RESEARCH ARTICLE

Consequences of nest site selection vary along a tidal gradient

Nicholas A. W. Brown[1,2] | Noah S. B. Houpt[1] | Nicole L. Yee[1] | Jennifer E. M. Curtis[2] |
Benjamin M. Bolker[3] | Francis Juanes[2] | Sigal Balshine[1]

[1]Department of Psychology, Neuroscience, and Behaviour, McMaster University, Hamilton, ON, Canada

[2]Department of Biology, University of Victoria, Victoria, BC, Canada

[3]Department of Mathematics & Statistics and Department of Biology, McMaster University, Hamilton, ON, Canada

Correspondence
Nicholas A. W. Brown
Email: brownn20@mcmaster.ca

Abstract

1. Parents providing care must sometimes choose between rearing locations that are most favourable for offspring versus those that are most favourable for themselves. Here, we measured how both parental and offspring performance varied in nest sites distributed along an environmental gradient.

2. The plainfin midshipman fish *Porichthys notatus* nests along a tidal gradient. When ascending from the subtidal to the high intertidal at low tide, both nest temperature and frequency of air exposure increase. We used one lab and two field experiments to investigate how parental nest site choices across tidal elevations are linked to the physiological costs incurred by parents and the developmental benefits accrued by offspring.

3. Under warmer incubation conditions, simulating high intertidal nests, offspring developed faster but had higher mortality rates compared to those incubated in cooler conditions that mimicked subtidal nests.

4. In the field, males in higher intertidal nests were more active caregivers, but their young still died at the fastest rates. Larger males claimed and retained low intertidal nests, where offspring survival and development rates were also highest.

5. Our results suggest that males compete more intensively for nest sites in the low intertidal, where they can raise their young quickly and with lower per-offspring investments. Smaller, less-competitive males forced into higher intertidal sites nest earlier in the season and provide more active parental care, possibly to bolster brood survival under harsh environmental conditions.

KEYWORDS
environmental gradient, fitness trade-offs, parental care, plainfin midshipman, reproductive strategies, reproductive success

1 | INTRODUCTION

During reproduction, care-giving parents face a critical decision: Where should they raise their young? Offspring accrue growth and survival benefits when raised under good developmental conditions, safe from predation and close to favourable juvenile habitat (Refsnider & Janzen, 2010). However, parents also need to consider the costs incurred on their own survival and future reproduction when choosing a place to rear offspring (Marshall & Uller, 2007). When these costs to parents outweigh the benefits offspring receive from favourable conditions, parents might even choose poor rearing sites to save energy that can be invested into future fecundity (Mayhew, 2001). In species that provide post-fertilization care at a single nesting site, parents are exposed to the same conditions

as their offspring. These parents can safeguard themselves and their offspring by avoiding areas with high predation risk or severe abiotic conditions (D'Alba et al., 2009; Eggers et al., 2006). However, when environmental conditions that favour parents and their offspring differ, parents choosing nesting sites face a trade-off between their future reproductive success and the fitness benefits accrued by their present offspring.

Few studies to date have considered nest site selection under this scenario of a parent–offspring conflict (Trivers, 1974). Such conflicts occur when parental and offspring fitness are maximized under different levels of parental investment; offspring are selected to demand more from parents than parents are selected to invest (Godfray, 1995; Parker et al., 2002). When offspring possess adaptations to elicit additional parental investments, an evolutionary stable strategy is attained at levels of parental investment somewhere between parental and offspring optima (Parker et al., 2002). However, offspring presumably have no ability to elicit additional investments from their parents during nest site selection, and so preferred sites should closely reflect what is optimal for parental fitness (Crespi & Semeniuk, 2004; Godfray, 1995; Janzen & Warner, 2009; Marshall & Uller, 2007; Refsnider & Janzen, 2010). In other words, ideal nesting conditions are those that favour parental survival (allowing parents to return over multiple breeding events) and that also confer benefits to the developing offspring. The aim of our study was to investigate how nest site selection is shaped by opposing factors, and particularly the extent to which preferred nests for parents deviate from optimal rearing conditions for offspring. To address this question, we examined how the reproductive costs to parents and developmental benefits to their offspring varied across nesting sites in a marine toadfish, the plainfin midshipman *Porichthys notatus*.

Each spring, plainfin midshipman migrate from deep waters (≤300 m) to beaches along the Pacific coast of North America to breed. Large males, called *guarder* males, excavate nest cavities under rocks and produce a vocalization that attracts females (Brantley

& Bass, 1994). Early in the breeding season, guarder males compete vigorously to acquire and retain nesting sites and larger males typically occupy the biggest nests, attract more females and sire larger broods (Bose et al., 2014, 2018; DeMartini, 1988). Successful guarder males spawn with several females and then remain alone in the nest for ≈60 days guarding and tending eggs until they develop into free-swimming juveniles (Cogliati et al., 2013; DeMartini, 1988; Figure 1a). Guarder males use their fins, nostrils and mouths to clean, oxygenate and hydrate embryos (see Appendix S2). However, during the parental care period, males feed only opportunistically, leading to severe declines in body condition (Bose et al., 2016). Furthermore, during low tide events, guarder males in intertidal nests endure several hours of daily emersion (air exposure) or hypoxia in small pools of increasingly warming waters. These events are more severe (more frequent and longer) in higher intertidal nests and during spring tides (Figure 1a; Bose, Borowiec, et al., 2019; Craig et al., 2014). Therefore, males in higher nests likely suffer higher costs of care as nesting in a harsher environment could lead to faster energy depletion, increased avian predation risk and a lower probability of survival to the subsequent breeding season (Bose, Borowiec, et al., 2019; Bryan & Bryant, 1999). In contrast, offspring development, which depends on parental care, might be most rapid under the warmer temperatures and frequent air exposure of higher intertidal nests. Warmer conditions likely lead to earlier hatching and a shorter parental care duration, which could curtail the window of mortality risk to both parents and offspring (MacDonald et al., 1995; Magnhagen, 1991; Warkentin, 1995). Offspring might also receive fitness benefits from hatching quickly if environmental conditions earlier in the breeding season (e.g. prey productivity; Doyle et al., 2002) are more favourable for juvenile growth and survival (Batten et al., 2016; Saino et al., 2012). Hence, we hypothesized that if the abiotic conditions at higher tidal elevations inflict greater physiological costs on guarder males but also enhance offspring development, then the best compromise for a parent between the costs and benefits of care might
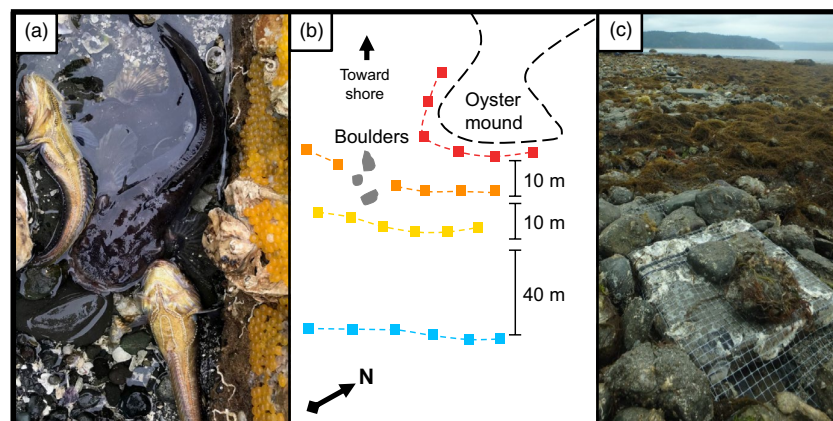

FIGURE 1 (a) A plainfin midshipman guarder male (centre) with two spawning (belly-up) females in an overturned natural nest. (b) Diagram of the field site. Coloured squares show every fifth tile along the high (red), middle (orange), low (yellow) and subtidal (blue) contours. High nests were wrapped around the oyster mound to match the 0.0-m contour on tidal charts. (c) An emersed, meshed experimental nest (foreground) and others (background) along the low contour during a spring tide. Images captured by S. Balshine and N. Brown

be to nest in the middle of the tidal gradient, where abiotic conditions are still favourable for offspring development but are not too harsh for parental males to endure.

Based on this hypothesis, we conducted a lab experiment and two field experiments to test the following two predictions: (a) body condition deterioration rates of caring males will increase with increasing tidal elevation and (b) offspring development rates will increase with increasing tidal elevation. This proposed divergence in environmental conditions favouring parents versus their offspring suggested three further questions: (c) at what elevation will offspring survival be highest? (d) where will the largest, highest quality males, which presumably have the greatest resource holding potential (Briffa & Sneddon, 2007), be found? and (e) will males provide more or less care as intertidal elevation increases and abiotic conditions harshen?

2 | MATERIALS AND METHODS

2.1 | Experiment 1: Effects of water temperature and emersion on offspring development rates and survival

We carried out a laboratory experiment to investigate how plainfin midshipman young are affected by abiotic conditions in their rearing environment. Specifically, we examined how development and mortality rates vary between cool and warm temperatures and in the presence or absence of daily emersion during embryonic, larval and juvenile life stages.

2.1.1 | Animal collection, housing and mating conditions

Guarder males and gravid females were collected by overturning large rocks during low spring tides between 2 May and 2 June 2018 at four sites in British Columbia, Canada: Ladysmith Inlet (49°01′N, 123°83′W), Lantzville (49°15′N, 124°04′W), Bowser (49°27′N, 124°41′W) and Crescent Beach (49°04′N, 122°88′W). Fish were transported in sex-specific bins filled with aerated seawater to the University of Victoria's Outdoor Aquatic Unit, where they were transferred to sex-specific, 400-L outdoor holding tanks (maximum of eight fish per tank) supplied with free-flowing, ambient temperature (c. 13°C) seawater and brick shelters.

After a minimum 24-hr recovery, males from holding tanks were placed individually in aerated 175-L glass spawning aquaria lined with gravel and supplied with free-flowing, ambient seawater. Each spawning tank contained an artificial nest made of bricks. Males were given 3 days to discover and excavate a nest under these bricks; males that failed to do so were swapped for a new male from the holding tanks. Once a male occupied a nest, a gravid female from the female holding tanks was weighed (±0.01 g), measured (standard length [SL]; ±1 mm) and then added to his tank. Like males, females were allowed up to 3 days to spawn with a partner; if no spawning
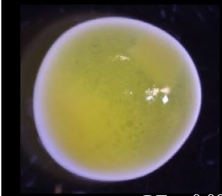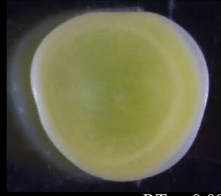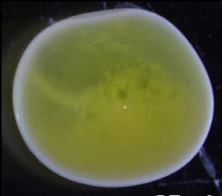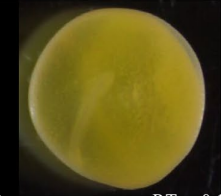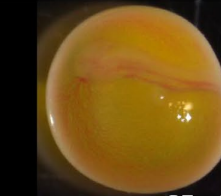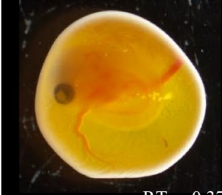
occurred, the female was moved into another male's tank. Females were given three opportunities to spawn before being removed from the study. Tanks were checked each morning for spawnings. In total, we collected fertilized eggs from 21 males and 41 females for this experiment (males were allowed to spawn twice).

2.1.2 | Rearing environments, experimental procedure and development staging

When eggs were detected (adhering to the roof of the nest), the parental male and female were immediately removed and measured. Concurrently, the four bricks constituting the roof of the nesting cavity, and hence the brood of fertilized eggs, were separated. Each brick with eggs was photographed alongside a ruler and then randomly assigned to one of four rearing environments: (a) cold (ambient) seawater (mean ± SD = 13.2 ± 0.6°C; N = 3,843 total hours in treatment) without prolonged daily emersion; (b) cold seawater (12.9 ± 0.4°C; 4,347 hr) with a 4-hr daily emersion; (c) warm seawater (19.6 ± 1.9°C; 2,018 hr) without prolonged daily emersion and (d) warm seawater (19.8 ± 1.4°C; 2,871 hr) with a 4-hr daily emersion. These conditions were chosen to match the average emersion duration and upper and lower thermal extremes experienced in the wild by plainfin midshipman during spring tides (Bose, Borowiec, et al., 2019). Each rearing environment was replicated in two continuously aerated *rearing tanks* (eight tanks in total; see tank-specific summaries in Table S3) that were identical in dimensions to spawning tanks. Rearing tanks were supplied with free-flowing seawater that fully replenished each tank every ≈2 hr. The warm seawater tanks contained two 250-W aquarium heaters (EHEIM GmbH & Co. KG). Bricks with young in emersion treatment tanks were removed daily for a 4-hr period (air temperature: mean ± SD = 18.4 ± 1.3°C; N = 3,178 hr). While emersed, bricks were covered with a plastic bin (to prevent light damage) and misted with seawater hourly (to prevent desiccation). All eggs attached to the bricks were inspected daily, so we could record the days when broods reached 10 standardized developmental stages (Table 1). All dead eggs were counted and then removed carefully with tweezers (caring males remove unhealthy eggs in the wild). Each brick was photographed every 3 days until all young reached the juvenile stage and detached. An enumerator, blinded to treatment group, counted the number of eggs or attached larvae in photos taken across the developmental period for all bricks. Counts continued until the young on a brick either perished entirely or started to become free-swimming. These time series of counts allowed us to track mortality rates across the developmental period. The enumerator also measured diameters (±0.1 mm) of 20 randomly selected eggs from their initial (day 1) photo.

When young finished detaching from bricks, we began daily counts of living and dead juveniles in each tank, allowing us to compare mortality rates across rearing environments. Counts continued until a tank's population reached ≤10 individuals and ranged from 23 to 63 days. Juveniles were fed 2 ml of SELCO-enriched live adult brine

TABLE 1 Ten discrete developmental stages in plainfin midshipman young. Specimens are representative of the morphologies observed across rearing conditions in Experiments 1 and 2. Using the data we collected during Experiment 1, we assigned to each stage a score corresponding to its average proportion of total development time across all treatments, RT_i (Klimogianni et al., 2004), which is overlaid on each photograph. Developed by N. Brown based on an index created by Karen Cogliati

1. New egg
A white blastodisc is visible on the surface of the yolk sac (white blob in the upper-right side of the egg).

2. Gastrula
Epiboly results in the formation of a thin, crescent-shaped blastoderm.

3. Early neurulation
The gastrula converges into a thin notochord (middle-left of egg).

4. Late neurulation
Dorso-ventral axis becomes apparent with the formation of a head at one end (top) of the notochord.

5. Heart
Organogenesis is clear: veins appear, and a faint heartbeat can be detected with the naked eye.

$RT_i = 0.001$ $RT_i = 0.094$ $RT_i = 0.135$ $RT_i = 0.154$ $RT_i = 0.326$

6. Eye
Advanced visceral organ development, most notably the darkly coloured eye.

7. Newly hatched larva
The new larva emerges from its yolk sac casing.

8. Swim bladder
The silver organ appears in the abdominal region. Coincides with flexion.

9. Melanophores
Darkening, striped pigmentation spreads across the dorsal surface, starting at the head.

10. Free-swimming juvenile
Attains all adult features. Yolk sac is nearly or fully absorbed. Can remain attached for some days before free-swimming.

$RT_i = 0.372$ $RT_i = 0.442$ $RT_i = 0.539$ $RT_i = 0.622$ $RT_i = 0.999$

shrimp daily on a per-fish basis supplemented with marine amphipods *Hyale* sp. Accordingly, any selective mortality we observed likely acted through differential success in transitioning to exogenous feeding. Following their use in this experiment, juveniles and adults were reused in additional experiments (e.g. Houpt, Borowiec, et al., 2020).

2.1.3 | Statistical analyses

All analyses in the present and following experiments were conducted in R (version 3.6.0; R Core Team, 2016; further details in Appendix S1). Rearing tank identity was included as a random intercept in all models to account for among-tank variation. First, we investigated the effects of water temperature and emersion on development rates in *demersal* young (those adhered to bricks) by fitting a linear mixed effects model (LMM) to total development times (days to reach free-swimming; square-root transformed). Fixed factors were water temperature, emersion, their interaction and average initial egg diameter. Female (dam) and male (sire) identities were included as additional random intercepts.

Second, we used a binomial GLMM with a complementary log–log link to investigate how water temperature and emersion affected mortality rates in demersal young, specifically mortality since the previous observation. Fixed factors were water temperature, emersion, brood age (days post fertilization), their interaction, average initial egg diameter and the time interval between observations (log-transformed and scaled). We included random intercept and slope terms for brick identity nested within female identity (Schielzeth & Forstmeier, 2009). We then subset the data by including only the final mortality count for each brick to investigate how survivorship to the free-swimming juvenile life stage varied across treatments. We used a model that was identical to the GLMM described above, except we removed the time interval between observations from the fixed factors (there were only two observations, initial and final, for each brick) and we removed the random slope term.

Third, we used a binomial GLMM with a complementary log–log link to investigate how water temperature and emersion affected mortality rates (mortality since the previous observation) in free-swimming juveniles. Fixed factors were water temperature, emersion (while demersal; free-swimming juveniles were never emersed), time (number of days since the beginning of each tank's time series), their interaction and the number of days between observations (log-transformed and scaled).

2.2 | Experiment 2: Costs and benefits of nest site selection along a tidal elevation gradient

The aim of this experiment was to investigate variation in parental costs and offspring benefits across different nesting sites in the wild.

We tracked the body conditions of individual males as well as development and mortality rates in their broods of eggs over the breeding period and along the tidal gradient. Additionally, we recorded videos of males providing care following nest emersion to investigate how parental care varied across the tidal gradient.

2.2.1 | Study site, nest construction and water quality measures

We studied plainfin midshipman fish nesting along the tidal gradient in Dabob Bay, Washington, United States (47°76′N, 122°86′W), from May to August 2018. Substrate composition at the site was a mixture of oyster reef (dominated by *Crassostrea gigas*) and beach rock, which descended into a subtidal macroalgae bed (mainly *Sargassum muticum* but with increasing depth *Zostera marina* became more abundant) interspersed with beach rocks (Figure 1c). From 14 to 16 May 2018, we constructed 110 artificial nests on this beach by deploying 30 square concrete tiles (929 cm^2; spaced 1 m apart) along intertidal contours demarcated by the waterline at −0.03, −0.40 and −0.61 m (relative to local tidal charts), which we refer to as *high*, *middle* and *low* respectively. These contours reflect the natural distribution of nesting plainfin midshipman at the site (Bose, Borowiec, et al., 2019). Twenty additional tiles were placed at a fourth *subtidal* contour (approximately −1.22 m; Figure 1b). We surveyed all artificial nests along these contours during low spring tides on 16–19 May, 13–18 and 28–29 June and 11–13 and 28–29 July 2018.

Digital temperature loggers (±0.1°C Onset HOBO Pendants and ±0.5°C Thermochron iButtons recording at one measurement per hour) were deployed in 10 nests along each intertidal contour and in three subtidal nests. Water quality tests were also carried out during the lowest tide of each spring cycle at three nests per intertidal contour (Table S1).

2.2.2 | Experimental procedure

The 20 northern-most tiles along each intertidal contour were designated *experimental* nests and covered with plastic mesh (1 cm^2 openings; Figure 1b,c) after a male excavated a cavity underneath and received eggs. Mesh prevented nesting males from leaving and most other intertidal animals from entering, allowing us to track the body condition of individual males while controlling for food availability, as well as brood development without the possibility of nest takeovers or avian predation, both of which are common in this species (Bose, Lau, et al., 2019; Cogliati et al., 2014; Houpt, Bose, et al., 2020). Mesh also prevented further spawnings, allowing us to track brood survival from a known spawning date. The remaining 10 tiles at each intertidal contour and all 20 tiles in the subtidal were designated *natural* nests and left uncovered. Logistical difficulties precluded meshing of subtidal nests during the present experiment, but we carried out follow-up work on subtidal nests in Experiment 3 (see below). We used natural nests to assess the impact of mesh covering on spawning success.

Nests were checked during ebbing tides, just after the sea receded below a contour. If no fish were present, the tile was checked again the following day. If a guarder male was discovered without eggs, we gently replaced the tile and checked it again the following day. Once a guarder male was discovered with a brood of eggs, we photographed the eggs and weighed (±0.01 g) and measured (SL; ±1 mm) the male. We also weighed and measured any females or cuckolder males in the nest and then released them into the sea, as these fish do not provide parental care and leave the nest immediately after spawning (Brantley & Bass, 1994). Following measurements, guarder males were returned to their nests and the tile was covered again with mesh (experimental nests only). Collectively, 87 guarder males took up residence in the experimental and natural nests. Once males were established in nests with broods of eggs, we returned to the nests during subsequent spring tides to measure the males and photograph the broods of eggs again, allowing us to track how the body masses and brood sizes of males changed over time (each male and brood was measured two to five times). An enumerator, blinded to nest elevation, counted the number of eggs present (brood size) in each nest photograph and scored their developmental stages. Following the methods of Klimogianni et al. (2004), each development stage was assigned a score (RT$_i$) corresponding to the average proportion of total development time it represented based on the developmental categories used in Experiment 1; scores ranged from 0.001 (a new egg) to 0.999 (a juvenile with no visible yolk sac; see Table 1).

Using digital cameras (GoPro Hero 5 Black), we collected 48 videos of 36 parental males tending broods of eggs: 13 videos (of 12 males) at the high elevation, 16 videos (of 14 males) at the middle and 19 videos (of 10 males) at the low elevation. Hence, some of the 36 males were repeatedly recorded, but most were recorded once (*N* measured once = 28; *N* measured twice = 2; *N* measured thrice = 6). We analysed all videos but statistically accounted for repeatedly recorded individuals (see below). Recordings began during the flood stage of the daily tidal cycle as soon as the sea returned to the focal nest. Videos recorded until camera batteries died and lasted 90 min, on average. A rater, blinded to nest elevation, counted or recorded the total durations of all parental behaviours from the first hour of each video recording (five videos <60 min were excluded). We defined parental care as the total time spent on egg hygiene (nosing eggs, egg squirting and egg fanning) and nest maintenance behaviours (sediment clearing, sediment carrying and sediment spitting; see Appendices S1 and S2 for tabular and video ethograms of these behaviours).

2.2.3 | Statistical analyses

To reflect our predictions, we applied successive differences contrasts (i.e. comparing the differences in responses between successive tidal elevations, using one-tailed tests) to the tidal elevation groups in some models. To test our assumption that thermal conditions increased in severity with tidal elevation, we calculated daily

mean temperatures, daily temperature standard deviations and daily maximum temperatures from measurements recorded by each digital logger ($N = 1,204$ daily measurements from 33 loggers). These data fluctuated with the tidal cycle (Figure 3), so we used generalized additive mixed models (GAMMs) to fit nonlinear regression curves to the time series. We fit three GAMMs—one each for average daily temperature, daily standard deviation and daily maximum temperature. Intertidal elevation was the only fixed effect in all models. We fit a separate function for each elevation to allow for variation in their temporal trends. Temperature logger identity was included as a random intercept to account for repeated measurements.

We fit a negative-binomial GLMM to brood size data to determine how spawning success varied across elevations. Nest elevation, manipulation (experimental or natural), Julian date and male SL were included as fixed factors. Nest identity was a random intercept.

Residuals from a log–log regression of each male's mass and SL were used as a body condition index (Bose et al., 2016; Schulte-Hostedde et al., 2005). To determine if body condition among males repeatedly measured in experimental nests ($N = 30$) deteriorated faster at higher elevations, we fit condition index values with an LMM. Fixed factors were elevation, observation day and their interaction. Male identity was included as a random intercept with a random slope for observation day.

To assess how development rates differed across elevations in experimental and natural nests, we fit a Beta GLMM to the development data. The response variable was the stage of the most developmentally advanced eggs in a nest on a given date (RT_j). Fixed factors were intertidal elevation, observation day, their interaction and the number of days (log-transformed and scaled) between the previous and focal observation. Brood identity was included as a random intercept.

We used a binomial GLMM with a complementary log–log link to investigate how egg mortality (disappearances of young since the previous observation) varied across intertidal elevations. Fixed factors were intertidal elevation, observation day, their interaction and the number of days (log transformed and scaled) between the previous and focal observation. Brood identity was included as a random intercept.

We used a log-LMM to test whether parental care decreased with increasing intertidal elevation. The response was the total duration of all parental behaviours exhibited during the trial. Egg squirts and sediment spits were brief events that were counted rather than timed, so we added their counts as 1-s bouts to the total parental care duration. Fixed factors were nest elevation, male size (SL) and brood size. Male identity and trial date were included as random intercepts to account for repeated measurements of individuals and any environmental differences between days respectively.

2.3 | Experiment 3: Spawning success and parental care in subtidal nests compared to intertidal nests

In Experiment 2, we made our first effort to study the subtidal rearing environment (where males and young are never emersed).

Our aim in this third experiment was to further compare the costs and benefits of nesting in the subtidal versus the intertidal by directly comparing male sizes, brood sizes and parental behaviours—including nest defence.

2.3.1 | Field survey and behavioural trials

We returned to the Dabob Bay site (where we conducted Experiment 2) in 2019 and constructed 30 artificial nests, spaced 1 m apart, along the middle intertidal and subtidal contours during low tides on 23–25 April 2019. We allowed 10 days for guarder males to discover, excavate and compete for nests. Then, during low tides on 5–7 May 2019, we sampled all nests in both the intertidal and subtidal groups. For intertidal nests, we followed Experiment 2 procedures (see above) to weigh (± 0.01 g) and measure (SL; ± 1 mm) all males. To capture fish from subtidal nests, two snorkelers worked together to lift each tile and cover the nesting cavity with a net. Fish were later returned to their original nest. On the rare occasion a subtidal fish escaped capture, we noted its presence in the nest. Broods within each nest were also photographed while the resident males were measured. We sampled all nests again during low tides on 3–4 June 2019 following the same procedures. In total, we captured and measured 46 males from subtidal nests (21 in May, 25 in June) and 57 males from middle intertidal nests (28 in May, 29 in June). An enumerator, blinded to nest elevation, counted brood sizes in nest photographs following the procedure described in Experiment 2 (above).

Defending young against predators is an important parental duty that we did not previously investigate experimentally (i.e. in Experiment 2). Hence, between 30 April and 24 May 2019, we used digital cameras (models: GoPro Hero5 Black and Sony AS300 & AS50 Action Cameras) to record behavioural trials investigating how parental care and nest defence varied between males in intertidal and subtidal nests during high tides, when nests were immersed at ≥1 m depth. Prior to each trial, snorkelers confirmed the presence of a single male with a brood of eggs under the focal nest, then covered it with mesh (see details in Experiment 2, Figure 1c) to prevent other animals from intruding. One snorkeler turned on the video camera, then both snorkelers left the nest and the fish was allowed a 10-min recovery. A 20-min *baseline* observation period then began wherein the focal fish's natural behaviour was recorded. Next, one snorkeler inserted into the nest a black-clawed crab *Lophopanopeus bellus* (carapace widths: 20–30 mm; cheliped lengths: 13–28 mm), attached with a small backpack harness to the end of a thin bamboo rod. These crabs are frequent predators of plainfin midshipman eggs (NAWB, NSBH, & SB, pers. obs.). The crab remained in the nest for a 20-min *intrusion* period. A snorkeler then removed the crab and recording continued for a 20-min *follow-up* period before snorkelers removed the camera and mesh. We recorded trials in 28 nests—14 in the middle intertidal and 14 in the subtidal. These nests were distributed evenly along the contours and were chosen opportunistically when snorkelers confirmed the presence of a lone male with eggs. Each nest was recorded only once. A rater, blinded to nest elevation,

counted or recorded the durations of parental care and nest defence behaviours during each trial period in the video recordings. We defined parental care as in Experiment 2 (see above), and nest defence as the total duration of all grunts, growls, bites and lunges exhibited during the intrusion period (see Table S2; Video S1). Four videos, all in subtidal nests, were excluded from statistical analyses because the focal male abandoned the nest during the trial.

2.3.2 | Statistical analyses

To determine how spawning success varied between middle intertidal and subtidal nests at *c*. 10 or 40 days post construction (5–7 May and 3–4 June), we fit a negative binomial GLMM to the brood size data. Fixed factors were elevation (middle intertidal or subtidal), month (May or June), their interaction and resident male size (SL). Nest identity was included as a random intercept to account for repeated measurements within nests (each nest was sampled twice; first in May and again in June).

For the behavioural data, we fit two separate models, one for parental care and a second for aggression. Many observations (64%) included no parental care at all; therefore, we used a GLMM with a Tweedie error distribution (for zero-inflated, non-negative continuous data; Jørgensen, 1987) to model these data. Nest elevation (middle or subtidal), trial period (baseline, intrusion, follow-up) and their interaction were included as fixed factors. Nest identity and trial date were included as random intercepts to account for repeated measurements across trial periods and environmental differences between days respectively. As no aggressive behaviours were observed during the baseline or follow-up periods, we used a log-LMM to model aggression during the intrusion period only. We included nest elevation as a fixed effect and trial date as a random intercept.

3 | RESULTS

3.1 | Experiment 1

Young incubated in warm water (*c*. 18°C) and without prolonged daily emersion developed fastest (median [IQR] days to reach free-swimming = 37 [35–38] days; Figure 2a). A slightly slower development time of 40 days (40–42) was observed among broods exposed to warm seawater with a 4-hr daily emersion. Young in cold water (*c*. 13°C) developed much slower—those that experienced both cold water and a 4-hr daily emersion were free-swimming by 105 days (102–107) while those not emersed took 108 days (106–112) to fully develop (GLMM, $N = 55$; temperature: $\chi_1^2 = 4{,}865.4$, $p < 0.001$; emersion: $\chi_1^2 = 2.3$, $p = 0.13$; water temperature × emersion: $\chi_1^2 = 15.4$, $p < 0.001$; Figure 2a). Egg diameters, measured on their first day post fertilization, ranged from 4.5 to 6.4 mm. Surprisingly, initial egg size did not have a clear effect on development times; a 1-mm increase in egg diameter corresponded to a 0.6-day (95% CI: −3.8–5.0) increase in development duration ($\chi_1^2 = 0.1$, $p = 0.76$).

When broods developed in warm water, young were exposed to an increased probability of mortality per day (a *hazard*) of approximately 3.6% (95% CI: 0.5%–6.6%) compared to broods that developed in cold water. Daily emersion for 4 hr (regardless of temperature) did not clearly affect the hazard (4-hr daily emersion–no emersion: est. [95% CI] = 0.9% [−2.3% to 4.1%]), nor did egg size (est. [95% CI] = −11% [−47% to 49%]; GLMM, $N = 309$;
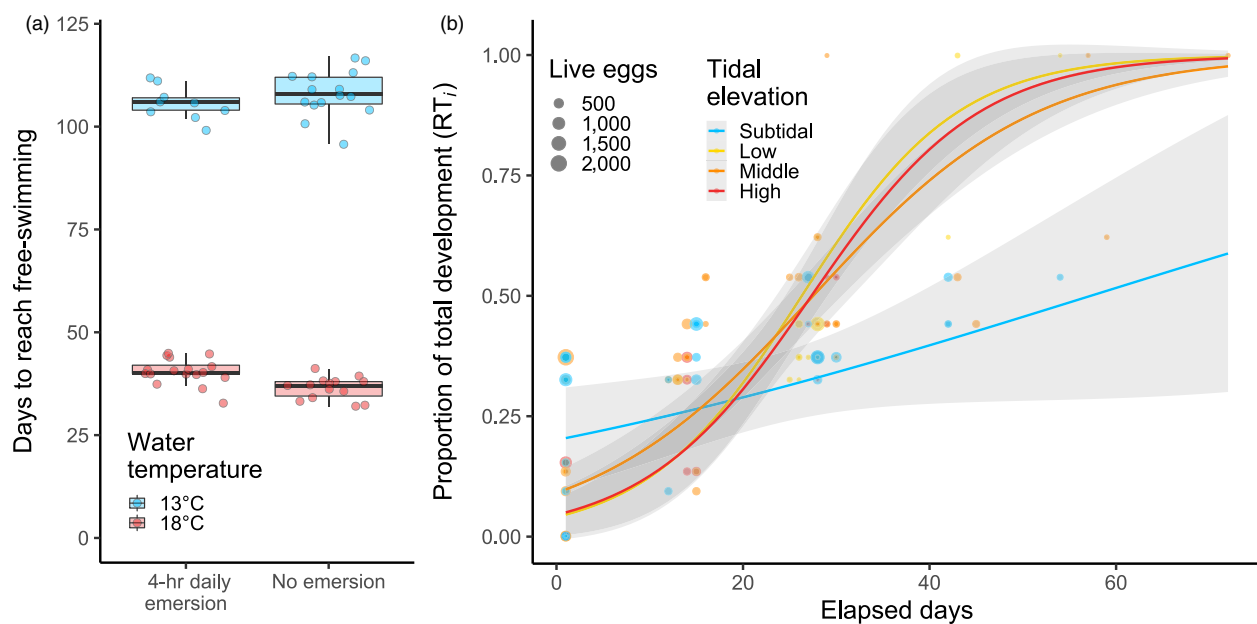

FIGURE 2 (a) Total development times of broods under different water temperature and emersion treatments in the lab (Experiment 1). (b) Development rates of broods in natural and experimental nests in the field (Experiment 2). Coloured lines show fitted population-level GLMM predictions, and the shaded areas their 95% CIs
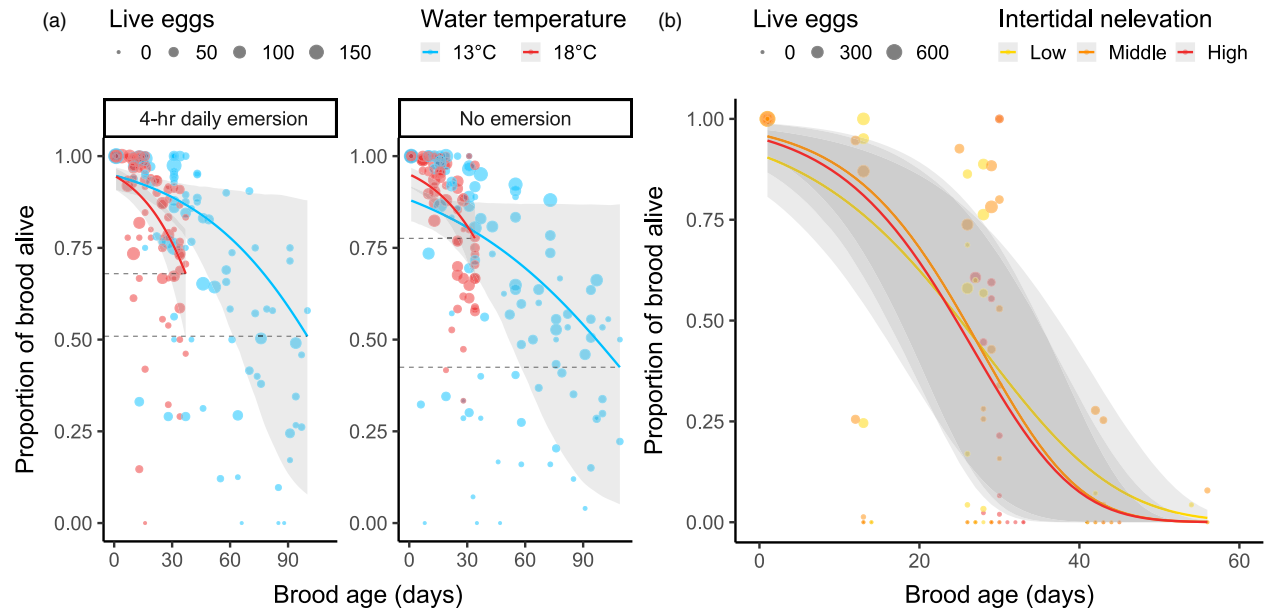
FIGURE 3 (a) Mortality rates of broods raised under combined water temperature and emersion manipulations in the lab (Experiment 1). (b) Mortality rates of broods in experimental nests in the field (Experiment 2). We could not accurately measure brood survival in subtidal nests. In both panels, coloured lines show population-level GLMM predictions, and shaded areas their 95% CIs

time × temperature: $\chi_1^2 = 5.0$, $p = 0.025$; time × emersion: $\chi_1^2 = 0.3$, $p = 0.59$; time × temperature × emersion: $\chi_1^2 = 0.0$, $p = 0.96$; time × initial egg diameter: $\chi_1^2 = 2.1$, $p = 0.15$; Figure 3a). Despite facing an increased hazard, total survivorship was actually higher among broods raised in warm water because they developed much faster—the percentage of young from each brick that survived to the free-swimming juvenile life stage was approximately 52% higher (95% CI: 29%–75%) in warm water compared to cold water (GLMM, $N = 73$; temperature: $\chi_1^2 = 16.2$, $p < 0.001$; emersion: $\chi_1^2 = 0.5$, $p = 0.50$; temperature × emersion: $\chi_1^2 = 1.7$, $p = 0.19$; initial egg diameter: $\chi_1^2 = 2.0$, $p = 0.16$; Figure 3a). However, hazards remained approximately 3.5% (95% CI: 0.9%–5.9%) higher for free-swimming juveniles reared in warm water compared to those reared in cold water, and a 4-hr daily emersion during embryonic development was associated with a hazard increase of approximately 2.7% (95% CI: 0.1%–5.4%) compared to no prolonged daily emersion (GLMM, $N = 178$; time × temperature: $\chi_1^2 = 6.9$, $p = 0.009$; time × emersion: $\chi_1^2 = 4.1$, $p = 0.042$; time × temperature × emersion: $\chi_1^2 = 0.01$, $p = 0.92$).

3.2 | Experiment 2

Across the experiment's 75-day span, artificial nests at the high contour were completely emersed on 49 days, while nests at the middle contour were emersed on 31 days and nests at the low contour were emersed on only 13 days; subtidal nests were never emersed (Table S1). Temperature loggers recorded the highest daily average temperatures at nests along the high and middle intertidal contours (successive differences contrasts; high–middle: est. [95%

CI] = 0.2 [−0.2 to 0.7]°C, $z_{1169} = 1.12$, $p = 0.26$; middle–low: est. [95% CI] = 0.3 [0.1–0.6]°C, $z_{1169} = 2.86$, $p = 0.004$; low–subtidal: est. [95% CI] = 1.0 [0.6–1.3]°C, $z_{1169} = 6.12$, $p < 0.001$; Figure 4a). We did not detect an equivalent pattern in daily temperature fluctuations (SD); the subtidal contour was less variable overall than any of the three intertidal contours, but the intertidal contours were similarly variable (successive differences contrasts: high–middle, est. [95% CI] = 0.19 [−0.63 to 1.02]°C, $z_{1132} = 0.56$, $p = 0.57$; middle–low, est. [95% CI] = 0.01 [−0.05 to 0.07]°C, $z_{1132} = 0.36$, $p = 0.72$; low–subtidal, est. [95% CI] = 0.10 [0.01–0.19]°C, $z_{1132} = 2.59$, $p = 0.01$; Figure 4b). Daily maximum temperatures followed the same pattern with elevation as daily average temperatures; maxima were highest in high and middle nests, and much higher in low than in subtidal nests (successive differences contrasts; high–middle: est. [95% CI] = 0.6 [−1.8 to 3.0]°C, $z_{1140} = 0.59$, $p = 0.55$; middle–low, est. [95% CI] = 0.6 [0.0–1.2]°C, $z_{1140} = 2.40$, $p = 0.02$; low–subtidal, est. [95% CI] = 1.7 [0.9–2.6]°C, $z_{1140} = 4.81$, $p < 0.001$; Figure 4c).

Males in natural nests received many more eggs than those in the experimental nests at every elevation (natural–experimental: est. [95% CI] = 1,062 [699–1,425] eggs; GLMM, $N = 95$; nest manipulation: $\chi_1^2 = 81.3$, $p < 0.001$; Table 2). However, brood size did not clearly differ across elevations once male size was accounted for (larger males received more eggs; elevation, $\chi_1^2 = 0.81$, $p = 0.67$; male SL: $\chi_1^2 = 5.4$, $p = 0.02$; Table 2).

The largest males were found in nests at the low elevation contour (one-way ANCOVA; date: $F_{1,82} = 2.63$, $p = 0.11$; elevation: $F_{2,82} = 3.33$, $p = 0.04$; post hoc Tukey's HSD: middle–low, $p_{adj} = 0.07$; high–low, $p_{adj} = 0.03$; high–middle, $p_{adj} = 0.82$; Table 2). Throughout the experiment, males nesting low in the intertidal also maintained better body conditions than males nesting in the middle

FIGURE 4 (a) Daily averages of temperature data collected from digital loggers between 14 May and 27 July 2018. (b) Daily standard deviations of temperature measurements. (c) Daily maximum temperatures. Each dot shows the daily value from one logger. Coloured lines show GAMM predictions, and the shaded areas their 95% CIs. Light grey lines show daily fluctuations in water heights (relative to local tidal charts)
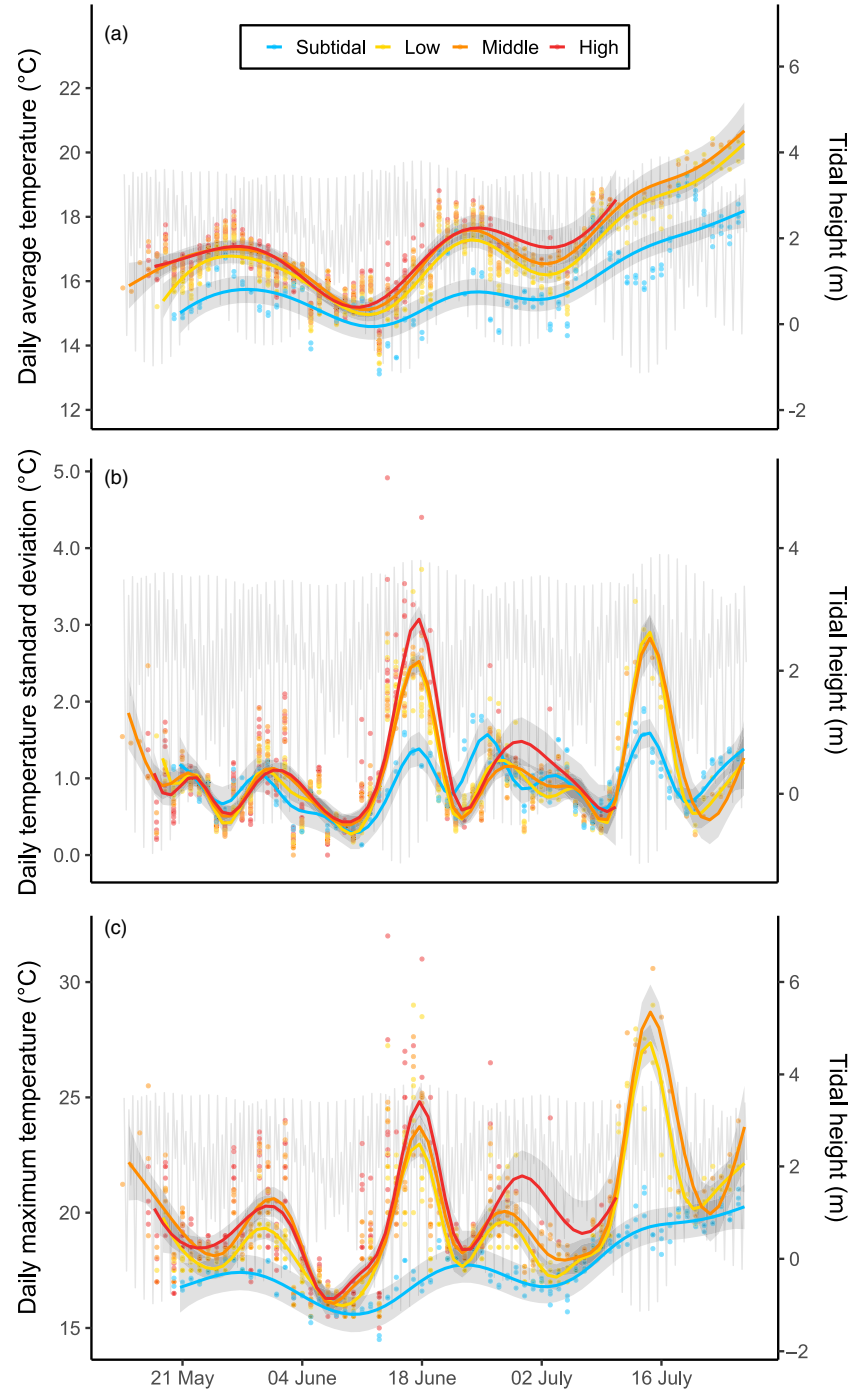
and high contours (est. [95% CI] body condition index scores: high–middle = −0.035 [−0.112 to 0.042]; middle–low = −0.054 [−0.137 to 0.028]; LMM, N = 84; elevation: χ^2_2 = 6.3, p = 0.04). Males persisted roughly 2 weeks longer in middle and low elevation nests than did males in high nests (median [IQR] number of days on a nest: high = 29 days [28–30], middle = 43 days [42–45], low = 42 days [35–54]; one-way ANCOVA; elevation: $F_{2,26}$ = 11.7, p < 0.001; initial male condition: $F_{1,26}$ = 5.0, p = 0.034). Body conditions of all guarder males, regardless of intertidal elevation, deteriorated by

approximately 4.3% (95% CI: 3.5%–5.3%) per day (time: χ^2_1 = 71.6, p < 0.001; successive differences contrasts: high–middle: est. [95% CI] = 0.0005% [−0.003%–0.004%] per day, t_{42} = −0.35, p = 0.72; middle–low: est. [95% CI] = 0.0006% [−0.004% to 0.003%] per day, t_{25} = 0.28, p = 0.78; Figure 5).

Development rates were slower among subtidal compared to low intertidal broods, but development rates did not differ clearly across the three intertidal contours (successive differences contrasts; high–middle: est. [95% CI] increase per day = 0.028% [−0.023% to

TABLE 2 Summary of male sizes, body conditions and spawning success among all artificial nests constructed in Experiments 2 and 3 (2018 and 2019 respectively). Male sizes (SL, in mm) and body conditions were calculated from individuals found in each nest. Body condition scores were calculated separately for fish in Experiments 2 and 3; see Section 2 for calculation. *Eggs* refer to brood sizes. Sample sizes (*N*) are in brackets

Tidal elevation	Year	Male SL	Male body condition	Eggs (natural nests)	Eggs (experimental nests)
		Mean $\pm$ *SD* (*N*)	Mean $\pm$ *SD* (*N*)	Median [IQR] (*N*)	Median [IQR] (*N*)
Subtidal	2018	—	—	0 [0–240] (20)[a]	—
Subtidal	2019	237 $\pm$ 22 (28)	0.01 $\pm$ 0.09 (28)	306 [0–706] (28)	—
Low	2018	234 $\pm$ 35 (24)	0.06 $\pm$ 0.11 (24)	1,010 [834–1,890] (8)	128 [61–221] (9)
Middle	2018	215 $\pm$ 35 (37)	0.06 $\pm$ 0.11 (37)	776 [116–1,673] (7)	87 [55–106] (15)
Middle	2019	237 $\pm$ 20 (37)	−0.01 $\pm$ 0.08 (37)	664 [237–1,141] (30)	—
High	2018	212 $\pm$ 29 (25)	0.06 $\pm$ 0.09 (25)	651 [494–1,216] (7)	99 [79–158] (15)

[a]These data were not statistically analysed because we did not capture subtidal males in 2018 and therefore could not account for male size.
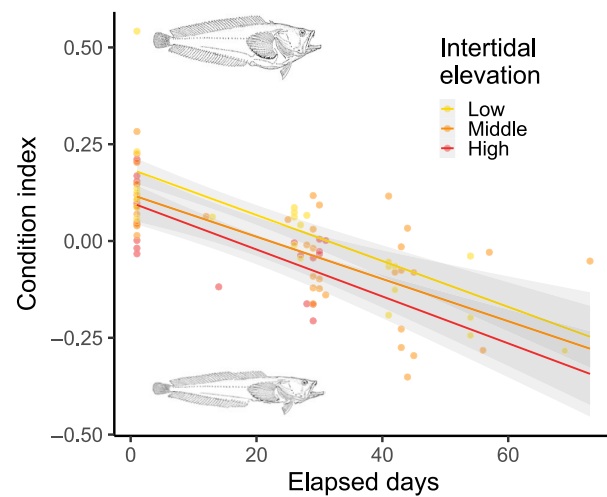

FIGURE 5 Change in body condition of males in experimental nests over the course of Experiment 2. Coloured lines show population-level LMM predictions, and the shaded areas their 95% CIs

0.079%], $t_{76} = 1.1$, $p = 0.27$; middle–low: est. [95% CI] = −0.036% [−0.078% to 0.005%], $t_{76} = −1.8$, $p = 0.083$; low–subtidal: est. [95% CI] = 0.096% [0.052%–0.140%], $t_{76} = 4.3$, $p < 0.001$; Figure 2b).

Broods developing in nests along the high and middle contour perished faster compared to broods in low elevation nests (GLMM, $N = 86$; elevation × time: $\chi_2^2 = 23.6$, $p < 0.001$; post hoc Tukey's HSD: est. [95% CI] middle–low = 3.2% [1.7%–4.7%] per day, $p_{adj} < 0.001$; est. [95% CI] high–middle = −0.4% [−5.4% to 4.3%] per day, $p_{adj} = 0.86$; Figure 3b).

Males in middle and high intertidal nests spent more time providing care compared to males in low intertidal nests (successive differences contrasts: low–middle: est. [95% CI] = −83% [−7% to −97%], $t_{48} = −2.10$, $p = 0.041$; middle–high: est. [95% CI] = −14% [−86% to 406%], $t_{46} = −0.17$, $p = 0.86$). However, neither brood size nor male body size clearly affected the duration of care provisioning (LMM, $N = 48$; brood size: $\chi_1^2 = 1.4$, $p = 0.23$; male size: $\chi_1^2 = 0.38$, $p = 0.54$).

3.3 | Experiment 3

In contrast to Experiment 2 (see above), brood sizes varied clearly between elevations even after accounting for male size. Broods were larger in middle intertidal nests than in subtidal nests in May and even more so in June (middle–subtidal in May: est. [95% CI] = 281 eggs [170–392]; middle–subtidal in June: est. [95% CI] = 437 eggs [168–706]; GLMM, $N = 103$; elevation × month: $\chi_1^2 = 12.0$, $p < 0.001$; male SL: $\chi_1^2 = 19.1$, $p < 0.001$).

Also in contrast to Experiment 2, male sizes did not clearly differ between the two elevation contours in May (subtidal–middle: est. [95% CI] = −6 mm [−18 to 6 mm]), and by June, males nesting in the subtidal appeared slightly larger than males in the middle intertidal (subtidal–middle: est. [95% CI] = 11 mm [−1 to 22 mm]; 2 × 2 factorial ANOVA; elevation × month, $F_{1,99} = 3.88$, $p = 0.052$). Body conditions did not clearly differ between males nesting in the subtidal and middle intertidal zone in May nor in June (2 × 2 factorial ANOVA; elevation: $F_{1,99} = 0.38$, $p = 0.54$; month: $F_{1,99} = 0.74$, $p = 0.39$; elevation × month: $F_{1,99} = 0.04$, $p = 0.84$; Table 2).

The duration of parental care behaviours performed by males in middle intertidal and subtidal nests did not clearly differ across nor within any of the trial periods (GLMM, $N = 72$; elevation: $\chi_2^2 = 0.37$, $p = 0.54$; elevation × trial period: $\chi_2^2 = 3.95$; $p = 0.14$). However, bouts of aggressive behaviour performed by males in subtidal nests were clearly longer by approximately 500% (95% CI: 6–3,301%) compared to the males in middle intertidal nests (LMM, $N = 24$; elevation: $\chi_1^2 = 4.1$, $p = 0.04$).

4 | DISCUSSION

We hypothesized that the best compromise between the costs and benefits of care for male plainfin midshipman when selecting nesting sites would be to nest in the middle intertidal; however, our data suggest that the best reproductive outcomes were realized by males that nested low in the intertidal zone, near the low water line. These males maintained better body conditions and persisted in

their nests for longer compared to males higher up on the tidal gradient. Offspring development rates were faster in intertidal nests than in subtidal nests, and offspring mortality was lowest in low intertidal nests, where males spent the least time providing care.

High rates of nest turnover, as well as the robust correlation between male body size and nest size, indicate that the plainfin midshipman breeding season is rife with male–male competition to control limited high-quality sites (Bose et al., 2014, 2018; DeMartini, 1988, 1991). As nest size was held constant in our study by the use of identical tiles, the presence of the largest males in low intertidal nests suggests competition was most intensive at this elevation (Bose, Borowiec, et al., 2019). It is conceivable that factors other than competition could explain the pattern of size-assortative nesting we observed. For example, if smaller males are less effective at fending off aquatic egg predators, nesting higher on the shore could provide a natural refuge for their broods (Tewksbury & Conover, 1987; Touchon & Worley, 2015). However, males in high intertidal nests are more frequently exposed to avian predation (Houpt, Bose, et al., 2020), and their broods might be exposed to an increase in terrestrial predation as well (Spencer, 2002). Therefore, it is unlikely that the potential benefit to smaller males of nesting high in the intertidal would outweigh the increased mortality risk. Furthermore, newly constructed high intertidal nests are slower to become occupied than nests lower in the intertidal (Bose, Borowiec, et al., 2019). We argue that the large sizes of males in low intertidal nests and the bottom-up pattern of nest residency previously observed reflect a preference for low intertidal sites.

In contrast to our first prediction, we found that body conditions of all males deteriorated at similar rates of ≈4% per day across tidal elevations. Nest emersion, which exposes resident fish to aquatic hypoxia and air (Bose, Borowiec, et al., 2019), occurred more frequently at higher intertidal elevations during our study. Hence, we expected males nesting higher in the intertidal to suffer higher energetic costs compared to males nesting at lower elevations because aquatic hypoxia and air exposure activate energetically inefficient anaerobic metabolism in other nearshore fishes (Boutilier, 2001; Richards, 2009; Speers-Roesch et al., 2013). It is possible that body condition deterioration differences across the tidal gradient do exist, but that the time span of our measurements was too short to capture this decline. The relatively rapid disappearances observed among males nesting high on the beach suggest that they either perished or abandoned their nests (by escaping under the mesh), possibly because of elevated physiological costs of remaining at the nest that we did not capture using a morphometric condition index (Bose, Borowiec, et al., 2019; Green, 2001). However, a recent study demonstrated that plainfin midshipman guarder males do not suffer high physiological disturbances in response to hypoxia and air exposure (Houpt, Borowiec, et al., 2020), which could explain why body condition deterioration rates did not clearly vary between tidal elevations in our study. During the breeding season, guarder males drastically reduce their food consumption or cease feeding altogether (Bose et al., 2016; Cogliati et al., 2015; Sisneros et al., 2009). Therefore, starvation was likely the main driver of the body condition deterioration we observed and affected all males similarly.

We found partial support for our second prediction; abiotic conditions in the intertidal zone were associated with faster development rates compared to subtidal conditions. Exposure to 18°C seawater in the lab dramatically reduced development times of plainfin midshipman young by 68 days compared to those exposed to 13°C seawater. Similarly, development rates in the field were increased by ≈4% per day in intertidal nests compared to subtidal nests. However, development rates varied little across the intertidal gradient. Daily average and maximum temperatures recorded in nests in the field were highest at the high and middle contours—maxima occasionally surpassed 30°C. Such extreme temperatures could have exceeded the thermal optima or tolerance thresholds of plainfin midshipman eggs, which could have temporarily arrested development and caused the higher mortality rates we observed in middle and high contour nests (Eyck et al., 2019). These extreme high temperatures might have negated any benefits accrued from more rapid development rates under higher average temperatures (Kinne & Kinne, 1962; Pörtner & Knust, 2007).

We also hypothesized that both the energetic costs of parental care and the benefits offspring receive from parental care would increase with tidal elevation as abiotic conditions harshen. Hence, we investigated whether males in higher elevation nests would provide more or less care compared to males in lower elevation nests (question 5). When nests were flooded by the returning tide, males in high and middle intertidal nests exhibited longer bouts of egg hygiene and nest maintenance behaviours than males in low nests. In videos recorded during high tides, when intertidal nests had been immersed for several hours or days, egg hygiene and nest maintenance behaviours were rarely observed in both intertidal and subtidal nests, but subtidal males defended their broods more actively against egg predators. When the intertidal zone floods, suspended sediments are added to nests, which likely necessitates parental cleaning to prevent eggs from suffocating (Järvi-Laturi et al., 2008). In contrast, protecting broods from aquatic predators is the primary parental duty at high tides, when suspended sediments are sparse. Subtidal males might be more alert to aquatic egg predators because their broods are constantly vulnerable. These results suggest that parental care was not energetically constrained by nesting in challenging conditions. Instead, plainfin midshipman males seemingly adjust their level of care to meet offspring needs, a strategy where males driven by competition into a harsher nesting environment can make the best of a bad situation (Bonsall & Klug, 2011; MacDonald et al., 1995). Conversely, males that retain low intertidal sites, where conditions are more favourable for their offspring, rear broods with higher survival and lower parental effort (Ens et al., 1992; Järvi-Laturi et al., 2008).

As the summer progresses, air and water temperatures increase in the intertidal and emersion is protracted during spring tides; higher intertidal nests thus become increasingly exposed to extreme temperature events and severe desiccation (Somero, 2002). Nesting in harsher, higher intertidal sites might preclude males from breeding several times but could afford a narrow window of prime breeding early in the season when temperatures are not too high (Candolin &

Voigt, 2003; Cargnelli & Neff, 2006). Capelin *Mallotus villosus* preferentially spawn intertidally until temperatures within spawning sediments exceed 12°C (typically late in summer), at which point they switch to subtidal spawning (Nakashima & Wheeler, 2002). Nesting lower in the intertidal might constitute a reproductive strategy adopted by males in prime condition; by persisting longer on the nest, these males could mate with more females and raise more broods across the entire breeding period (Cargnelli & Neff, 2006; Dickerson et al., 2005; Verboven & Verhulst, 1996). Conversely, smaller males or those in worse condition might need to complete their reproduction quickly and early. In many birds, individuals that arrive earlier in the season attain high quality territories and enhanced breeding success (Becker et al., 2008; Gunnarsson et al., 2008; Kokko, 1999). For example, male collared flycatchers *Ficedula albicollis* exhibit condition-dependent reproductive tactics related to time of arrival at the breeding grounds (Qvarnström, 1999). High-condition males invest heavily in mate attraction early in the season and their later parental care is energetically constrained as a result (Qvarnström, 1997). Female breeding success is enhanced when males provide high quality parental care, so males in relatively poor condition can enhance their attractiveness by arriving early in the season and making greater parental investments (Qvarnström et al., 2000). Thus, plainfin midshipman guarder males might exhibit divergent reproductive strategies, where small males forced into high intertidal nests make the best of a bad situation, whereas larger males compete for nests low in the intertidal and rear more offspring by remaining longer in the breeding grounds.

The vertical zonation of rocky intertidal shorelines has provided one of the most fruitful testbeds for classical ecological theory and climate change effects (Helmuth et al., 2006; Underwood, 2000). In this study, we highlight how steep ecological gradients and the creatures that inhabit them can enrich our understanding of parental care trade-offs. At the narrow interface of land and sea, costs and benefits change dramatically with depth, which allowed us to study parents and offspring under a broad range of conditions at the same site. We were able to simulate the extremities of these conditions in the lab to isolate the abiotic effects on offspring development. Estimating the fitness consequences of intertidal nest site choices across multiple generations remains an important challenge for future research.

AUTHORS' CONTRIBUTIONS
N.A.W.B. and S.B. conceived the project with inputs from F.J. and B.M.B.; N.A.W.B., F.J. and S.B. designed the methodologies; N.A.W.B., S.B., N.S.B.H. and J.E.M.C. conducted field and lab work; J.E.M.C. and N.L.Y. conducted video analyses; N.A.W.B., B.M.B., N.L.Y. and J.E.M.C. analysed the data; N.A.W.B. wrote the first manuscript draft with input from S.B. All authors contributed to subsequent drafts and approved the final version.

DATA AVAILABILITY STATEMENT
Data and R script are available on Dataverse: https://doi.org/10.5683/SP2/XLIM93 (Brown et al., 2020).

ORCID
Nicholas A. W. Brown https://orcid.org/0000-0002-9093-4098
Noah S. B. Houpt https://orcid.org/0000-0003-2696-9058
Benjamin M. Bolker https://orcid.org/0000-0002-2127-0443
Francis Juanes https://orcid.org/0000-0001-7397-0014
Sigal Balshine https://orcid.org/0000-0003-3671-0517

REFERENCES
Batten, S. D., Moffitt, S., Pegau, W. S., & Campbell, R. (2016). Plankton indices explain interannual variability in Prince William Sound herring first year growth. *Fisheries Oceanography*, *25*(4), 420–432. https://doi.org/10.1111/fog.12162

Becker, P. H., Dittmann, T., Ludwigs, J. D., Limmer, B., Ludwig, S. C., Bauch, C., Braasch, A., & Wendeln, H. (2008). Timing of initial arrival at the breeding site predicts age at first reproduction in a long-lived migratory bird. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(34), 12349–12352. https://doi.org/10.1073/pnas.0804179105

Bonsall, M. B., & Klug, H. (2011). The evolution of parental care in stochastic environments. *Journal of Evolutionary Biology*, *24*, 645–655. https://doi.org/10.1111/j.1420-9101.2010.02203.x

Bose, A. P. H., Borowiec, B., Scott, G., & Balshine, S. (2019). Nesting on high: Reproductive and physiological consequences of breeding in the intertidal zone. *Evolutionary Ecology*, *33*(1), 21–36. https://doi.org/10.1007/s10745-006-9094-1

Bose, A. P. H., Cogliati, K. M., Howe, H. S., & Balshine, S. (2014). Factors influencing cannibalism in the plainfin midshipman fish. *Animal Behaviour*, *96*, 159–166. https://doi.org/10.1016/j.anbehav.2014.08.008

Bose, A. P. H., Cogliati, K. M., Luymes, N., Bass, A. H., Marchaterre, M. A., Sisneros, J. A., Bolker, B. M., & Balshine, S. (2018). Phenotypic traits and resource quality as factors affecting male reproductive success in a toadfish. *Behavioral Ecology*, *29*, 496–507. https://doi.org/10.1093/beheco/ary002

Bose, A. P. H., Lau, M. J., Cogliati, K. M., Neff, B. D., & Balshine, S. (2019). Cannibalism of young is related to low paternity and nest takeovers in an intertidal fish. *Animal Behaviour*, *153*, 41–48. https://doi.org/10.1016/j.anbehav.2019.04.018

Bose, A. P. H., McClelland, G. B., & Balshine, S. (2016). Cannibalism, competition, and costly care in the plainfin midshipman fish, *Porichthys notatus*. *Behavioral Ecology*, 27(2), 628–636. https://doi.org/10.1093/beheco/arv203

Boutilier, R. G. (2001). Mechanisms of cell survival in hypoxia and hypothermia. *Journal of Experimental Biology*, 204(18), 3171–3181.

Brantley, R. K., & Bass, A. H. (1994). Alternative male spawning tactics and acoustic signals in the plainfin midshipman fish *Porichthys notatus* Girard (Teleostei, Batrachoididae). *Ethology*, 96, 213–232. https://doi.org/10.1111/j.1439-0310.1994.tb01011.x

Briffa, M., & Sneddon, L. U. (2007). Physiological constraints on contest behaviour. *Functional Ecology*, 21(4), 627–637. https://doi.org/10.1111/j.1365-2435.2006.01188.x

Brown, N. A. W., Houpt, N. S. B., Yee, N. L., Curtis, J., Bolker, B. M., Juanes, F., & Balshine, S. (2020). Data and R script for 'Consequences of nest site selection vary along a tidal gradient'. *Scholars Portal Dataverse*, https://doi.org/10.5683/SP2/XLIM93

Bryan, S. M., & Bryant, D. M. (1999). Heating nest-boxes reveals an energetic constraint on incubation behaviour in great tits, *Parus major*. *Proceedings of the Royal Society B: Biological Sciences*, 266(1415), 157–162. https://doi.org/10.1098/rspb.1999.0616

Candolin, U., & Voigt, H. R. (2003). Size-dependent selection on arrival times in sticklebacks: Why small males arrive first. *Evolution*, 57(4), 862–871. https://doi.org/10.1111/j.0014-3820.2003.tb00297.x

Cargnelli, L. M., & Neff, B. D. (2006). Condition-dependent nesting in bluegill sunfish *Lepomis macrochirus*. *Journal of Animal Ecology*, 75(3), 627–633. https://doi.org/10.1111/j.1365-2656.2006.01083.x

Cogliati, K. M., Danukarjanto, C., Pereira, A. C., Lau, M. J., Hassan, A., Mistakidis, A. F., Bolker, B. M., Neff, B. D., & Balshine, S. (2015). Diet and cannibalism in plainfin midshipman *Porichthys notatus*. *Journal of Fish Biology*, 86(4), 1396–1415. https://doi.org/10.1111/jfb.12649

Cogliati, K. M., Mistakidis, A. F., Marentette, J. R., Lau, A., Bolker, B. M., Neff, B. D., & Balshine, S. (2014). Comparing population level sexual selection in a species with alternative reproductive tactics. *Behavioral Ecology*, 25(6), 1524–1533. https://doi.org/10.1093/beheco/aru147

Cogliati, K. M., Neff, B. D., & Balshine, S. (2013). High degree of paternity loss in a species with alternative reproductive tactics. *Behavioral Ecology and Sociobiology*, 67(3), 399–408. https://doi.org/10.1007/s00265-012-1460-y

Craig, P. M., Fitzpatrick, J. L., Walsh, P. J., Wood, C. M., & McClelland, G. B. (2014). Coping with aquatic hypoxia: How the plainfin midshipman (*Porichthys notatus*) tolerates the intertidal zone. *Environmental Biology of Fishes*, 97(2), 163–172. https://doi.org/10.1007/s10641-013-0137-3

Crespi, B., & Semeniuk, C. (2004). Parent-offspring conflict in the evolution of vertebrate reproductive mode. *The American Naturalist*, 163(5), 635–653. https://doi.org/10.1086/382734

D'Alba, L., Monaghan, P., & Nager, R. G. (2009). Thermal benefits of nest shelter for incubating female eiders. *Journal of Thermal Biology*, 34(2), 93–99. https://doi.org/10.1016/j.jtherbio.2008.11.005

DeMartini, E. E. (1988). Spawning success of the male plainfin midshipman. I. Influences of male body size and area of spawning site. *Journal of Experimental Marine Biology and Ecology*, 121(2), 177–192. https://doi.org/10.1016/0022-0981(88)90254-7

DeMartini, E. E. (1991). Spawning success of the male plainfin midshipman. II. Substratum as a limiting spatial resource. *Journal of Experimental Marine Biology and Ecology*, 146(2), 235–251. https://doi.org/10.1016/0022-0981(91)90028-U

Dickerson, B. R., Brinck, K. W., Willson, M. F., Bentzen, P., & Quinn, T. P. (2005). Relative importance of salmon body size and arrival time at breeding grounds to reproductive success. *Ecology*, 86(2), 347–352. https://doi.org/10.1890/03-625

Doyle, M. J., Mier, K. L., Busby, M. S., & Brodeur, R. D. (2002). Regional variation in springtime ichthyoplankton assemblages in the northeast Pacific Ocean. *Progress in Oceanography*, 53, 247–281. https://doi.org/10.1016/S0079-6611(02)00033-2

Eggers, S., Griesser, M., Nystrand, M., & Ekman, J. (2006). Predation risk induces changes in nest-site selection and clutch size in the Siberian jay. *Proceedings of the Royal Society B: Biological Sciences*, 273(1587), 701–706. https://doi.org/10.1098/rspb.2005.3373

Ens, B. J., Kersten, M., Brenninkmeijer, A., & Hulscher, J. B. (1992). Territory quality, parental effort and reproductive success of oystercatchers (*Haematopus ostralegus*). *Journal of Animal Ecology*, 61(3), 703–715. https://doi.org/10.2307/5625

Eyck, H. J. F., Buchanan, K. L., Crino, O. L., & Jessop, T. S. (2019). Effects of developmental stress on animal phenotype and performance: A quantitative review. *Biological Reviews*, 94(3), 1143–1160. https://doi.org/10.1111/brv.12496

Godfray, H. C. J. (1995). Evolutionary theory of parent-offspring conflict. *Nature*, 376, 133–138. https://doi.org/10.1038/376133a0

Green, A. J. (2001). Mass/length residuals: Measures of body condition or generators of spurious results? *Ecology*, 82(5), 1473–1483. https://doi.org/10.1890/0012-9658(2001)082[1473:MLRMOB]2.0.CO;2

Gunnarsson, T. G., Gill, J. A., Sigurbjörnsson, T., & Sutherland, W. J. (2008). Arrival synchrony in migratory birds. *Nature*, 488, 485–488.

Helmuth, B., Mieszkowska, N., Moore, P., & Hawkins, S. J. (2006). Living on the edge of two changing worlds: Forecasting the responses of rocky intertidal ecosystems to climate change. *Annual Review of Ecology, Evolution, and Systematics*, 37(1), 373–404. https://doi.org/10.1146/annurev.ecolsys.37.091305.110149

Houpt, N. S. B., Borowiec, B. G., Bose, A. P. H., Brown, N. A. W., Scott, G. R., & Balshine, S. (2020). Parental males of the plainfin midshipman are physiologically resilient to the challenges of the intertidal zone. *Physiological and Biochemical Zoology*, 93(2), 111–128. https://doi.org/10.1086/707408

Houpt, N. S. B., Bose, A. P. H., Warriner, T., Brown, N. A. W., Quinn, J. S., & Balshine, S. (2020). Foraging behaviour of four avian species feeding on the same temporarily available prey. *Canadian Journal of Zoology*, 98, 581–590. https://doi.org/10.1139/cjz-2019-0286

Janzen, F. J., & Warner, D. A. (2009). Parent-offspring conflict and selection on egg size in turtles. *Journal of Evolutionary Biology*, 22(11), 2222–2230. https://doi.org/10.1111/j.1420-9101.2009.01838.x

Järvi-Laturi, M., Lehtonen, T. K., Pampoulie, C., & Lindström, K. (2008). Paternal care behaviour of sand gobies is determined by habitat related nest structure. *Behaviour*, 145(1), 39–50. https://doi.org/10.1163/156853908782687197

Jørgensen, B. (1987). Exponential dispersion models. *Journal of the Royal Statistical Society, Series B*, 49(2), 127–162. Retrieved from https://www.jstor.org/stable/2345415

Kinne, O., & Kinne, E. M. (1962). Rates of development in embryos of a cyprinodont fish exposed to different temperature-salinity-oxygen combinations. *Canadian Journal of Zoology*, 40, 231–253. https://doi.org/10.1139/z62-025

Klimogianni, A., Koumoundouros, G., Kaspiris, P., & Kentouri, M. (2004). Effect of temperature on the egg and yolk-sac larval development of common Pandora, *Pagellus erythrinus*. *Marine Biology*, 145(5), 1015–1022. https://doi.org/10.1007/s00227-004-1382-y

Kokko, H. (1999). Competition for early arrival in migratory birds. *Journal of Animal Ecology*, 68, 124–940–950. https://doi.org/10.1046/j.1365-2656.1999.00343.x

MacDonald, J. F., Bekkers, J., MacIsaac, S. M., & Blouw, D. M. (1995). Intertidal breeding and aerial development of embryos of a stickleback fish (*Gasterosteus*). *Behaviour*, 132(15), 1183–1206.

Magnhagen, C. (1991). Predation risk as a cost of reproduction. *Trends in Ecology & Evolution*, 6(6), 183–186. https://doi.org/10.1016/0169-5347(91)90210-O

Marshall, D. J., & Uller, T. (2007). When is a maternal effect adaptive? *Oikos*, 116(12), 1957–1963. https://doi.org/10.1111/j.2007.0030-1299.16203.x

Mayhew, P. J. (2001). Herbivore host choice and optimal bad mother-hood. *Trends in Ecology & Evolution*, *16*(4), 165–167. https://doi.org/10.1016/S0169-5347(00)02099-1

Nakashima, B. S., & Wheeler, J. P. (2002). Capelin (*Mallotus villosus*) spawning behaviour in Newfoundland waters – The interaction between beach and demersal spawning. *ICES Journal of Marine Science*, *59*(5), 909–916. https://doi.org/10.1006/jmsc.2002.1261

Parker, G. A., Royle, N. J., & Hartley, I. R. (2002). Intrafamilial conflict and parental investment: A synthesis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *357*(1419), 295–307. https://doi.org/10.1098/rstb.2001.0950

Pörtner, H. O., & Knust, R. (2007). Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science*, *315*(5808), 95–97. https://doi.org/10.1126/science.1135471

Qvarnström, A. (1997). Experimentally increased badge size increases male competition and reduces male parental care in the collared flycatcher. *Proceedings of the Royal Society B: Biological Sciences*, *264*(1385), 1225–1231. https://doi.org/10.1098/rspb.1997.0169

Qvarnström, A. (1999). Different reproductive tactics in male collared fly-catchers signalled by size of secondary sexual character. *Proceedings of the Royal Society B: Biological Sciences*, *266*(1433), 2089–2093. https://doi.org/10.1098/rspb.1999.0892

Qvarnström, A., Pärt, T., & Sheldon, B. C. (2000). Adaptive plasticity in mate preference linked to differences in reproductive effort. *Nature*, *405*(6784), 344–347. https://doi.org/10.1038/35012605

R Core Team. (2016). *R: A language and environment for statistical computing* (3.3.1). R Foundation for Statistical Computing.

Refsnider, J. M., & Janzen, F. J. (2010). Putting eggs in one basket: Ecological and evolutionary hypotheses for variation in oviposition-site choice. *Annual Review of Ecology, Evolution, and Systematics*, *41*(1), 39–57. https://doi.org/10.1146/annurev-ecolsys-102209-144712

Richards, J. G. (2009). Chapter 10 metabolic and molecular responses of fish to hypoxia. In J. G. Richards, A. P. Farrell, & C. J. Brauner (Eds.), *Hypoxia* (Vol. 27, pp. 443–485). Academic Press. https://doi.org/10.1016/S1546-5098(08)00010-1

Saino, N., Romano, M., Ambrosini, R., Rubolini, D., Boncoraglio, G., Caprioli, M., & Romano, A. (2012). Longevity and lifetime reproductive success of barn swallow offspring are predicted by their hatching date and phenotypic quality. *Journal of Animal Ecology*, *81*(5), 1004–1012. https://doi.org/10.1111/j.1365-2656.2012.01989.x

Schielzeth, H., & Forstmeier, W. (2009). Conclusions beyond support: Overconfident estimates in mixed models. *Behavioral Ecology*, *20*(2), 416–420. https://doi.org/10.1093/beheco/arn145

Schulte-Hostedde, A. I., Zinner, B., Millar, J. S., & Hickling, G. J. (2005). Restitution of mass-size residuals: Validating body condition indices. *Ecology*, *86*(1), 155–163. https://doi.org/10.1890/04-0232

Sisneros, J. A., Alderks, P. W., Leon, K., & Sniffen, B. (2009). Morphometric changes associated with the reproductive cycle and behaviour of the intertidal-nesting, male plainfin midshipman *Porichthys notatus*. *Journal of Fish Biology*, *74*(1), 18–36. https://doi.org/10.1111/j.1095-8649.2008.02104.x

Somero, G. N. (2002). Thermal physiology and vertical zonation of intertidal animals: Optima, limits, and costs of living. *Integrative and Comparative Biology*, *42*(4), 780–789. https://doi.org/10.1093/icb/42.4.780

Speers-Roesch, B., Mandic, M., Groom, D. J. E., & Richards, J. G. (2013). Critical oxygen tensions as predictors of hypoxia tolerance and tissue metabolic responses during hypoxia exposure in fishes. *Journal of Experimental Marine Biology and Ecology*, *449*(2013), 239–249. https://doi.org/10.1016/j.jembe.2013.10.006

Spencer, R. J. (2002). Experimentally testing nest site selection: Fitness trade-offs and predation risk in turtles. *Ecology*, *83*(8), 2136–2144. https://doi.org/10.1890/0012-9658(2002)083[2136:ETNSSF]2.0.CO;2

Tewksbury, H. T. I., & Conover, D. O. (1987). Adaptive significance of intertidal egg deposition in the Atlantic silverside *Menidia menidia*. *Copeia*, *1987*(1), 76–83. https://doi.org/10.2307/1446040

Touchon, J. C., & Worley, J. L. (2015). Oviposition site choice under conflicting risks demonstrates that aquatic predators drive terrestrial egg-laying. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1808), 20150376. https://doi.org/10.1098/rspb.2015.0376

Trivers, R. L. (1974). Parent-offspring conflict. *American Zoologist*, *264*, 249–264. https://doi.org/10.1093/icb/14.1.249

Underwood, A. J. (2000). Experimental ecology of rocky intertidal habitats: What are we learning? *Journal of Experimental Marine Biology and Ecology*, *250*(1–2), 51–76. https://doi.org/10.1016/S0022-0981(00)00179-9

Verboven, N., & Verhulst, S. (1996). Seasonal variation in the incidence of double broods: The date hypothesis fits better than the quality hypothesis. *Journal of Animal Ecology*, *65*(3), 264–273. https://doi.org/10.2307/5873

Warkentin, K. M. (1995). Adaptive plasticity in hatching age: A response to predation risk trade-offs. *Proceedings of the National Academy of Sciences of the United States of America*, *92*(8), 3507–3510. https://doi.org/10.1073/pnas.92.8.3507

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.