

# Land colonisation by fish is associated with predictable changes in life history

Edward R. M. Platt<sup>1</sup> · Ashley M. Fowler<sup>2</sup> · Terry J. Ord<sup>1</sup>

Received: 17 June 2015 / Accepted: 17 February 2016 / Published online: 1 March 2016  
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**Abstract** The colonisation of new environments is a central evolutionary process, yet why species make such transitions often remains unknown because of the difficulty in empirically investigating potential mechanisms. The most likely explanation for transitions to new environments is that doing so conveys survival benefits, either in the form of an ecological release or new ecological opportunity. Life history theory makes explicit predictions about how traits linked to survival and reproduction should change with shifts in age-specific mortality. We used these predictions to examine whether a current colonisation of land by fishes might convey survival benefits. We found that blenny species with more terrestrial lifestyles exhibited

faster reproductive development and slower growth rates than species with more marine lifestyles; a life history trade off that is consistent with the hypothesis that mortality has become reduced in younger life stages on land. A plausible explanation for such a shift is that an ecological release or opportunity on land has conveyed survival benefits relative to the ancestral marine environment. More generally, our study illustrates how life history theory can be leveraged in novel ways to formulate testable predictions on why organisms might make transitions into novel environments.

**Keywords** Age-specific mortality · Blenny · Gonad development · Trade-offs · Ecological release

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Communicated by Steve Swearer.

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*Highlighted student paper* We use the study of life history in a novel way to investigate the potential consequences of the colonisation of a novel habitat. Much has been made of how transitions into new environments promote adaptive evolution and speciation but our understanding of why organisms make these transitions in the first place is far more limited. Our study provides a unique perspective on this question by leveraging an extraordinary vertebrate example of a major ecological transition: the colonisation of land by marine fish.

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**Electronic supplementary material** The online version of this article (doi:10.1007/s00442-016-3593-6) contains supplementary material, which is available to authorized users.

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✉ Terry J. Ord  
t.ord@unsw.edu.au

<sup>1</sup> Evolution and Ecology Research Centre and the School of Biological, Earth and Environmental Sciences, University of New South Wales, Kensington, NSW 2052, Australia

<sup>2</sup> School of Life Sciences, University of Technology Sydney, Ultimo, NSW 2007, Australia

## Introduction

It is now well established that the colonisation of novel environments can be a vital ingredient for adaptation and potential speciation. This is because new environments frequently result in new selection pressures that can stimulate adaptive differentiation among populations (e.g. Münzing 1963; Rainey and Travisano 1998; Kornfield and Smith 2000; Streebman and Danley 2003; Rundle and Schluter 2004; Arbogast et al. 2006). However, why organisms should make the transition into a new environment in the first place—especially one that is drastically different in its biotic or abiotic conditions—remains an open question. At a general level, ecological release or ecological opportunity are two hypotheses for why an organism might colonise a novel environment: the new environment offers reduced predation or competition for resources (an ecological release), or the new environment offers new resources that are absent or rare in the ancestral environment, respectively (an ecological opportunity; Wilson 1961; Lister 1976;

Jeffries and Lawton 1984; Losos and Mahler 2010). In both cases, the new environment offers an improved chance of survival.

The colonisation of land from an aquatic environment arguably represents one of the most dramatic ecological transitions possible given the distinct change in conditions experienced. In the case of fish, there are a number of groups that have—or are in the process of—colonising land (Sayer and Davenport 1991). These fishes have been the focus of numerous physiological and morphological studies of the adaptations required for a successful transition to land (reviewed by Sayer 2005; Gibb et al. 2013; Pace and Gibb 2014; Martins 2014, 2015). However, the question remains why present-day fish so well adapted to one environment (water) would make the shift into such a vastly different environment (land) (Sayer and Davenport 1991; Vermeij and Dudley 2000; Graham and Lee 2004). Amphibious behaviour in extant fish living in closed water bodies (e.g. ponds, small lakes) might be explained by abiotic factors such as adverse fluctuations in water temperature or chemistry that push fish to temporarily strand themselves on land (Sayer and Davenport 1991; Martins 2014). Such fluctuations in abiotic factors are probably less acute in open marine environments and subsequently less likely to explain why many marine fish initially moved onto land. Instead, the best explanations centre on factors relating to a release from predation or competition or some new opportunity found only on land (Sayer and Davenport 1991; Bhikajee and Green 2002; Shimizu et al. 2006).

If ecological release or ecological opportunity prompted present-day marine fish to make the transition onto land, then this presumably resulted in increased survival for land fish compared to their marine relatives. Quantifying changes in survival directly is difficult without long-term study, but its signature should be apparent in differences in life history among taxa that can be measured over the short term. In particular, there is an extensive body of life history theory that predicts how organisms should balance growth and reproduction depending on the probable survival of different age classes in a given environment (Gadgil and Bossert 1970; Stearns 1976; Law 1979; Michod 1979;

Stearns 1992). By comparing life history strategies among closely related species, it might be possible to reveal how settlement on land could have improved survival.

Classic life history theory works on the assumption that organisms have a fixed amount of energy at any one point in time that must be split between characteristics that promote survival or reproduction (Gadgil and Bossert 1970). For example, allocating resources to reproduction will necessarily divert resources away from growth (Stearns 1992). Natural selection is expected to generate a balance in this allocation of resources that maximises the cumulative fitness of an organism over its lifetime (Smith and Fretwell 1974). Theory shows that this optimum balance in energy allocation depends on the probability of survival at different stages of an organism's lifetime (Gadgil and Bossert 1970; Pianka and Parker 1975; Law 1979). Investment in current reproduction will also come at the expense of future survival [and consequently future reproduction (Pianka and Parker 1975)]. This leads to several predictions for how investment in reproduction (current versus future) should change as the chance of survival at a given age shifts for individuals within a population or species (Gadgil and Bossert 1970; Law 1979; Michod 1979; Hutchings 1993).

Age-dependent survival takes two general forms (Gadgil and Bossert 1970; Taylor et al. 1974; Law 1979; Michod 1979; Hutchings 1993): survival declines with age (e.g. the probability of survival is higher for younger individuals compared to older individuals in the population), or survival increases with age (e.g. mortality is higher in younger individuals compared to older individuals). In principle, a third scenario is also possible in which survival is not age dependent and all age classes have an equal probability of survival. In the context of the colonisation of land by fish, Table 1 summarises the expected change in life history under each of these three scenarios as the probability of survival improves in certain age classes as species move from an aquatic to terrestrial environment.

In general, theory predicts that reproduction should be concentrated in age classes that experience increased survivorship (Michod 1979). For example, if improvements in survival following the colonisation of land were largely

**Table 1** Predicted changes to age-specific survival and life history following the colonisation of land by fish

| Scenario   | Expected change in life history   |             |                         |                         |  |
|--|---|-------------|-------------------------|-------------------------|--|
|  | Reproductive effort   | Growth rate | Egg number              | Egg size                |  |
| 1. Early age survival increases relative to older ages | Increases   | Decreases   | No change, or increases | No change, or decreases |  |
| 2. Older age survival increases relative to early ages | Decreases   | Increases   | No change, or decreases | No change or increases  |  |
| 3. Survival increases uniformly across age classes     | No change, or increase if survival increases because of resource availability | No change   | Increases               | Decreases               |  |

confined to younger age classes (Scenario 1; Table 1), then land species should concentrate reproduction in these earlier life stages and emphasize current reproduction over future reproduction (high reproductive effort) at the expense of growth rate (Gadgil and Bossert 1970; Pianka and Parker 1975; Law 1979; Michod 1979; Hutchings 1993). In contrast, if improvements in survival were largely confined to older age classes in the population (Scenario 2; Table 1), then investment in reproduction should be concentrated in older individuals and growth rate should generally be higher (Gadgil and Bossert 1970; Law 1979; Michod 1979; Hutchings 1993). This emphasis on growth occurs because an individual would do better to invest more in growth and delay reproduction to later in life to increase the chances of surviving through the earlier (higher mortality) life stages (Gadgil and Bossert 1970; Pianka and Parker 1975; Law 1979). It is also possible—although probably rare in nature—that survival following the colonisation of land increased uniformly for all age classes (Scenario 3; Table 1; Law 1979). In this scenario, the optimum distribution of reproductive effort (emphasis on current or future reproduction) should not have changed among aquatic and terrestrial fish, and life history strategies would be broadly consistent among species (Gadgil and Bossert 1970; Taylor et al. 1974; Law 1979; Michod 1979). The only circumstance where life history would differ among species would be where all age classes had increased survival on land specifically because of greater resource availability (i.e. because of an ecological opportunity on land). If so, this should have resulted in higher reproductive effort across all reproductive ages in land species, with little or no compromise in growth rate (Gadgil and Bossert 1970; Table 1).

Finally, in addition to the broad trade-off between reproduction and survival, there is another classic life history trade-off between the size and number of offspring produced. In general, an increase in an individual offspring's size will improve its chance of survival (Smith and Fretwell 1974), but offspring size comes at the expense of the number of offspring that can be produced (Smith and Fretwell 1974). How offspring size improves an individual offspring's chance of survival is predicted to be a result of either improving competitive ability, or by reducing the duration of time spent in an early vulnerable life history stage (Smith and Fretwell 1974; Brockelman 1975; Sibly and Calow 1983; Hutchings 1991). If the ecological release or opportunity associated with the transition onto land improved early age survival (Scenario 1; Table 1), either by reducing competition, predation, or increasing resource availability, then those species on land should produce a higher number of offspring at the cost of size (Smith and Fretwell 1974; Sibly and Calow 1983). A matching outcome is expected if the move onto land improved survival across all age classes (Scenario 3; Table 1), because the

absolute value of early age survival should still increase. These expectations are based on the assumption that higher resources, or lower competition or predation, should reduce the selective pressure for competitive ability in offspring, increasing the benefits of having a higher number of offspring at the expense of offspring size (Smith and Fretwell 1974; Brockelman 1975; Sibly and Calow 1983; Hutchings 1991). If this was not the case, then we expect little change in offspring (egg) size and number with the transition onto land.

Using the predictions from life history theory presented in Table 1, we evaluated the evidence for predictable changes in life history among several closely related tropical species of fish from the family Blenniidae. Within this family, there are species that remain in the ancestral marine environment, species that exhibit varying degrees of amphibious behaviour, and species that spend their entire adult life out of the water on rocks in the splash zone (Patzner et al. 2009; Hsieh 2010; Ord and Hsieh 2011; Morgans and Ord 2013). In the latter case of land blennies, these fish are exceptional in their degree of terrestrially: they are highly agile on land (Hsieh 2010), actively avoid immersion and track changes in tide level to remain above the waterline (Ord and Hsieh 2011), and appear to spend the vast majority of their adult life out on the rocks in the splash zone (Ord and Hsieh 2011). Past studies have examined a range of respiratory, metabolic and locomotor characteristics of amphibious blennies in terrestrial environments in an effort to understand *how* fish make the transition to land (e.g. Martin and Lighton 1989; Brown et al. 1992; Rozemeijer and Plaut 1993; Hsieh 2010; Dabruzzi et al. 2011). The focus of our study was to provide a first look into *why* fish might colonise land. To this end, we used the variation in amphibious behaviour among species within the Blenniidae to examine how life history characteristics might have changed following the progressive colonisation of land by fish, and the extent that this major ecological transition might have been associated with changes in survival, consistent with an ecological release or new ecological opportunities on land.

To this end, we examined species representing the marine, amphibious and terrestrial life styles from the island of Guam to obtain data on reproductive investment, growth rate, egg number and egg size. Changes in these characteristics with the progressive transition onto land that matched those outlined in Table 1 would provide general support for the expected improvements in survival for fish on land. Future study would then be justified in attempting to document the specific changes in age-specific survival, and whether the colonisation of land has been associated with factors related to an ecological opportunity or release [e.g. a change in the availability of key resources or likelihood of predation (see Platt and Ord 2015)]. However, if

life history characteristics were broadly consistent among blenny species, or differed among species in a pattern unrelated to their degree of terrestriality, then this would suggest that fish made the transition onto land in response to factors other than an ecological release or ecological opportunity [e.g. to escape adverse fluctuations in the abiotic conditions of aquatic environments (see Martins 1996)].

## Materials and methods

### Specimen collection

We obtained live-caught specimens over a broad range of body sizes for five blenny species exhibiting different levels of terrestriality on the island of Guam: *Alticus arnoldorum* (terrestrial), *Entomacrodus striatus* (highly amphibious), *Prealticus labrovittatus* (mildly amphibious), *Prealticus poptae* (mildly amphibious), and *Istiblennius lineatus* (largely marine). Opportunistic sampling of a limited number of females for a sixth species, *Istiblennius edentulus* (largely marine), was also made and included in our analyses but was not a main focus of our study. Sample sizes for each life history characteristic varied depending on the number of available specimens. Sample sizes are given in Table S1 (Online Resource) and ranged from 14 to 46 fish for each of the five focal species. Specimens examined and reported in Table S1 (Online Resource) comprised juveniles, immature females and mature females; this emphasis on females was because they were the sex most likely to exhibit the strongest trade-off between growth and reproduction. Categorization of lifestyle (degree of terrestriality) was based on detailed observations of behaviour during this study (see also Morgans and Ord 2013). The predominantly marine species (*Istiblennius* spp.) were typically observed in water (e.g. swimming in large rock pools in the inter-tidal zone at low tide). Mildly amphibious species (*Prealticus* spp.) were frequently observed immersed in rock pools above the tide waterline, but attempted to escape capture by hopping out of the water and across exposed rocks to other rock pools or open water. The highly amphibious species (*Entomacrodus striatus*) was similar to other amphibious species in being found immersed in rock pools, but were also frequently found on exposed rocks or in rock holes above the waterline. The terrestrial species (*Alticus arnoldorum*) was the only fish that remained exclusively out of the water at all times.

The phylogenetic relationships of sampled species are given in Fig. S1 (Online Resource; Cooke and Ord, unpublished data) and showed that species exhibiting the same lifestyle are closely related (Fig. S1 also depicts the relative

sizes of each species; see also Table S1, Online Resource). We subsequently viewed species within the same lifestyle category as ecological replicates (with species identity included as a random effect in our analyses; see “[Statistical analyses](#)” below) rather than independent evolutionary origins of a given lifestyle. Importantly, the progressive colonization of land was less dependent on phylogeny: the highly amphibious species was more closely related to marine species than the exclusively terrestrial species, while the mildly amphibious species were more closely related to the exclusively terrestrial species than the marine species (Fig. S1, Online Resource).

Sampling was conducted by hand using aquaria nets at seven locations around the island: Pago Bay (13°25'39"N, 144°47'56"E), Taga'chang (13°24'16"N, 144°46'53"E), Talofofu (13°20'34"N, 144°46'21"E), Umatac (13°17'40"N, 144°39'29"E), Inarajan (13°16'18"N, 144°44'53"E), Tangisson (13°32'43"N, 144°48'32"E), and Adelup Point (13°28'52"N, 144°43'44"E). Our sampling was conducted in July 2012 and fell within the known breeding period for blenny genera in the region (marine and terrestrial), which is April–September (Carlson 1992; Sunobe et al. 1995; Shimizu et al. 2006; Ord and Hsieh 2011). Collections were made along transects that traversed the water–land interface from below the waterline in the intertidal zone to above the waterline in rock pools and exposed rocks in the supralittoral splash zone. Once caught, fish were euthanised and then preserved in 10 % neutral-buffered formalin.

### Body measurements and dissections

Standard length, body weight, and gonad weight were recorded for specimens in the following ways. Standard length was measured as the length (millimetres from the anterior of the upper jaw to the caudal peduncle using digital calipers (>0.03 mm accuracy, 0.01 mm resolution; Traceable Digital Caliper, Control Company). Body weight was measured using a semi-micro analytical balance (model GR-200,  $e = 1$  mg,  $d = 0.1$  mg; A&D) after all surface moisture had been removed from the fish. Specimens were then dissected to confirm sex and to estimate the stage of maturity based on the macroscopic appearance of the gonads (see “[Quantifying egg size and number](#)”). Gonads were then removed, dried of all surface moisture, and weighed to the nearest milligram using the semi-micro analytical balance. In the case of very small gonads (<0.002 g), a Cahn c-33 microbalance was used to obtain a weight to nearest 10  $\mu$ g. Gonads were then stored in 10 % buffered formalin and later used for egg analysis. To age fish, sagittal otoliths were removed, cleaned in distilled water and stored dry in microtubes.

## Determining fish age

Age (in days) was determined by counting the number of microincrements visible in sagittal sections of the right otolith. Microincrements appear as alternating light and dark bands and have been shown to correspond to daily cycles of otolith deposition in nearly all fish species tested (Brothers et al. 1976; Campana and Neilson 1985), including blennies (Hernández-Miranda et al. 2009). While daily deposition of microincrements has yet to be empirically confirmed for the species examined in the current study, the absolute time period is incidental given that it will almost certainly be consistent among the closely related species examined here. Sagittal sections were prepared by mounting the otolith on a microscope slide using thermoplastic cement (CrystalBond 509). The proximal surface of the otolith was then ground down using 3-, 9- and then 12- $\mu\text{m}$  grade lapping film. Once the primordium was reached, the otolith was turned over and the distal surface was ground down to produce a thin (~100–150  $\mu\text{m}$ ) section through the otolith centre (core). Sections were then imaged at 600 $\times$  magnification using an Olympus BX50 microscope connected to an image analysis system (Spot Flex digital camera integrated with Image Pro Plus version 5.1; Media Cybernetics, Rockville, MD). Oil immersion was used to increase the clarity of section images. Microincrements were then counted along a transect extending from the core to the otolith edge. Total counts were made three times until a consistent number was attained (counts differing by no more than three rings). These counts were then averaged to provide a single estimate of age for a given fish (corresponding to the number of days post-hatch). In one or two cases for some species, a consistent count could not be obtained and these individuals were excluded from subsequent age analyses.

## Quantifying egg size and number

The development stage, size and number of eggs were measured from one ovary for at least 14 of the largest females per species (Table S1, Online Resource). Egg staging was used to ensure that differences in egg size and number between species reflected factors of interest, and not simply differences in brood cycles (see Table S2, Online Resource).

Using a dissecting microscope (Olympus BX50), eggs were first separated from the ovarian tissue in a petri dish using a probe and dilute soapy water to keep eggs separated. Egg developmental stage was then determined for a subsample (40–50 eggs) representing every size and phenotype found in the ovary. These eggs were imaged at 63 $\times$  magnification and then classified into one of five developmental stages [based on Selman et al. (1993), Tyler

and Sumpter (1996), Clelland et al. (2007) and Núñez and Duponchelle (2009); see criteria outlined in Table S2, Online Resource]: stage I (primary growth), stage II (cortical alveolus stage), stage III (vitellogenesis), stage IV (a combination of maturation/mature), and stage V (atresia; very few eggs were found in this stage).

The subsamples were then grouped with the rest of the eggs and light threshold functions applied by the image analysis software (Image Pro Plus) were used to compute the size and number of all eggs within the ovary of each individual. Thresholds were first used to filter out non-egg objects, such as ovarian tissue. This was done manually by observing images and varying threshold settings such that the exclusion of non-egg material was maximized without inadvertent loss of actual eggs. After initial filtering, the mean diameter of each remaining object (egg) was measured using the image software (diameters were in micrometres based on image calibration). The size range of eggs classified by developmental stage for a particular individual was then used to help identify ‘developmental cohorts’ in a frequency distribution of all the eggs found in the ovary. These cohorts were subsequently used to determine the number and mean size of eggs in each developmental stage. This approach was used instead of attempting to measure egg number from laid clutches in the wild because blennies deposit eggs across multiple clutches in a laying period (Bhikajee and Green 2002; Shimizu et al. 2006). Indeed, our examination of eggs in the latest development stage (IV) supported females laying eggs across multiple clutches (see “Statistical analyses” below). Any measure of egg number from individual clutches would therefore obscure the true developmental relationship between egg number and size that is predicted by theory (Smith and Fretwell 1974) and that is relevant for our study (i.e. the total number of eggs in a given developmental stage relative to the ultimate size those eggs will achieve immediately before laying).

Given eggs were only removed from one ovary; total egg number for a female was estimated by calculating the number of eggs per unit mass of the ovum examined, multiplied by the total ovarian weight (i.e. the combined weight of both ovaries).

## Statistical analyses

Unless stated otherwise, statistical comparisons were performed using mixed-model multivariate regressions in the lme4 package, version 0.99999911-8 (Bates 2008) implemented in R version 2.15.3 (R Development Core Team, R Foundation for Statistical Computing, Vienna). These analyses tested the extent that progressive increases in terrestriality (the factor Lifestyle, coded as 0 for largely marine, 1 for mildly amphibious, 2 for highly amphibious, and 3 for terrestrial)

were associated with progressive changes in life history characteristics. We chose not to focus on phylogenetic analyses when applying statistical tests for two reasons. First, the number of species examined, and their overall distribution across the blenny phylogeny as a whole (e.g. see Morgans and Ord 2013), made the estimate of phylogenetic structure in the data poor and essentially meaningless (e.g. the estimated phylogenetic signal in data converged on zero in all cases; see Table S4, Online Resource). Second, and more importantly, the direct inclusion of biologically relevant random effects was difficult in phylogenetic regressions and these random effects were expected to have potentially important impacts on final parameter estimates (see below). While we report the outcome of phylogenetic regressions in Table S4 (Online Resource), we do so largely for completeness and as a general confirmation of the main results obtained from the analyses described below (in all cases, results were qualitatively equivalent).

#### *Growth rate*

Growth for each species was initially modelled separately to determine the best model for describing growth rate for each species. This was done by regressing standard length on total microincrement count (age) using several different regression functions (linear, natural log linear, quadratic and power). The power function was consistently found to be the best-fitting model for all species (based on  $r^2$ -values). Length data for juveniles, immature females, and females for all species were subsequently entered into a multivariate power function with a random effect for species and fixed effects for age, lifestyle and an age by lifestyle interaction. This interaction specifically tested for differences in growth rate among species as a function of the level of terrestriality exhibited.

#### *Reproductive investment*

A linear regression of natural log-transformed ovarian weight on natural log-transformed standard length was used to quantify the relative investment of tissue for reproduction as a function of terrestriality (lifestyle). This analysis was performed using data on juveniles, immature females and females, and used a regression model with a random effect for species and fixed effects for standard length, lifestyle and their interaction. This model estimated the proportion of body weight dedicated to reproductive tissue among species exhibiting different degrees of terrestriality (represented by the intercept values) and the rate at which reproductive tissue developed in those species (represented by the slope value).

To assess the impact of any difference in the maturity of individuals that happened to be surveyed for a given species, a second more complex model was applied that included an additional random effect for the estimated

reproductive status of each female. Reproductive status was determined by the latest developmental stage of eggs found in ovaries for those females examined in egg analyses (see “[Quantifying egg size and number](#)”) or by detailed descriptions of ovaries noted during the initial dissection of the gonads (N.B. this latter classification was validated by cross-referencing ovary descriptions for females that had also been subject to detailed egg analysis).

#### *Egg size and number*

Total number of eggs likely to be laid during the breeding season was measured as the number of eggs found in the developmental stage that had the largest number of eggs. This was done instead of simply counting all the eggs found in the ovary (irrespective of development stage) because females were collected during the breeding period (see “[Specimen collection](#)” above) and may have already started to lay eggs prior to capture (this was especially likely for eggs in the latest developmental stage, stage IV; see Table S2, Online Resource). The number of eggs in earlier developmental stages, however, reflected the number that would ultimately be laid over an egg-laying period in the near future. This means that the largest number of eggs found in any developmental stage represented the largest number of eggs that a particular female was likely to lay in a given laying period. Using this estimate of egg number removed the potential confound on egg number if a female had started to lay, and also controlled for differences in the reproductive status of females that might also occur among species (due to seasonal effects).

Egg number was natural log transformed to improve normality, and data for all species were entered into a regression model with a random effect for species and fixed effects for standard length (natural log transformed), lifestyle and their interaction. In this model, intercept values corresponded to the relative number of eggs produced among species exhibiting different degrees of terrestriality, while slope values measured the relative rate of egg production among those species.

Egg size on laying was determined by modelling the trajectory of egg development within females using a regression of natural log-transformed egg size on egg development stage. Here, all species were entered into a single regression with a random effect for species and fixed effects for egg development stage, standard length and lifestyle, with separate interactions between lifestyle, egg stage and length. In this model, intercept values measured the relative size of eggs among species, while the slope value of egg stage measured the rate of development of eggs. Differences in egg size and development by body size were controlled for by the covariate of standard length entered into the model. Given that standard length was not found to be a significant predictor of egg size or development, a second

analysis was performed with standard length removed to provide more accurate parameter estimates of the relationship between lifestyle and egg size and development.

*Life history trade-offs*

Finally, the trade-offs predicted by life history theory between growth and reproduction (Stearns 1992), and between offspring size and number (Smith and Fretwell 1974), were examined by correlating the relevant parameter estimates computed from regression models described above using a Pearson correlation. N.B. we used these computed parameter values rather than raw means because the parameter values explicitly controlled for body size and differences in maturity among species.

**Results**

**Life history variation as a function of terrestriality**

*Growth and ovary development*

There was a significant interaction between age and lifestyle that indicated growth rate progressively decreased in species with an increasingly terrestrial lifestyle (Fig. 1; Table 2). Conversely, there was an increase in the rate of

ovarian weight gain with an increasingly terrestrial lifestyle (Fig. 2b, lower panel; Table 2). This latter pattern was consistent regardless of whether the maturity of individuals within species was controlled for or not (Tables 2B, S3A, Online Resource). This implies there has been a shift towards earlier sexual maturity as blennies have moved from a marine environment to one on land.

*Egg number and size*

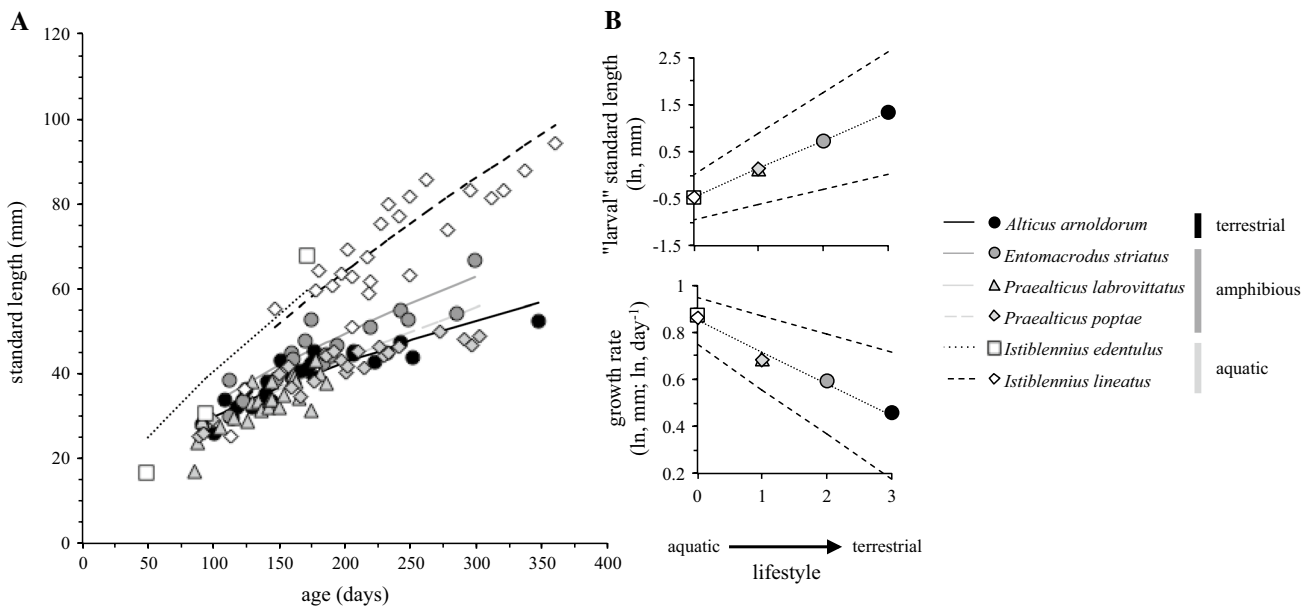
Egg number increased significantly with body size such that differences in egg number among species could be entirely attributed to differences in overall body size (Fig. 3; Table 2). Lifestyle had no impact on the number of eggs produced.

The only factor predicting egg size was the developmental stage of eggs, with eggs becoming increasingly larger at each developmental stage. Neither body size nor lifestyle accounted for any variance in egg size among species (Fig. 4; Table 2). Lifestyle continued to have low predictive power in a model with body size removed (Table S3B, Online Resource).

**Trade-offs between life history characteristics**

*Growth versus reproduction*

There was a prominent, negative relationship between growth rate and the rate of ovarian development



**Fig. 1** Female growth rate among blennies that vary in degree of terrestriality (**a**;  $n_{\text{observations}} = 119$ ,  $n_{\text{species}} = 6$ ). Age was measured as the total number of microincrements in an individual’s otolith. **b** Also shown are species coefficients computed from the fitted model reported in Table 2. Dashed lines around coefficients represent 95 % confidence intervals. Symbols are shaded according to species life-

style, from *white* (aquatic) to *black* (terrestrial). N.B. larvae size was not measured directly and values shown in the upper panel of **b** are the intercept values computed from growth curves in **a**. The extent to which these values reflect actual larvae sizes on hatching is unknown and we make no interpretation of their relationship with lifestyle, as a consequence

**Table 2** Variation in life history among blenny species as a function of lifestyle and other factors

| Variable                                  | $\beta$ | 95 % CI (lower, upper) | <i>t</i> |
|---|---------|------------------------|----------|
| <b>Growth rate</b>                        |         |                        |          |
| Intercept                                 | -0.47   | -0.95, 0.01            | -1.93    |
| Age                                       | 0.85    | 0.75, 0.95*            | 16.81    |
| Lifestyle                                 | 0.60    | 0.33, 0.87*            | 4.28     |
| Age $\times$ lifestyle                    | -0.13   | -0.19, -0.07*          | -4.62    |
| <i>n</i> <sub>observations, species</sub> | 119, 6  |                        |          |
| <b>Reproductive effort</b>                |         |                        |          |
| Intercept                                 | -17.69  | -23.19, -12.19*        | -6.31    |
| Length                                    | 3.85    | 2.60, 5.10*            | 6.03     |
| Lifestyle                                 | -7.61   | -11.71, -3.51*         | -3.64    |
| Length $\times$ lifestyle                 | 1.95    | 0.96, 2.94*            | 3.85     |
| <i>n</i> <sub>observations, species</sub> | 161, 6  |                        |          |
| <b>Egg number<sup>a</sup></b>             |         |                        |          |
| Intercept                                 | -3.30   | -6.77, 0.17            | -1.87    |
| Length                                    | 2.62    | 1.83, 3.41*            | 6.54     |
| Lifestyle                                 | -0.19   | -0.43, 0.05            | -1.59    |
| <i>n</i> <sub>observations, species</sub> | 77, 6   |                        |          |
| <b>Egg size<sup>a</sup></b>               |         |                        |          |
| Intercept                                 | 4.43    | 3.90, 4.96*            | 16.45    |
| Length                                    | 0.07    | -0.06, 0.20            | 0.99     |
| Egg stage                                 | 0.53    | 0.48, 0.57*            | 22.32    |
| Lifestyle                                 | 0.04    | -0.01, 0.08            | 1.69     |
| <i>n</i> <sub>observations, species</sub> | 170, 6  |                        |          |

The lifestyle of species was coded 0–3 depending on the prepotency of terrestrial behaviour exhibited by the species. A random effect for species identity was included in all models. Equivalent phylogenetic analyses are reported in Table S2 (Online resource)

\*  $p < 0.05$  [parameter values with 95 % confidence intervals (CIs) that do not overlap zero are considered statistically significant effects]

<sup>a</sup> Interaction terms between length and lifestyle, or between egg stage and lifestyle, were initially included in Egg number and Egg size, but failed to account for significant variation in egg number or size and were subsequently removed from final models

exhibited by species (Pearson correlation,  $n = 6$ ,  $r = -0.92$ ,  $p = 0.005$  one-tailed; Fig. 5a). These contrasting life history strategies were also consistent with the lifestyle exhibited by species: the slow reproductive development and high growth rate found in aquatic species progressively shifted to high reproductive development and slow growth rate as species became increasingly more terrestrial (Fig. 5a; see also Table 2; Figs. 1, 2).

#### Egg number versus egg size

There was a prominent, negative relationship between the number and size of eggs produced by species (Pearson correlation,  $n = 6$ ,  $r = -0.83$ ,  $p = 0.02$  one-tailed; Fig. 5b). Species either produced many, small eggs (e.g.

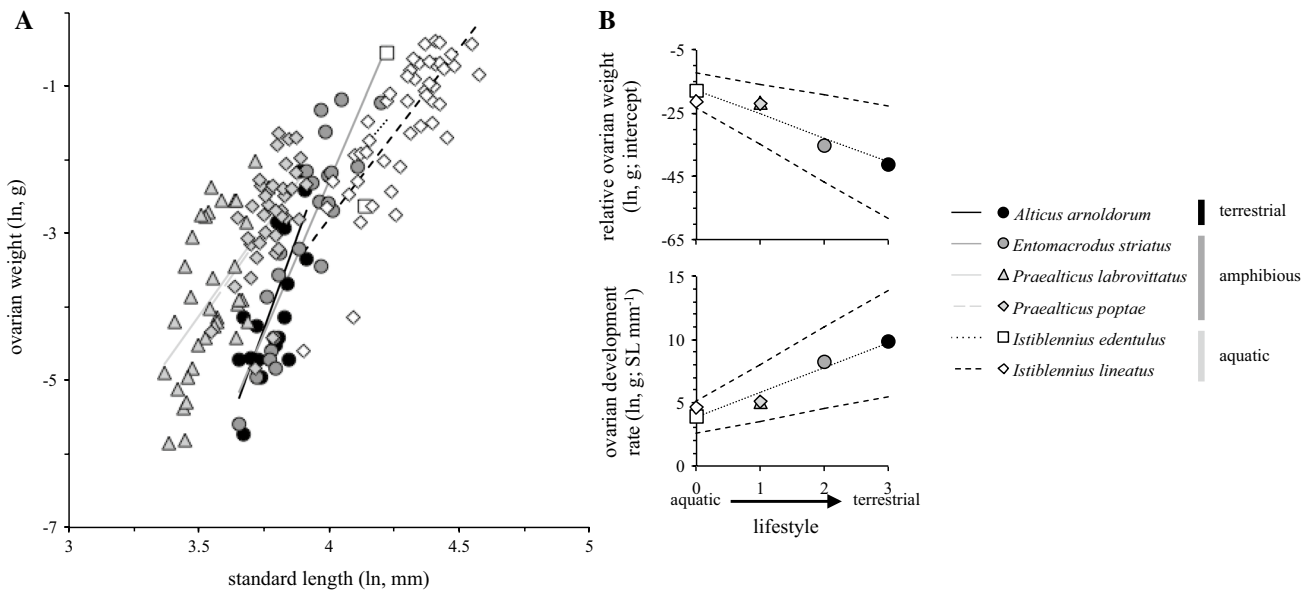
*Entomacrodus striatus*) or few, large eggs (e.g. *Praealticus labrovittatus*). Not surprisingly given the lack of relationship between lifestyle and egg production (Table 2), there was no obvious relationship between the egg production strategy exhibited by species and their degree of terrestriality.

## Discussion

As blennies have colonised land, there appears to have been an increase in female reproductive effort in the form of ovary development at the expense of growth rate. This trade-off between reproduction and growth is consistent with life history theory (Gadgil and Bossert 1970; Stearns 1992; see “Introduction”) and has commonly been observed in a variety of taxa (Robinson and Doyle 1985; Berglund and Rosenqvist 1986; Ryser 1989; Geber 1990; Schwarzkopf 1993). However, it is the direction of this change that is of special interest because it infers settlement on land has increased survival for younger females relative to older females (Table 1). This might occur, for example, if the transition onto land released fish from resource competition or predation that tended to reduce the survival of younger individuals in the aquatic environment (e.g. Osenberg et al. 1992; Belk 1995; Platt and Ord 2015). Marine fishes are subject to extremely high mortality during the juvenile stage (Victor 1986; Myers and Cadigan 1993), usually due to size-selective predation (Almany and Webster 2006), but also because of competition for resources (Forrester 1990), such as habitat (Shulman 1985). High mortality rates have also been specifically confirmed for marine blenny species relative to other fish species (Hunte and Côté 1989; Wilson 2004). A transition away from the marine environment may therefore provide fish with considerable scope for reduction in predative and competitive pressures.

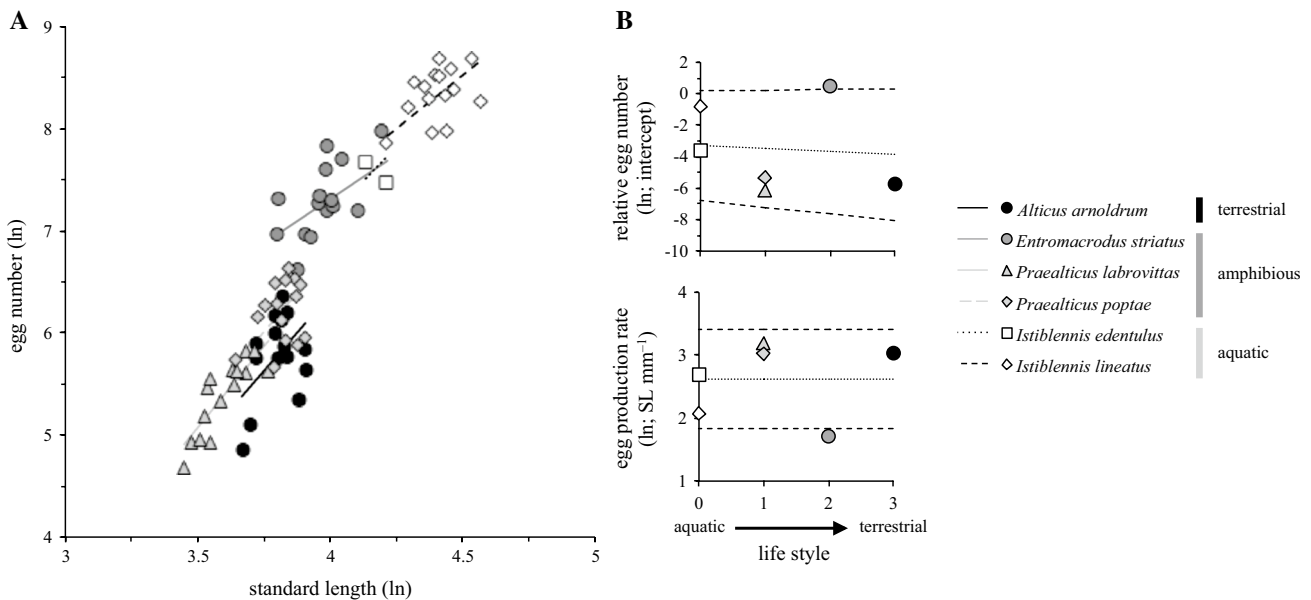
While the trade-off between egg number and egg size (Fig. 5b) implies there are also differences in egg or larval survival among species [i.e. species that produce large eggs will tend to improve the survival of their offspring, but at the expense of the total number of offspring that can be produced (Smith and Fretwell 1974)], these differences were unrelated to the degree of terrestriality exhibited by species (Figs. 3, 4). It seems, then, that there are gross similarities in egg or larval ecology between aquatic and land species. Although females of land blennies lay egg clutches in rock holes above the waterline (Bhikajee and Green 2002; Shimizu et al. 2006), these rock holes are frequently inundated by waves (Platt and Ord, personal observation), such that the abiotic conditions experienced by eggs could be similar to those laid by aquatic species [e.g. see Martin et al. (2004); N.B. increased oxygen exchange for eggs laid in terrestrial environments might facilitate increased





**Fig. 2** Ovarian development as a function of body size (standard length; SL) among blennies that vary in degree of terrestriality (**a**;  $n_{\text{observations}} = 161$ ,  $n_{\text{species}} = 6$ ). **b** Also shown are species coefficients

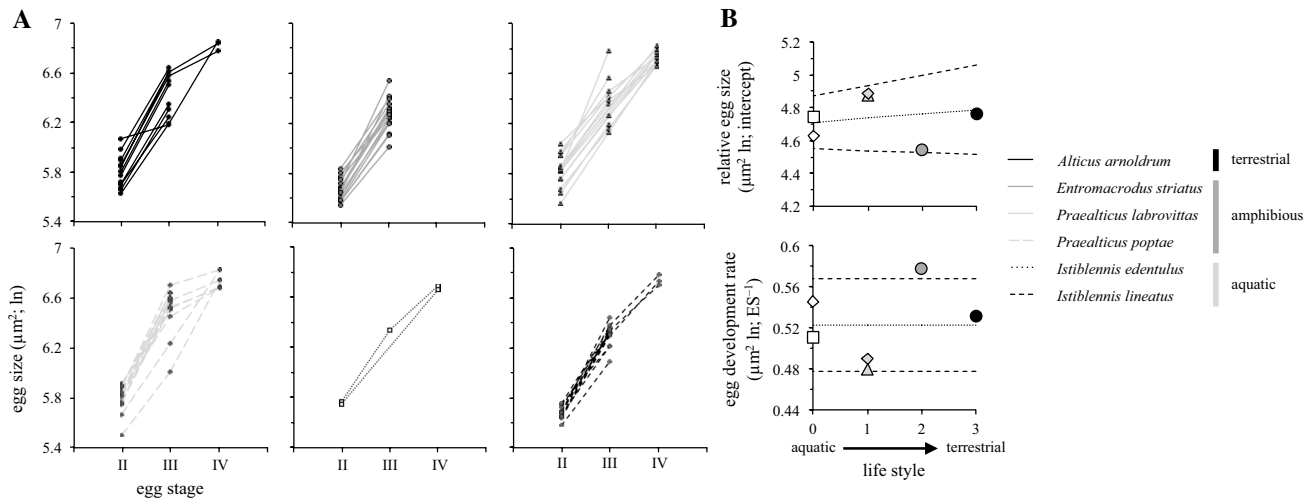
computed from the fitted model reported in Table 2. See Fig. 1 legend for other details



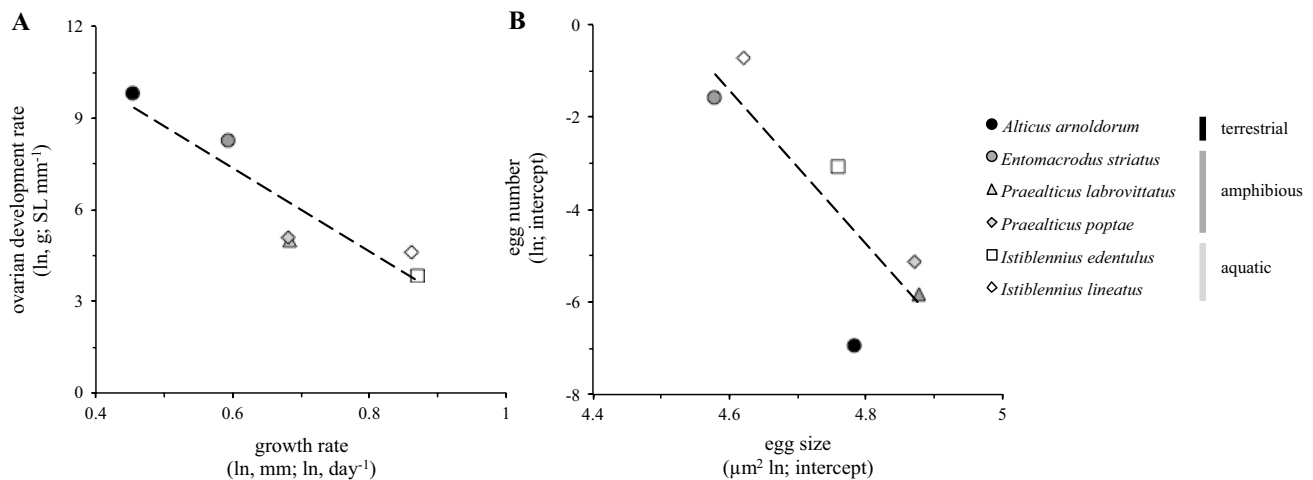
**Fig. 3** The number of eggs produced by female blennies that vary in degree of terrestriality (**a**;  $n_{\text{observations}} = 77$ ,  $n_{\text{species}} = 6$ ). **b** Also shown are species coefficients computed from the fitted model reported in Table 2. See Fig. 1 legend for other details

egg size (Martin and Carter 2013; Martin 2015), but this does not seem to have been the case in the blennies studied here; Fig. 4b]. Furthermore, there is almost certainly a pelagic larval phase for all the species examined [irrespective of the degree of terrestriality exhibited by adults (see Morgans et al. 2014)]. Therefore, larvae of land species probably spend part of their life floating freely in the water

column in the same way as larvae of aquatic species, before emerging onto land in later life stages [probably within 36 days of hatching based on the microincremental counts of the estimated settlement age for *A. arnoldorum* (Platt and Ord, unpublished data)]. While the colonisation of land by blennies has obviously resulted in a substantial change in environment for juveniles and adults (those life stages



**Fig. 4** Differences in egg size produced by female blennies as a function of developmental stage (**a**;  $n_{\text{observations}} = 170$ ,  $n_{\text{species}} = 6$ ). **b** Also shown are species coefficients computed from the fitted model reported in Table 2. *ES* Egg stage. See Fig. 1 legend for other details



**Fig. 5** Trade-offs between **a** growth and reproduction, and **b** egg size and number in female blennies ( $n_{\text{species}} = 6$ ). Plots show species coefficients computed from the fitted model reported in Table 2 (N.B.

parameter estimates for egg size and number were taken after removing lifestyle from the models as lifestyle did not account for significant variation in size or number)

actually observed on land), there may have been very little change in the conditions experienced (and subsequent survivorship) of eggs and larvae, and therefore little difference in the selection pressures required to shift the trade-off between egg size and egg number. Nevertheless, future study is needed to determine the conditions experienced by eggs of these species and why differences are apparent in size and number that are otherwise not accounted for by differences in amphibious lifestyle.

Given amphibious behaviour in fish has evolved in a diverse range of marine species (Graham 1997; Horn et al. 1999; Gibb et al. 2013; Knope and Scales 2013), the advantages apparently offered by a life on land are unlikely to

be unique to the amphibious and terrestrial blennies studied on Guam, but frequently experienced by marine fish. The most likely hypothesis for organisms to make such a large transition in environment is a selection advantage associated with an ecological release or new ecological opportunity (Wilson 1961; Lister 1976; Jeffries and Lawton 1984; Losos and Mahler 2010). The key factors commonly associated with these hypotheses are a reduction in predation or density-dependent resource competition in the new environment. Future work will need to confirm that these ecological factors result in changes in reproductive effort and growth rate reported here in blennies. However, there are a number of precedents leading us to expect this could be

the case (e.g. Martin 1995; Johansson et al. 2001; Benard 2004), most notably the impact of predation and resource availability on the freshwater guppy that has been experimentally confirmed in the wild to induce differences among populations in reproductive effort, growth rate and a range of other life history characteristics (Reznick and Ender 1982; Reznick and Bryga 1987; Reznick et al. 1990). Conducting similar experimental manipulations is likely to be impractical for blennies. However, we do know that populations of the land species *A. arnoldorum* on Guam vary in predation pressure and density (Morgans et al. 2014), and that these populations exhibit differences in reproductive effort and growth rate in a way consistent with the notion that increases in reproductive effort (at the expense of growth rate) reflect a reduction in predation [and to some extent competition (Platt and Ord 2015)]. These data provide support for the general hypothesis in the current study that improvements in female survival may have prompted the observed changes in life history following the transition to land, with this probable change in survival potentially reflecting some form of ecological release such as a reduction in predation.

In itself, our study illustrates that a comparison of life history strategies among closely related taxa in contrasting environments can provide useful insights on the probable ecological conditions affecting reproduction and survival within those taxa. By leveraging the large body of life history theory, our study confirmed the plausibility of the most likely explanation for why organisms might colonise novel environments (an ecological release or opportunity). In doing so, future work can now focus on attempting to examine the specific ecological factors that differ between aquatic and terrestrial environments that might have initially pushed fish to make the seemingly drastic transition out of the water and onto land. Blennies offer a powerful model system to test hypotheses on the causes, processes and consequences of such colonization events given that closely related aquatic, amphibious and terrestrial species effectively represent snapshots of one of the largest ecological transitions possible.

There is now an extensive body of literature documenting the evolutionary consequences of populations living in different environments (e.g. Schluter 2009; Losos and Mahler 2010; Yoder et al. 2010; Nosil 2012). There is also much interest in how the colonization process unfolds and the sorts of phenotypes that might allow some species to be more invasive than others (e.g. Hayes and Barry 2008; Simberloff 2009; Sol et al. 2012). However, it remains unclear what prompts organisms adapted to one environment to move into another environment in which the conditions experienced are very different. Our data suggest that the study of life history may offer a useful starting point for investigating this topic. Although

life history traits do not measure survival directly, many studies have demonstrated strong relationships between life history strategies and survival, including growth rate and reproductive output (e.g. Reznick et al. 1990; Hutchings 1993). Life history variation among closely related taxa could therefore be used to indirectly assess population and species differences in age-specific mortality. Life history strategies that are consistent with theoretical predictions could then be used to focus investigation on the specific ecological variables believed to cause differences in mortality among those taxa. This would be especially valuable for systems in which such direct ecological study is logistically challenging and difficult to justify without some a priori evidence that it will likely prove fruitful.

**Acknowledgments** We would like to thank Alex Kerr and Brett Taylor for logistical support on Guam, Georgina Cooke for assistance in specimen collection, Iain Suthers for the use of his lab equipment and David Chapple and several anonymous reviewers for comments on previous versions of this paper. This work was supported by an Australian Research Council grant to T. J. O., and a postgraduate research award from the School of Biological, Earth and Environmental Sciences to E. R. M. P. This study was covered by the University of New South Wales Animal Care and Ethics Committee protocol 11/36b initially approved on 10 March 2011 and most recently reviewed on 28 February 2013. All data from this publication have been archived in the Dryad Digital Repository (doi:10.5061/dryad.55f35). The authors declare no conflict of interest.

**Author contribution statement** T. J. O. conceived the project. E. R. M. P. collected the data and performed the analyses. A. M. F. contributed to processing specimens. E. R. M. P., A. M. F. and T. J. O. wrote the paper.

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