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Integrating Development and Environment to Model Reproductive Performance in Natural Populations of an Intertidal Gastropod[1]

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SYNOPSIS. Functional challenges can differ among life-history stages, yet performance at one stage may be linked to the outcome of performance at others. For example, adult performance, in terms of the location or timing of reproduction in response to environmental signals, can set conditions that affect the performance of developmental stages. In marine invertebrates, however, early performance has been studied primarily in the laboratory. I outline an integrative approach to the study of field reproductive performance in a marine gastropod that undergoes development in intertidal habitats. Embryos within gelatinous masses experience high variability in development temperature and frequent exposure to thermal stress. In laboratory experiments, developmental performance was measured as a function of maximum temperature (T_{max}) experienced during fluctuations that mimicked field tidal profiles. Performance curves showed declines that coincided with temperature thresholds for heat shock protein (Hsp) expression, a signal of cellular stress. Application of laboratory results to field records of T_{max} predicted large variation in the survival of embryos deposited on different days. Timing of field reproduction was non-random with respect to T_{max}, suggesting that adults could help to buffer embryos from environmental stress. Embryo survival, however, was not predicted to benefit from the non-random pattern of adult reproduction. Adults may be constrained to respond to information that only weakly predicts conditions that embryos will experience. Studies that incorporate linkages between life cycle stages in the field may better reveal how performance capacities and constraints at one stage can influence performance and selection at others.

INTRODUCTION

Life cycles are composed of stages that face different functional challenges (Werner, 1988). Success at a given stage can depend on particular aspects of performance, but stages can also be functionally linked if processes at one stage influence performance at others (Pechenik *et al.*, 1996; Phillips, 2001; Marshall *et al.*, 2002). For marine invertebrates, much of what is understood about performance at early stages and linkages among stages comes from studies in the laboratory, where small individuals can be handled and cultured in large numbers, subjected to controlled treatments, and measured with technical equipment (Boidron-Metairon, 1988; Pechenik *et al.*, 1993; Hoegh-Guldberg and Manahan, 1995; Mead and Denny, 1995; Hart, 1996; Emlet and Hoegh-Guldberg, 1997; Hilbish *et al.*, 1999; Pechenik and Rice, 2001; Podolsky, 2001; Marshall *et al.*, 2002; Strathmann *et al.*, 2002). In contrast, relatively little is known about performance capacities or selection on functional traits for these stages under natural conditions (Pechenik, 1987; Young, 1990). Unlike for terrestrial taxa, early stages are usually microscopic and dispersing (Strathmann, 1990) and therefore impractical for *in situ* tests of performance. Field-based tests of performance are typically limited to stages that are brief, sedentary, or unusually large (Bingham and Young, 1991; Stoner, 1994; Levitan, 1996; Meidel and Yund, 2001; Moran and Emlet, 2001; Phillips, 2002). Such examples, however, are far outnumbered by laboratory studies, which are often used to infer consequences in the field.

Laboratory studies can reveal how performance varies under controlled conditions, but cannot establish the relevance of those conditions to selection. In nature, early stages typically encounter conditions relevant to performance that vary on multiple spatial or temporal scales (Pechenik, 1987; Olson and Olson, 1989; Rodriguez *et al.*, 1993; Levitan and Petersen, 1995; Walters and Wethey, 1996; Helmuth and Hofmann, 2001). Understanding selection and the evolution of performance in variable environments has been a long-standing challenge to evolutionary theory (Levins, 1968; Hedrick *et al.*, 1976; Slatkin and Lande, 1976; Gilchrist, 1995), and environmental variability poses special challenges to the empirical study of selection on performance (Bennett and Huey, 1990; Kingsolver, 2000, see also Kingsolver and Gomulkiewicz, 2003). For example, the frequency, duration, and order of exposure to conditions can be difficult to measure or characterize, making it difficult to integrate the effects of performance over space or time. The persistent challenge (Arnold, 1983) is to find ways to integrate controlled performance measures in the laboratory with information about conditions experienced in the field.

In this paper I briefly outline an approach I am developing to assess the relationship between performance measures at two life cycle stages of a marine gastropod: developmental performance of embryos in response to temperature variability, and performance of adults in timing their reproduction to reduce embryo risks. The situation is a departure from the more typical marine life cycle, and involves internal fertiliza-

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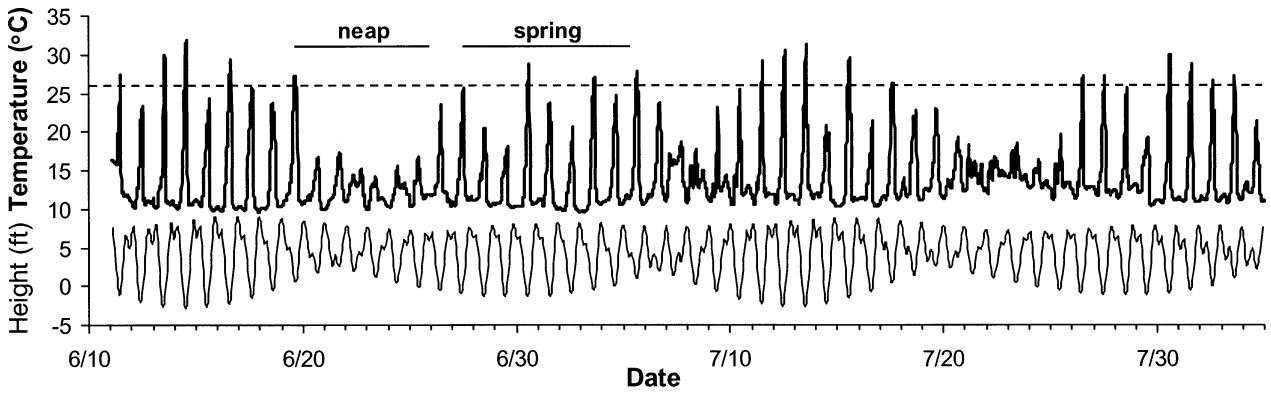

FIG. 1. Variation in tide height and tide pool water temperature over two months of the 1999 *M. diomedea* reproductive season at False Bay, WA. Lower tracing shows tide height relative to annual mean low-low water as predicted by X-tide (Flater, 1996). Upper tracing shows temperatures recorded by Tidbit data loggers (Onset Corp., MA) in tidal channels at the height of egg masses. The dotted line shows the temperature (26°C) at which stress protein expression is induced in embryos. Neap and spring tide series are indicated as periods of positive and negative low-low tides, respectively.

tion, embryonic development within a benthic gelatinous mass, and planktonic larval dispersal (Mileikovsky, 1971). The focal stage for this analysis is the early period of embryo encapsulation, a mode of development that has evolved several times among gastropods, polychaetes, nemerteans and flatworms (Pechenik, 1979). One benefit of encapsulation may be reduced predation risk, because mortality, in large part from predation (Morgan, 1995), is estimated to be lower for benthic broods than for independent equivalent stages in the plankton (Rumrill, 1990). Placement of broods in intertidal areas can provide refuge from diverse subtidal predators (De Martini, 1978), but the extreme variability of physical conditions in such habitats poses other developmental risks for embryos (Pechenik, 1987) as well as considerable challenges for biologists to measuring performance in the field.

Temperature variability during intertidal development

Melanochlamys diomedea (Bergh) is a small (approx. 1 cm) cephalaspidean opisthobranch mollusc found on tidal flats from central California to southern Alaska (Behrens, 1991). Adults produce balloon-shaped gelatinous masses (1–2 cm) that hold tens of thousands of encapsulated embryos. Masses are deposited in tidal channels or shallow pools that retain water at low tide, and are secured in place by a long sand-mucus tether buried firmly in the substrate. At low tide, adults behaviorally regulate their exposure by burrowing into sediment, but embryos within masses are exposed to surface conditions for their first week of development. After hatching, they then spend an undetermined period feeding in the plankton before settlement. Reproduction at study sites on San Juan Island, WA occurs during late spring and summer, when low tides typically expose tidal flats to mid-day conditions.

Temperature fluctuations at False Bay, measured by data loggers placed near masses in tide pools, range from mild during neap tides to extreme during spring tides (Fig. 1). Temperatures can exceed 33°C and fluctuate more than 22°C during a single exchange. Patterns of fluctuation result from both predictable tidal cycles and less predictable variation in climatic conditions (*e.g.,* cloud cover, precipitation, and winds). Because both immersed egg masses and data loggers equilibrate rapidly with surrounding water temperatures, logger records provide a reliable estimate of developmental temperatures experienced by embryos. In addition, because tidal flats are topographically simple and spatially homogeneous, field temperatures can be characterized for large portions of the population.

As a result of intertidal development, embryos of *M. diomedea* are exposed to temperatures that are not only highly variable but also frequently stressful. Induction of heat-shock protein (Hsp70 and Hsp90 family) expression, an indicator of cellular stress (Anathan *et al.,* 1986; Hofmann and Somero, 1995; Kregel, 2002), begins around 26°C for embryos after brief (15–30 min) exposures in the laboratory (R. Podolsky and G. Hofmann, unpublished data). Temperatures during the reproductive season reach or exceed this stress threshold on many days and on the majority of spring tides (Fig. 1). Protein expression profiles for masses collected from the field confirm that induction of stress protein induction begins within one hour of pools reaching 26°C (Podolsky, unpublished data), indicating that laboratory signatures of stress are relevant to field conditions.

Embryo developmental performance in the laboratory

Temperature variability and stress on tidal flats are likely to have complex effects on development, depending on the particular temperature range and performance measure. For example, increases in fixed developmental temperature generally increase development rate (Clarke, 1982; Hoegh-Guldberg and Pearse, 1995) but can have the opposite effect on growth (Berrigan and Charnov, 1994). Performance can improve under mild temperature increases but decline at higher

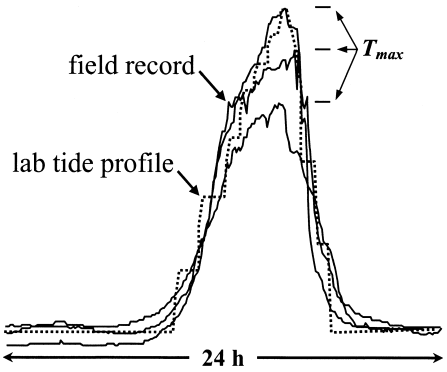

FIG. 2. Tide pool temperatures on three successive days at False Bay (solid lines), reaching T_{max} = 26.7, 30.2, and 33.1°C, with high temperatures roughly aligned. The dotted line shows the 9-hour temperature profile created by the tidal gradient block to match the upper field profile.

ranges, as temperatures become physiologically suboptimal or stressful (Huey and Kingsolver, 1989; Kingsolver and Woods, 1997). Furthermore, fluctuating temperatures can influence performance measures in ways that can not be predicted from average, fixed temperatures (McDonald, 1990; Stamp, 1994; Manel and Debouzie, 1995; Brakefield and Kesbeke, 1997). Given the high temperature variability and frequent stress encountered by embryos of *M. diomedea*, there exist considerable challenges to characterizing the relationship between performance and fitness under field conditions (Bennett and Huey, 1990).

Can controlled measurements of performance in the laboratory provide insight into selection in the field? Although field conditions are extremely variable, daily fluctuations in temperature follow a common pattern, such that the rise and fall occur over similar time scales each day but with varying amplitudes (Fig. 2). In order to estimate the effect of field exposures, I measured three aspects of developmental performance (development rate, growth, and survival) under temperature profiles in the laboratory that approximated natural conditions. Laboratory profiles were generated by cycling a programmable water bath in a sequence to match the shape and duration of typical field profiles (Fig. 2).

To generate performance curves, egg masses were collected during their first low tide before stress conditions and within 12 hours of deposition, as gauged by embryo staging. Each of six masses (sibships) was divided and distributed among nine culture tubes that were individually aerated and received daily water changes. To create a graded series of profiles with different temperature maxima (T_{max}), I placed culture tubes in a thermal gradient block with a fixed (12°C) cold end and a fluctuating warm end. Eight different positions along the block gave a series of profiles that differed in T_{max} ranging from 20 to 34°C, in 2°C increments, with a common T_{min} (12°C). A ninth tube for each replicate was held at a nearly constant 12°C. Experimental temperature regimes were repeated daily starting on the day after collection.

Results from this experiment showed that embryo survival (Fig. 3A), size at hatching, and development rate all varied as a function of T_{max}. Survival peaked at T_{max} = 24°C and declined regularly at 26°C and above, a temperature threshold that coincides with the onset of physiological stress as indicated by stress protein expression. Similar patterns resulted for hatching size and development rate, with performance maxima at 24°C and 28°C, respectively. The survival data showed a decline of about 30% (3.8% per °C) with variation in T_{max} from 24 to 34°C; this decline represents a cumulative effect of repeated daily exposures. Because embryo survival showed the greatest treatment differences and likely had the strongest fitness consequences, I focus on this one aspect of performance to estimate consequences of field exposures.

Modeling the relationship between hatching success and T_{max} is not straightforward. Performance curve data are typically skewed and not well-represented by simple functions (*e.g.,* quadratic or Gaussian; DeWitt and Friedman, 1979; Huey and Kingsolver, 1989). The cubic spline, a function with a less restrictive shape, assumes a smooth underlying functional relationship (Schluter, 1988) and therefore does not represent well

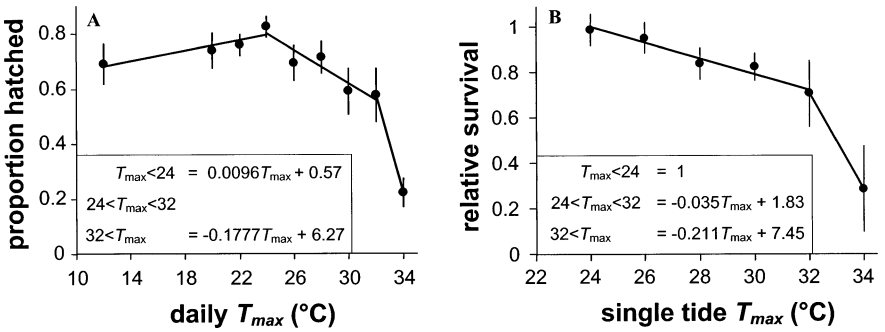

FIG. 3. Embryo survival to hatching during laboratory experiments. Typically 300–500 embryos embedded in gel were used for each treatment. Each value is the mean ± 1 SE for six sibships. Boxes show linear regression equations used in the model for different ranges of T_{max} (see text). (A) Survival after daily (beginning day 2) exposure to temperature fluctuations varying in T_{max}. (B) Survival following a single tidal exposure on day 1 relative to the average survival for single exposures on days 2, 3 or 4 (averaged within replicates) for exposures varying in T_{max}.

a function with mechanistic stress thresholds (in this case, at the onset of hsp expression near 26°C and at the disruption of total protein synthesis above 32°C). More complex functions that have been used to model temperature dependence of performance (*e.g.*, Logan *et al.*, 1976) are also not appropriate because they use information drawn from traditional performance curves (measurements at a series of constant T rather than under fluctuating profiles that vary in $T_{\max}$). Development in *M. diomedea* is arrested at constant temperatures above the stress threshold of 26°C, so it was not possible to generate standard performance curves for integrating effects of variable temperature exposures (see Kingsolver and Gomulciewicz, 2003). For this preliminary analysis I chose to fit simple linear regressions that break at the two biologically relevant critical values for the onset of stress. Assuming other shapes for functions did not alter any of the qualitative conclusions of the analysis.

One additional aspect of the embryo stress response is important to interpreting developmental performance. Protein labeling experiments indicate that Hsp expression is not inducible within the first 20 to 30 hours of development, making early embryos particularly vulnerable to heat stress (Podolsky and Hofmann, unpublished data). As a result, the effect on development of temperatures that exceed stress thresholds is qualitatively different on an embryo's first day as compared with later days.

I used a second experiment to distinguish the importance of day 1 tide exposures for embryo survival. Six masses were collected from the field at the very start of their first tide, partitioned in the laboratory, and subjected to treatments in a factorial design, with two factors: (1) the day when embryos were exposed to a single tidal temperature profile (day 1, 2, 3 or 4, where day 1 is the day of collection), and (2) T_{max} of the single profile (6 levels: T_{max} = 24, 26, 28, 30, 32, 34°C). Apart from the single tide profile, development was completed in mesh bottom trays in flowing seawater at relatively constant temperature (11–13°C). Because each treatment consisted of one exposure against a background of relatively cold and suboptimal temperatures, absolute survival rates from this experiment could not be combined directly with those from the first experiment. Instead, I compute ''relative survival'' as the ratio of survival for day 1 exposures relative to survival for single exposures on later days. Note that, because fitness for a given laying date in the model is ultimately scaled relative to the best day of the season (see below), the absolute scale for this index has no bearing on conclusions drawn from the model. Percentage data were arcsin-square root transformed before statistical analysis.

Results of this second experiment show an effect of early high temperature exposure on the relative probability of survival. Exposure day had a significant effect on survival probability (mixed-model ANOVA, $F_{3,15} = 5.09$, $P < 0.02$); multiple comparison tests showed a significant difference between day 1 and each of days 2 through 4, but no significant differences among days 2 through 4 (Tukey's HSD, $P < 0.05$; Neter *et al.*, 1985). To simplify the model, values for exposure days 2 through 4, when stress protein expression is inducible and a qualitative difference was therefore expected, were averaged within each replicate for comparison with day 1. Relative survival was similar for day 1 *versus* later single exposures at nonstress temperatures (T_{max} = 24°C) but declined regularly as T_{max} exceeded the stress threshold (Fig. 3B). Relative survival showed a decline of about 28% (3.6% per °C) with variation in T_{max} from 24 to 32°C. As in experiment 1, relative survival declined abruptly when T_{max} = 34°C, coinciding with the threshold at which protein synthesis is disrupted. Again, I model this relationship as a set of linear functions that break at the critical stress thresholds (Fig. 3B).

Predicting developmental performance in the field

I now integrate results of the two laboratory experiments (Fig. 3) with records of temperature variation in the field (Fig. 1) to predict relative embryo survival for masses deposited on each date during the 1999 reproductive season. Given the simplified structure of the laboratory data, I make the following assumptions in applying the model to field conditions. (1) Embryo development is completed over 6 tidal fluctuations (days) in the field, which is the average median (50% hatch) development time among treatments in experiment 1 (range: 5.3 days for $T_{\max}$ = 28°C to 6.6 days for $T_{\max}$ = 34°C). Marked masses in the field typically hatch out between their sixth and seventh tides (unpub. data), but sometimes later. (2) Effects of exposures on days 2 through 6 are independent: exposure to a given T_{max} has the same effect on survival (calculated from results of experiment 1) regardless of when it occurs or what exposures precede or follow it. Survival probability was calculated as the cumulative probability of independent effect of $T_{\max}$ on each of days 2–6 as estimated from laboratory data (Fig. 3A). (3) Day 1 exposure reduces survival by the same percentage regardless of later exposures, and $T_{\max}$ below the stress threshold (24°C) on day 1 has no effect on relative survival (Fig. 3). (4) Overall fitness (embryo survival) is the product of probabilities described in #2 and #3. This probability was then scaled relative to a maximum fitness of 1 on the best date for egg mass deposition over the 1999 reproductive season.

According to the model, predicted embryo loss ranged as high as 39.3% and averaged around 10.8% relative to the best day of the season (Fig. 4). Losses were predicted to be greater within each of the four spring tide series, averaging 18%, 6%, 18%, and 14%, respectively. Predicted losses were correlated between adjacent days over the entire season (r = 0.43, N = 54, $P < 0.002$), but not within spring tide series (r = 0.29, N = 29, $P < 0.13$). Thus, given the jagged form of variation in $T_{\max}$ (Fig. 1), risks to embryos were not always predictable across days.

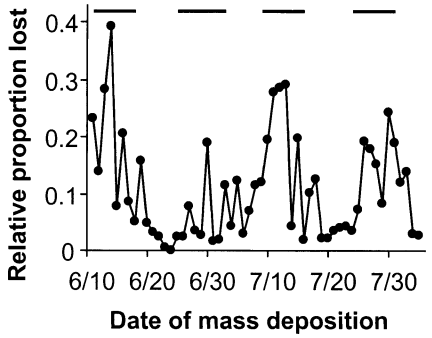

FIG. 4. Model prediction of percent embryo mortality for egg masses deposited on each day relative to mortality on the best day of the 1999 reproductive season. Solid bars indicate spring tides.

Adult reproductive performance in the field

Parental care is absent in *M. diomedea*, so adult control over developmental conditions is limited to the location or timing of mass production. Because soft-sediment habitats in which *M. diomedea* reproduces provide no physical refuge for embryos (*cf.* Pechenik, 1978; Brawley and Johnson, 1991; Leonard, 1999), tidepool locations show relatively little variation in temperature. Model predictions based on laboratory performance data and field temperature data, however, suggest that reproductive timing has important fitness consequences. If adults can detect conditions relevant to development on preceding tides, and if such cues predict conditions on following tides, then they would be expected to temporally pattern their reproduction in accord with future risks to embryos. In terms of adult performance, the model results predict that reproductive patterns should be (i) non-random in time, (ii) responsive to environmental information that predicts conditions under which embryos will develop, and (iii) beneficial to embryo survival.

Limited data are available to address these predictions. During the 1999 reproductive season, I recorded egg mass deposition along five strip transects (approx. 50 × 1.25 m) in tidal channels at False Bay. To avoid disturbing animals, transect lines were attached to and removed from permanent markers at each census. Transects were visited daily when the bay was exposed during spring tides, and egg masses were marked or cleared to record new mass production. In total, 1,493 masses were deposited over 29 days of the four spring tide series. Production was not recorded during intervening neap tide series, but counting masses at the start of each spring tide series gave a record of accumulation on transects during neap tides. Because production showed a seasonal decline among series, to aid the presentation I standardized the number of masses produced within each series to zero mean and unit variance (shown as Z-scores). Analyses were done on non-standardized data.

The transect data show patterns of egg mass production that are non-random within each of the four tide series (tests for equal production across days: $\chi^2 = 56.2, 41.8, 13.3, 26.5$; df = 6, 6, 6, 7; all $P < 0.05$) and similar among tide series (Fig. 5). In striking fashion, reproduction in the population crashed consistently toward the middle of each series, dropping from a high of 10 to 40 per transect to on average about 0.5 per transect. This general pattern supports the prediction that reproduction would decline at times of higher heat stress, typically toward the middle to late part of each series when tides are low and overlap more of the mid-day hours.

Even more striking is the detailed pattern of change in reproduction by adults relative to their recent thermal history. Except for a few days at the start of the second spring tide series, the direction of change in daily mass production exactly opposes the direction of change in daily T_{max} as recorded *two tides prior* (hereafter $T_{max(-2)}$, where the subscript denotes the number of tides prior to the daily census when masses were recorded; Figure 5; $\chi^2 = 11.0$, df = 1, N = 24, $P < 0.001$). As a result, mass production was strongly negatively associated with $T_{max(-2)}$ (multiple regression controlling for tide series; $F_{1,23} = 11.30$, N = 29, $P < 0.003$; Fig. 6) but, surprisingly, not with $T_{max(-1)}$ ($F_{1,23} = 0.25$, $P = 0.62$). During the 1999 reproductive season, the ability of T_{max} to predict conditions on future

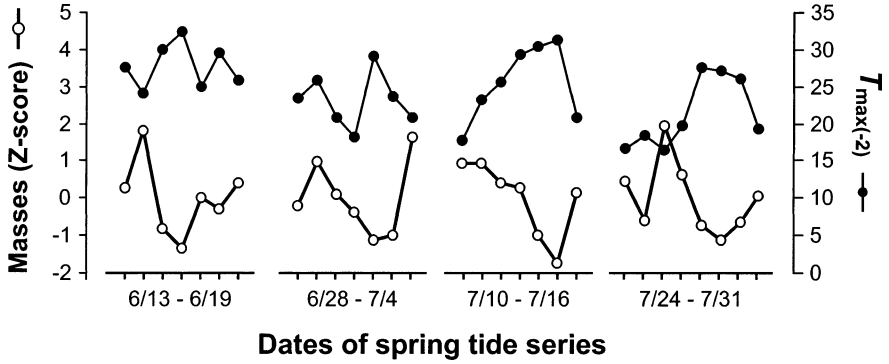

FIG. 5. Average egg mass production per transect (open symbols) each day during four spring tide series in summer 1999 (N = 652, 339, 258, 244) and corresponding values of $T_{max(-2)}$, the maximum temperature on the low tide two days prior (closed symbols). T_{max} is shifted two days forward in this way, and mass production is standardized within each series (Z-scores) to remove variation across series, in order to show more clearly how changes in mass production oppose changes in $T_{max(-2)}$.

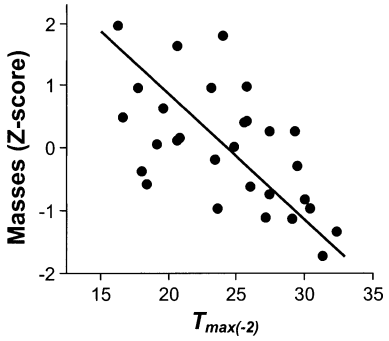

FIG. 6. Relationship between mass production on transcects (Z-scores) and $T_{max(-2)}$ for all spring tide census days. The regression line is the reduced major axis ($R^2 = 0.34$).

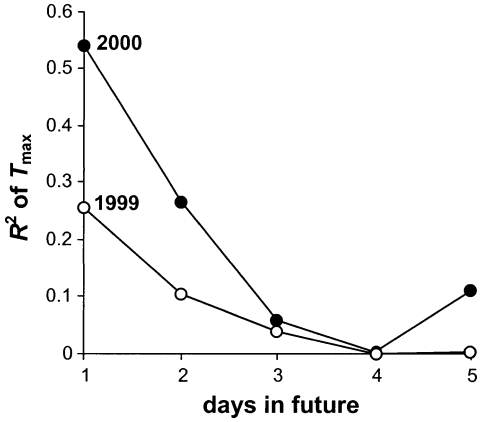

FIG. 7. Temporal autocorrelations in T_{max} for different time intervals over two months (early June to early August) during the reproductive seasons of 1999 and 2000.

tides dropped off rapidly as a function of time (Fig. 7). Thus, reproduction within spring tides (i) was non-random and (ii) appeared to change in response to an environmental signal, though not one more strongly predictive of future conditions for developing offspring.

Despite the association between reproduction and thermal history, and the consistent decline in mass production toward the middle of tide series, population-level patterns of reproduction do not appear to have been beneficial to offspring. On a given day, egg mass production was not positively associated with predicted embryo survivorship (linear regression controlling for tide series; $t_{24} = 1.688$, $P = 0.95$). The same conclusion follows from comparing total embryo survival within each tide series to survivorship of embryos in simulations where masses were distributed at random among days. In all four tide series, the actual distribution of masses among days had no better survivorship by chance than 1,000 such random distributions (randomization tests, $P \geq 0.05$; Efron and Tibshirani, 1993). Interestingly, survivorship in series 4 would have been significantly better than chance if masses had been deposited one day earlier, as if in response to $T_{max(-1)}$ rather than $T_{max(-2)}$ (randomization test, $P < 0.034$).

What constrains reproductive performance in natural populations?

The data and model predictions present something of a paradox concerning adult reproductive performance in *M. diomedea*. On one hand, egg mass production by adults is non-random and appears, from patterns of reciprocal change with T_{max}, to respond to environmental information with daily temporal resolution. On the other hand, adult reproduction responds not to immediate signals but rather to more temporally remote information, which only weakly predicts conditions likely to be experienced by embryos. As a result, reproduction among this sample of field days occurred at times when the model predicts no significant enhancement of offspring survival.

Although this paradox cannot yet be resolved, observations presented here raise several hypotheses for consideration and future work. First, perhaps reproduction occurs mainly during neap tides in the absence of heat stress, and what I observe during spring tides plays a minor role in selection on reproductive performance. The regular decline in mass production toward the middle of spring tide series suggests that adult reproduction could be entrained to a lunar cycle, and not actually responsive to temperature. In the absence of neap tide transect data this hypothesis cannot be tested directly, but three pieces of indirect evidence weigh against it as a complete explanation. (1) $T_{max(-2)}$, a variable with some unpredictability given variation in weather conditions, accounted for 34% of variance in mass production. In contrast, mass production was less strongly predicted by tidal height (H_t; maximum $R^2 = 0.18$ for $H_{t(-3)}$), a variable that is tied to lunar cycles and is likely more predictable than T_{max}. Coincident reversals in $T_{max(-2)}$ and mass production (Fig. 5) indicate an association between the two that goes beyond a potential background effect of lunar phase. (2) From the day they were brought into the laboratory, a captive population of adults maintained steady egg mass output (unpub. data), showing no evidence of lunar entrainment as seen in some organisms that reproduce on lunar cycles (Saigusa, 1980; Battaglene *et al.*, 2002; Ferrero *et al.*, 2002). (3) The accumulation of masses on transects over neap tide series did not consistently indicate higher production compared with spring tides, even assuming measured rates of daily loss from transects (unpublished data).

Second, the model as developed here might fail to take into account other environmental conditions that affect embryo survival, growth, or hatching size. Other risks can influence developmental success in intertidal habitats, some in parallel with (*e.g.,* UV exposure, oxidative stress) and some opposed to (*e.g.,* dislodgement risk, predation) conditions that lead to thermal stress (Biermann *et al.*, 1992; Trussell *et al.*, 1993; Abele-Oeschger and Oeschger, 1995). In addition, the assumption that effects of T_{max} are independent across days may be violated if consequences of heat stress

are more severe early in development, or if stress protection is accumulated from previous exposures, as seen over longer time scales in adult stages (Roberts *et al.*, 1997; Buckley *et al.*, 2001). Also, I lack information about the relative effect of day 1 exposures for $T_{max} < 24$°C, which could raise the cost of reproducing during neap tides or on cool days during spring tides. The model ignores other complications, such as the effects of oxygen deficit at interior positions within masses (Strathmann and Strathmann, 1995). Given the strong effect of high temperature on oxygen demand, and the weaker effect on oxygen supply through diffusion (Woods, 1999), this assumption likely makes my estimates of temperature risk conservative. Several of these assumptions will be addressed in future laboratory and field work.

Third, evidence that adults respond to environmental cues, but not necessarily to those with the greatest predictive power, raises the intriguing hypothesis that physiological constraints on reproduction could limit the ability of adults to respond on an optimal time scale (Hoffmann, 1978; Kingsolver and Huey, 1998). Given that masses are deposited at high tide within a few hours of the most recent low tide, information from $T_{max(-1)}$ (or a correlated variable) could be too recent to alter the process underlying production of an egg mass. Perhaps in some years the capacity to respond with a one tide-lag could still benefit offspring. The summer of 1999 may have been especially poor for temporal predictability, as the autocorrelation of T_{max} was weaker and appears to have been influenced by variable weather conditions more strongly than in 2000, another year when temperature data were logged (Fig. 7).

Finally, reproductive timing could be a passive physiological consequence of temperature rather than an adaptive response. According to this hypothesis, physiological processes underlying egg mass production would be negatively associated with increasing temperatures. Non-stress temperatures, however, typically have a positive effect on metabolism and egg production (Fusaro, 1980; Smith and Lane, 1985). It is possible that high temperatures could induce adult physiological stress or limit mating opportunities, but adults characteristically avoid surface conditions by burrowing at low tide and, based on laboratory tests, can store sperm for long periods. Although passive physiological responses to temperature could have led to diminished reproduction at both low temperatures and stressful high temperatures (Venkataraman and Job, 1980), this pattern was not apparent in the data (Fig. 6).

Although this analysis was presented at a population level, the study system lends itself to analyzing selection on performance of individual adults and their embryo clutches (see Kingsolver and Gomulciewicz, 2003). Gel maintains the integrity of clutches, so that sibships can be sampled repeatedly in the field, and measures of developmental performance in the laboratory can be related to field measures and to the timing of mass production by individual adults. In addition, large differences in physical characteristics and heat stress among field sites where *M. diomedea* reproduces offer the opportunity to examine consequences of performance in different selective environments. Given planktonic dispersal of larvae, sites are likely to be genetically coupled, so that plasticity may evolve in response to local conditions. Examination of plasticity and performance at this larger spatial scale is underway.

Studies that incorporate linkages between life cycle stages, especially in a field context, may better reveal how performance capacities at one stage can influence performance and selection at others. ''Ecological simulations'' in the laboratory (*e.g.*, Boule and Fitzgerald, 1989; Sulkin and McKeen, 1996; Marsh and Manahan, 2000) can contribute where it proves difficult to measure performance directly in the field (Bennett and Huey, 1990). This study used ecologically relevant simulations to examine the interaction between embryo and adult performance under field conditions, and revealed that adults may be constrained in their ability to influence selection on embryos. Other work has begun to focus on the network of performance consequences that connect gametes, larvae, juveniles, and adult stages of marine invertebrates (Levitan and Young, 1995; Walters and Wethey, 1996; Moran and Emlet, 2001; Franke *et al.*, 2002; Phillips, 2002). These studies are providing insight into how performance capacities structure life histories and thereby shape the evolution of organism form and function over life cycles.

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