological basis	Indicative references
Thermal stress above optimum	Reduced	Increased	Ingestion declines beyond the thermal optimum; maintenance rises with temperature	Montalto et al., (2016); Sarà et al. (2011)
Harmful algal blooms	Strongly reduced	Increased	Valve closure and reduced clearance with toxic cells; detoxification cost	Bricelj and Shumway (1998)
Turbidity, suspended sediment	Strongly reduced	Slightly increased	Pseudofaeces and reduced ingestion efficiency; particle-sorting cost	Widdows et al. (1979)
Chemical contamination	Reduced	Increased	Reduced clearance; detoxification and repair cost	Widdows and Donkin (1992)
Hypoxia	Strongly reduced	<i>Sign not constant within event</i>	Valve closure suppresses ingestion; metabolic depression then oxygen debt	Sobral and Widdows (1997)
Ocean acidification	Reduced	Increased	Reduced clearance; acid-base regulation and calcification cost	Fernández-Reiriz et al. (2011)

treated only as a hypothesis for future comparative testing.

4.6. Translation to real stressors

The two perturbation axes correspond to identifiable classes of coastal stressor (Table 2). The mapping is qualitative, a translation device, not a calibration: it identifies stressors whose events can be long enough to engage the duration mechanism, but does not establish that a given event crosses the survival transition, which depends on the intensity of the flux reduction as well as its duration. A thermal event of 30 h reducing assimilation by a few percent is not equivalent to 30 h of complete feeding cessation.

4.7. Limitations and testable predictions

The critical duration D50 is a model prediction whose value depends on parameterisation and hazard form; it should be read as a falsifiable hypothesis - that a continuous feeding interruption beyond roughly a day suppresses juvenile survival in the native under Mediterranean conditions - testable in a mesocosm. The interspecific and duration-deficit analyses rest on the two shared forcing scenarios; the reserve-margin ordering on six non-independent combinations. The feeding and maintenance axes are not on a common energetic scale. The translation of real stressors onto the fluxes is qualitative. Extrapolation from individual pre-maturity mortality to recruitment failure and mass mortality remains a testable population-level hypothesis. None of these undermines the core result: duration and cumulative deficit act on distinct components of reproductive performance, survival and conditional investment respectively, and the temporal continuity of the deficit is the operative currency for survival. The correspondence between modelled structural volume and observable shell length under strong starvation also requires empirical verification.

4.8. Conclusion

Decomposing the reproductive response of an individual energy budget along the life course separates a nonlinear survival transition, governed by the uninterrupted duration of an energetic deficit, from a graded reduction of conditional reproductive investment, governed by the cumulative deficit. The position of the survival transition is ordered by the reserve margin an organism maintains and modulated by its distance from maturation. Four practical consequences follow. First, exposure indicators that sum stress over a fixed window cannot separate one long interruption from several short ones that remove the same energy, so monitoring programmes should record the longest uninterrupted interval of an event alongside its total magnitude. Second, size-based endpoints understate the damage: at the longest durations examined here the modelled native lost about half of its conditional reproductive investment but only about a fifth of its shell length, so surveys that track length alone will miss reproductive failure that has already occurred. Third, because the transition is ordered by the reserve

margin measured in undisturbed conditions, a pre-disturbance measure of reserve state offers a way to rank populations by exposure before an event arrives, and populations at food-poor sites or in seasons of low reserve are the ones to watch. Fourth, the two species differ in this margin, so a lengthening disturbance regime is expected to shift the balance towards the invader. Each of these follows from a model of two species under four forcing scenarios and requires field testing before use in management.

These consequences map onto the monitoring obligations of the Marine Strategy Framework Directive. Under Descriptor 1, criterion D1C3 covers the demographic characteristics of a population, including body size structure together with fecundity and survival rates, while criterion D1C6 covers the condition of the habitat types that foundation species build. The results reported here indicate that the size component of D1C3 and the extent component of D1C6 can remain close to reference conditions while reproductive output has already fallen, so a mussel bed may be assessed in good environmental status on structural grounds while its capacity for renewal is impaired. Two additions would close this gap at modest cost: recording the longest uninterrupted duration of temperature, oxygen or food anomalies alongside their cumulative magnitude in the pressure layer, and pairing the size-based indicator with a measure of reserve condition or gamete output in the sentinel beds already sampled under Descriptors 1 and 6.

Declaration of generative AI and AI-assisted technologies in the manuscript preparation process

During the preparation of this work, the author used CLAUDE OPUS for language fine tuning. The author reviewed and edited the output as needed and take full responsibility for the content of the published article.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Gianluca Sara' reports article publishing charges was provided by University of Palermo. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2026.108411>.

Data availability

The model code, the four hourly forcing series, the full factorial output and the analysis scripts are available at Mendeley Data: Sarà, G., 2026. Disturbance duration governs mortality risk while cumulative energetic deficit shapes reproduction in Mediterranean mussels. Mendeley Data, V1. <https://doi.org/10.17632/r2h822zxp.1>.

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