Life-history trade-offs and ecological dynamics in the evolution of longevity

Michael B. Bonsall[1,2]* and Marc Mangel[2]

[1]*Department of Biological Sciences and NERC Centre for Population Biology, Imperial College London, Silwood Park Campus, Ascot SL5 7PY, UK*
[2]*Department of Applied Mathematics and Statistics, and Center for Stock Assessment Research, University of California, Santa Cruz, CA 95064, USA*

Longevity is a life-history trait that is shaped by natural selection. An unexplored consequence is how selection on this trait affects diversity and diversification in species assemblages. Motivated by the diverse rockfish (*Sebastes*) assemblage in the North Pacific, the effects of trade-offs in longevity against competitive ability are explored. A competition model is developed and used to explore the potential for species diversification and coexistence. Invasion analyses highlight that life-history trait trade-offs in longevity can mitigate the effects of competitive ability and favour the coexistence of a finite number of species. Our results have implications for niche differentiation, limiting similarity and assembly dynamics in multispecies interactions.

Keywords: competition; coexistence; evolutionary stable strategies; invasion dynamics; rockfish

1. INTRODUCTION

Longevity is of fundamental importance to a broad range of disciplines and is central in population biology, demography and gerontology (Gavrilov & Gavrilova 1991; Carey 2003). It underpins, for example, life-table analyses (e.g. the Euler–Lotka equation), the statistical analysis of failure (Cox 1972) and the emerging synthetic approaches of biodemography (Carey 2001, 2003). However, longevity is a life-history trait that is shaped by selection acting on the processes of genetics, behaviour and physiology of organisms (see Rose 1991; Charlesworth 2001; Mangel 2002; Mangel & Bonsall 2004).

Although the demographic and gerontological aspects of longevity are important, one of the principal unexplored consequences of longevity is how this life-history trait might affect the diversity of species assemblages. Understanding how species assemble into guilds has been a major theme in community ecology (May 1975; Connell & Slayter 1977; Pimm 1984; Drake 1990) and ecological theory has shown the conditions under which species may coexist. For instance, pertinent theory has illustrated that the coexistence of two or more species competing for the same resource can occur owing to differences in their life-history traits (Hutchinson 1951, 1965; Skellam 1951; Levins & Culver 1971; Horn & MacArthur 1972; Armstrong 1976). In particular, Levins & Culver (1971) succinctly demonstrated that by expressing the problem of coexistence as the proportion of habitat occupied, the equilibrium fraction of habitat occupied by two rare species is a balance between the rate of local immigration and extinction. More recently, the role of local immigration (colonization) and competitive ability has been the focus of considerable attention (Tilman 1994; Kinzig *et al.* 1999; Yu & Wilson 2001; Levine & Rees 2002). The emerging consensus is that as colonization rate trades off against competitive ability, coexistence is possible (Tilman 1994; Kinzig *et al.* 1999). This occurs as asymmetries in competition reduce the strength and intensity of interspecific interactions. Moreover, rather than affecting the potential for coexistence *per se*, colonization–competition trade-offs have also been shown to determine the patterns of relative abundance of species in assemblages (Levine & Rees 2002).

Whereas the colonization–competition trade-off is well supported, the second trade-off originally highlighted by Levins & Culver (1971) between extinction (death rate) and competitive ability has received somewhat less attention. Levins & Culver (1971) argued that coexistence of competitors is possible if one species is a superior competitor but the other species is longer lived. By decreasing death rate (increasing longevity), again a species effectively reduces the strength of interspecific competition and this can favour coexistence. Moreover, the evolutionary responses by species faced with intense competition are either to avoid competitors, or for selection to act to reduce death rate (increase longevity) (Levins & Culver 1971). However, these may not be mutually exclusive processes and the avoidance of competitors may arise through differences in longevity such that long-lived species are relatively unaffected by interspecific interactions. For instance, Bonsall *et al.* (2002) illustrated that differences in longevity can influence the coexistence of predators by mitigating the effects of interspecific competition for prey resources. This is an included niche in the life history of the animals: predators that live longer have access to scarce resources that would otherwise be consumed by the superior competitor.

The conditions under which one species might exclude another based on differences in life-history trait trade-offs can be determined by evaluating a species' invasion potential (Levins & Culver 1971). Invasion criteria demonstrate that a species will persist if, and only if, it can increase whenever it is rare, and coexistence requires that this invasion condition holds for each species in an interaction

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(Armstrong & McGhee 1980). Such ecological invasion analyses can be more formally linked to evolution (Metz *et al.* 1992; Dieckmann 1997) and the notion of evolutionary stable strategies (ESSs). If a species cannot be replaced by any other species with a different life-history trait then the system is considered non-invadable and may be classed as evolutionary stable. It is widely accepted that frequency-dependent mechanisms underlie the persistence of different evolutionary plausible strategies and that the ESS is the fixed point favouring the persistence of a particular or fixed group of life histories or behaviours (Maynard-Smith 1982). More recently, this idea has been expanded to couple ecological dynamics and evolutionary processes to consider how invasion and replacement by species with different life histories can affect individual single-species dynamics (Dieckmann & Doebeli 1999; Geritz *et al.* 1999), competitive interactions (Kisdi 1999; Doebeli & Dieckmann 2000) and more complex multispecies interactions (Jansen & Mulder 1999).

Predicting the patterns and mechanisms of coexistence among potential competitors, therefore, requires knowledge of the life-history traits of species (Vincent *et al.* 1996): species cannot simply be Darwinian demons. The ability to trade competitive ability against particular (or a suite) of life-history traits is a compelling explanation for the persistence of complex ecological assemblages. As first postulated by Levins & Culver (1971) it is a testable but relatively unexplored hypothesis that a longevity–competitive ability trade-off can affect species interactions, invasions, coexistence and, ultimately, species diversity. Our principal objective is to attempt to address this hypothesis.

(a) Biological motivation

The second aim of this work is to understand and predict how life-history traits can influence the diversity and diversification of multispecies assemblages. In particular, we are motivated to explain the high degree of endemism in the rockfishes (*Sebastes*) in the North Pacific. Rockfish are a diverse group of fishes (*ca.* 100 species) within the order Scorpaeniformes (and are related to the scorpionfishes and lionfishes). In the northeast Pacific, 65 species are known to co-occur, with the highest diversity (56 species) occurring in southern Californian waters (Love *et al.* 2002). The rockfishes show a wide variability in their life-history traits (Love *et al.* 2002), and their longevity strategies span at least an order of magnitude. For example, one of the shorter-lived species, calico rockfish, *Sebastes dalli*, lives for *ca.* 12 years whereas one of the longest-lived species (and longest-lived vertebrates), rougheye rockfish, *Sebastes aleutianus*, lives for at least 200 years.

To explore how longevity and competitive ability interact to affect rockfish assemblage diversity and coexistence we develop a mathematical model that accounts for the physiological (individual fish growth), ecological (population dynamics) and evolutionary dynamics of species interactions. We begin by presenting a competition model. From its analysis, we show how species coexistence and assemblage diversity is determined by trade-offs in longevity and correlations with other life-history parameters, and that only a finite number of species are predicted to coexist. We conclude with the implications of this study for understanding the processes of community assembly and species diversification.

2. MATERIAL AND METHODS

We consider a stylized interaction between rockfish competing for a limiting resource in which there is no *a priori* partitioning of this resource so that multiple types of rockfish can feed on this resource. At the foundation, we develop the physiological model and trade-off function to represent the precise form of the interaction between competing species. This provides an explicit link to the population dynamics of the system and the replacement (evolutionary) dynamics. We use invasion analysis and support functions to explore the consequences of fitness differences (based on life-history trait trade-offs) on the potential for coexistence and diversification.

(a) Model structure

At a physiological level, changes in mass (m) for the ith species can be described by an allometric relationship such that anabolic resource uptake rate scales to the βth power of mass (West *et al.* 2001) and is weighted by population biomass, while catabolic processes scale linearly with mass

$$\frac{\mathrm{d}m_i}{\mathrm{d}t} = \frac{a_i \times m_i^{\beta}(t)}{1 + \sum_j \gamma_{ij} \times m_j^{\beta}(t) \times N_j(t)} - b_i \times m_i(t),\qquad(2.1)$$

where γ_{ij} is the strength of density dependence, N_j is the size of the jth population, a_i is the resource uptake rate and b_i is the resource utilization rate.

The population dynamics of the ith species follow a simple age-structured formulation (Gurney *et al.* 1983) such that

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = r_i \times N_i(t) - \left(\mu_i + \sum_j \gamma_{ij} \times m_j^{\beta}(t) \times N_j(t)\right) \times N_i(t) - S_i(t,\tau_i),$$

$$(2.2)$$

where r_i is the maximum *per capita* reproductive rate for the ith species, μ_i is the natural mortality rate and $S_i(t,\tau_i)$ is the through class survival

$$S_i(t,\tau_i) = r_i \times N_i(t - \tau_i) \times \exp\left(-\int_{t-\tau_i}^{t} \left(\mu_i + \sum_j \gamma_{ij} \times m_j^{\beta} \times N_j\right)\mathrm{d}x\right),$$

which is determined by maximum lifespan (τ_i). Rockfish population size increases through recruitment at rate r_i and declines through density-independent (μ_i) and density-dependent mortality

$$\left(\sum_j \gamma_{ij} \times m_j^{\beta}(t) \times N_j(t)\right)$$

over the total lifespan (τ_i).

While there is a well-established formal relationship between lifespan (τ) and mortality rate (μ) and survival ($e^{-\mu \times \tau}$), it may be that if μ is high, then a maximum lifespan (τ) is never achieved. However, we separate these into distinct life-history characters. Understanding how these traits (natural mortality rate and lifespan) independently affect future reproductive success of different strategies is the third aim of this study.

(b) Trade-offs and competition functions

Differences in these traits (natural mortality rate (μ) and lifespan (τ)) determine the strength of interspecific competitive ability (γ_{ij}) and consequently the strength of selection. Central to our argument, we describe the life-history trait trade-off in terms of the effective strength of interspecific competition (γ_{ij}).

This can be expressed as

$$\gamma_{ij} = \gamma_{jj} \times \exp\left(-\frac{1}{2}\left(\frac{x_i - x_j}{\sigma_x}\right)^2\right), \qquad (2.3)$$

where γ_{jj} is the strength of intraspecific competition, x_i is the trait of a mutant strategy, x_j is the trait of a resident strategy and σ_x governs the width of the competition window. Species with similar life histories (smaller σ) experience more intense competition while species that differed markedly in life histories experience diffuse competition. This is a relatively unexplored hypothesis but developments in ESS theory and our understanding of multispecies interactions now allow trade-offs in competition and longevity (Levins & Culver 1971) to be investigated.

To investigate how life-history trait correlations might affect coexistence we allow the life-history trait (natural mortality or lifespan) and resource utilization parameters (a or b) to covary. We assume that the correlated traits of the invader are given, for example, by

$$x_i = x_j + \sigma_x^2 \times z_1,$$
$$a_i = a_j + \sigma_a^2 \times \left(z_1 \times \rho + z_2 \times \sqrt{1 - \rho^2}\right), \qquad (2.4)$$

where z_1 and z_2 are normally distributed with mean 0 and variances, σ_x^2 and σ_a^2 are the variances of the life-history traits and ρ is the strength of correlation between traits x and a. Differences in covarying life-history characters can both have an influence on competitive ability. This impact of resident species on an invader (γ_{ij}) can be determined from a bivariate normal distribution:

$$\gamma_{ij} = \gamma_{jj} \times \exp\left(-\frac{1}{2(1-\rho^2)}\left[\left(\frac{x_i - x_j}{\sigma_x}\right)^2 \right.\right.$$
$$\left.\left. - 2\rho\frac{x_i - x_j}{\sigma_x^2}\frac{a_i - a_j}{\sigma_a^2} + \left(\frac{a_i - a_j}{\sigma_a}\right)^2\right]\right), \qquad (2.5)$$

where γ_{jj} is the strength of intraspecific competition, x_i is the trait of a mutant strategy, a is the rate of resource uptake by the resident (j) or mutant (i) strategy, x is the trait of a resident (j) or mutant (i) strategy, ρ is the correlation between traits and σ_x and σ_a governs the width of the competition window.

(c) *Invasion analysis and support functions*

From an evolutionary perspective, we are interested in how changes in the life-history trait under selection affect the ESSs and invasion conditions. To explore this we specify the fitness function of a rare mutant in terms of the life-history trait trade-off. This fitness function can be used to determine the evolutionary stable states (i.e. when the rate of change in fitness is zero) and the invasion dynamics. By taking a Taylor expansion (to second order) of the fitness function the curvature around the evolutionary steady states can be specified and this provides a measure of the strength of selection. It also provides an indication of how broad the ESS is in terms of similar life-history traits. This is known as the support function (Edwards 1972).

Invasion and replacement (evolutionary) dynamics must be explored from knowledge of both the mass gain (equation (2.1)) and population dynamics (equation (2.2)). To do this, we evaluate the invasion potential of a rare mutant that has a different set of life-history characters (to resident strategies) and determine whether this species can invade and outcompete any or all of the resident species. To determine invasion potential we use the fitness function evaluated when equal to zero (using a Newton–Raphson algorithm coupled with the demographic equilibrium for the resident ($\hat{m}_j^\beta, \hat{N}_j$)) for different values of the life-history

trait. Understanding the invasion and replacement dynamics compliments the ESS approach outlined above.

3. RESULTS

(a) *Evolutionary stable strategies*

The fitness function of an initially rare mutant invading a resident assemblage can be expressed in terms of the *per capita* population growth rate (R) of the mutant population:

$$R_i = r_i - \left(\mu_i + \sum_j \gamma_{ij} \times \hat{m}_j^\beta \times \hat{N}_j\right)$$
$$- r_i \times \exp(-(\gamma_{ij} \times \hat{m}_j^\beta \times \hat{N}_j + \mu_i) \times \tau), \qquad (3.1)$$

where γ_{ij} is the strength of interspecific competition described by the Gaussian model for the life-history trade-offs (equation (2.3)) and $\hat{m}_j^\beta$ and $\hat{N}_j$ are the equilibrium conditions for the resident strategy. As outlined above, this fitness function can be used to determine the evolutionary stable states (i.e. when the rate of change in fitness (growth rate) is zero) and the invasion dynamics for the longevity–competitive ability trade-off.

(i) *Natural mortality rate (μ)*

The fitness function for changes in mutant natural mortality rate is illustrated in figure 1a. The derivative of this function (equation (3.1)) with respect to natural mortality rate μ) for a mutant invading an assemblage with a single resident allows the ESS conditions to be determined:

$$\frac{\mathrm{d}R_i}{\mathrm{d}\mu} = \gamma_{jj} \times \exp\left(-\frac{1}{2}\left(\frac{\mu_i - \mu_j}{\sigma_\mu}\right)^2\right) \times \hat{m}_j^\beta \times \hat{N}_j \times (\mu_i - \mu_j)$$
$$- r_i \times \exp\left(-\left(\gamma_{jj} \times \exp\left(-\frac{1}{2}\left(\frac{\mu_i - \mu_j}{\sigma_\mu}\right)^2\right)\right.\right.$$
$$\left.\times \hat{m}_j^\beta \times \hat{N}_j + \mu_i\right) \times \tau_i\Big) \times \left(\gamma_{jj} \times \exp\left(-\frac{1}{2}\left(\frac{\mu_i - \mu_j}{\sigma_\mu}\right)^2\right)\right.$$
$$\left.\times \hat{m}_j^\beta \times \hat{N}_j \times (\mu_i - \mu_j) \times \tau_i - \tau_i\right). \qquad (3.2)$$

There are two evolutionary stable states where the gradient of the fitness function is zero (figure 1b). One of these points is a fitness maximum (where $\mu \sim 2.3$) whereas the other is a fitness minimum (where $\mu \sim 0.9$) (figure 1c). The span of the support function (estimated from the difference in μ for a known $f(\mu)$) reveals that functionally equivalent strategies are more likely to occur at the fitness minimum (span in μ at 80% $\mu_{ESS} \sim 0.6$) than at the fitness maximum (span in μ at 80% $\mu_{ESS} \sim 0.1$).

From this we predict that selection at the fitness minimum could allow several similar strategies to co-occur and promote phenotypic divergence. At this minimum point, selection is predicted to drive phenotypes away from this point albeit at a slow rate. This can happen in one of three ways. First, phenotypes only move to the left (that is rockfish with increased longevity only evolve). If this occurs evolution to maximum longevity can be favoured. Second, phenotypes move only to the right (that is rockfish with shorter longevities evolve). If this occurs, phenotypes should eventually converge to the fitness maximum. Finally, a branching occurs and phenotypes of increased and shorter longevities evolve (and possibly coexist). While at the fitness maximum selection will have a stabilizing influence on phenotypes and a monomorphic strategy may be expected to persist. Below, we explore these predictions (see § 3c).
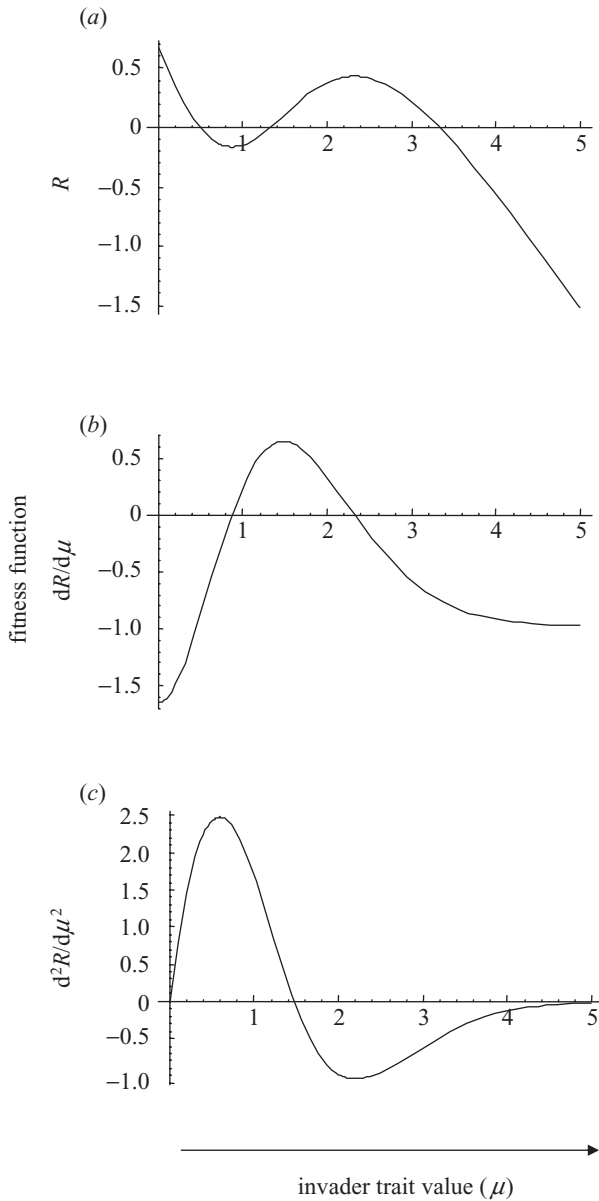
Figure 1. Fitness surfaces for changes in invader natural mortality rate (μ_i) expressed as (*a*) the fitness function (equation (3.1)), (*b*) the first derivative and (*c*) the second derivative of fitness. The fitness surface shows both evolutionary maximum ($\mu \sim 2.3$) and evolutionary minimum points ($\mu \sim 0.9$) (resident steady states: $\hat{m}^{\beta} = 0.175^{0.75}$ and $\hat{N} = 10.754$).

(ii) *Lifespan (τ)*

Similarly, the fitness function for changes in longevity for a mutant strategy is illustrated in figure 2. The derivative of the fitness function (equation (3.1)) with respect to lifespan (τ) is

$$
\begin{aligned}
\frac{dR_i}{d\tau} &= \gamma_{jj} \times \exp\left(-\frac{1}{2}\left(\frac{\tau_i - \tau_j}{\sigma_\tau}\right)^2\right) \times \hat{m}_j^{\beta} \times \hat{N}_j \times (\tau_i - \tau_j) \\
&\quad - r_i \times \exp\left(-\left(\gamma_{jj} \times \exp\left(-\frac{1}{2}\left(\frac{\tau_i - \tau_j}{\sigma_\tau}\right)^2\right) \times \hat{m}_j^{\beta} \times \hat{N}_j + \mu_i\right) \times \tau_i\right) \\
&\quad \times \left(-\mu_i + \gamma_{jj} \times \exp\left(-\frac{1}{2}\left(\frac{\tau_i - \tau_j}{\sigma_\tau}\right)^2\right) \times \hat{m}_j^{\beta} \times \hat{N}_j \times (\tau_i - \tau_j)\right) \\
&\quad \times \tau_i - \gamma_{jj} \times \exp\left(-\frac{1}{2}\left(\frac{\tau_i - \tau_j}{\sigma_\tau}\right)^2\right) \times \hat{m}_j^{\beta} \times \hat{N}_j\right).
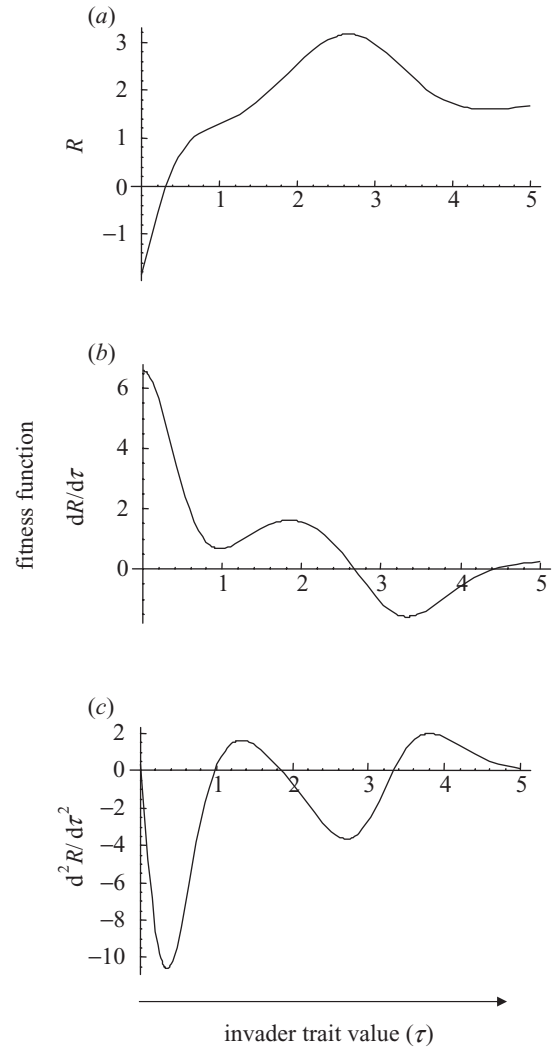\end{aligned} \tag{3.3}
$$

Figure 2. Fitness surfaces for changes in invader lifespan (τ_i) expressed as (*a*) the fitness function (equation (3.1)), (*b*) the first derivative and (*c*) the second derivative of fitness. The fitness surface shows a single evolutionary maximum ($\tau \sim 2.8$) (resident steady states: $\hat{m}^{\beta} = 0.175^{0.75}$ and $\hat{N} = 10.754$).

This derivative reveals that there is a single maximum to lifespan (figure 2) (where $\tau \sim 2.8$). The support function of the fitness function with respect to τ about this ESS point reveals that the span is relatively broad (span in τ at 80% of $\tau_{ESS} > 1.0$). Again, we predict from this that there is potential for evolutionary divergence. Similar strategies (in terms of τ) have similar fitness values and divergence away from the ESS will be relatively slow. Below, we explore these predictions and the potential for coexistence when lifespan is allowed to evolve (see § 3c).

(**b**) *Invasion dynamics*

The pairwise invasion boundaries and regions of coexistence for two species (*i* and *j*) with different life-history trait values are illustrated in figure 3. In particular, invasion is successful for species *i* above the grey line and for species *j* to the right of the black line. The point where the two lines cross illustrated in figure 3 is the fitness minimum (highlighted above for a particular strategy from the ESS analysis): fitness (*per capita* growth rate) is zero for both species at this point. At this fitness minimum
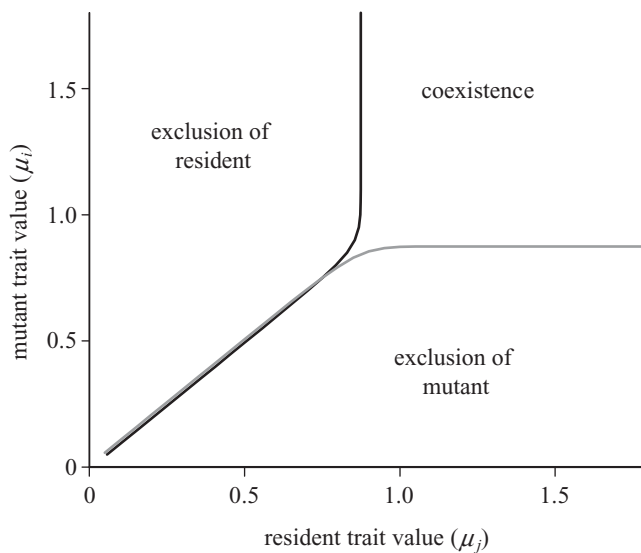
Figure 3. Reciprocal invasion boundaries for natural mortality rate (μ). Grey line: boundary for mutants invading residents. Mutants are successful above the line. Black line: boundary for resident invading mutant. Residents are successful to the right of the line. The area for coexistence allows long-lived and short-lived species to potentially coexist.

perturbations through selection will lead to a number of evolutionary outcomes. For species i invading species j (grey line), mutants are successful only above the line so replacement occurs by phenotypes with higher trait values (shorter lifespans). This is reciprocal and holds for species j invading species i. As such, there is a region of mutual invasibility for shorter-lived strategies. However, once perturbed away from this point by repeated invasion and replacement of species with a shorter-lived strategy long-lived phenotypic strategies can reinvade. These replacement dynamics predict that the evolution of a variety of longevity strategies may co-occur.

(c) *Patterns of coexistence*

Numerical solutions of the model (equations (2.1) and (2.2)) in which species with different longevity strategies (in terms of μ or τ), may arise (through mutation) and replace existing species show how patterns of coexistence can occur. In particular, we are interested in whether multiple species with different mortality rates or lifespans can co-occur and persist.

Following on from the predictions of the invasion and ESS analysis, it is possible for multiple species to coexist provided that there is sufficient difference in the natural mortality (μ) between species (figure 4a). Within these assemblages, invading strategies may persist as transients for long periods of time and the number of different species that can ecologically coexist at any point in time may exceed the number observed in the terminal assemblage. Similarly, evolution of lifespan (τ) can also favour species diversification and coexistence (figure 4b). In contrast to the evolution of natural mortality rate, variation in lifespan allows fewer species to persist in the assemblage, and relative differences in lifespan span a more restricted range (a twofold difference) than variation in mortality rate (a sevenfold difference). In comparison, variation in
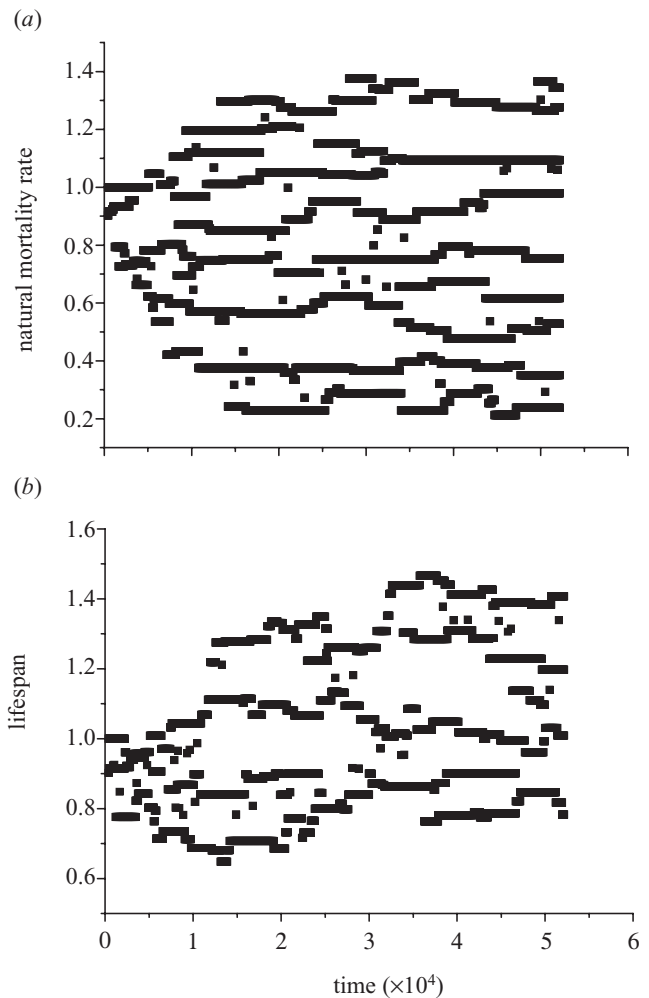

Figure 4. Evolutionary dynamics and branching processes for life-history trait evolution for (a) natural mortality rate (μ) and (b) lifespan (τ). Single mutation event (in an extant population selected at random) in the life-history trait occurs with a probability of 0.5 every 150 generations (after the population dynamics asymptote). Evolutionary dynamics were numerically integrated for 50 000 generations.

longevity traits allows fewer species to coexist and this form of coexistence can give rise to a form of limiting similarity. Coexistence is possible and occurs because of asymmetric competition between species: more similar strategies experience greater effects of interspecific competition than more distinct strategies. Thus, persistence of multispecies assemblages occurs as a result of distinct differences in trait values.

Allowing more than one life-history trait to evolve permits similar levels of diversity in species coexistence as observed under evolution of a single trait. Again, this arises because the effects of competition are only manifest around the local neighbourhood of existing species. If there is no correlation in the life-history traits ($\rho = 0$) these traits evolve independently, and relationships between life-history traits of species present in the final assemblage can emerge because of the feedbacks in the interaction between within-species mass gain and between-species population biomass. In particular, we observe negative correlations between natural mortality rate (μ) and anabolic rate (a) (figure 5a) and lifespan (τ) and anabolic rate (a) (figure 5b) whereas a weak positive correlation is
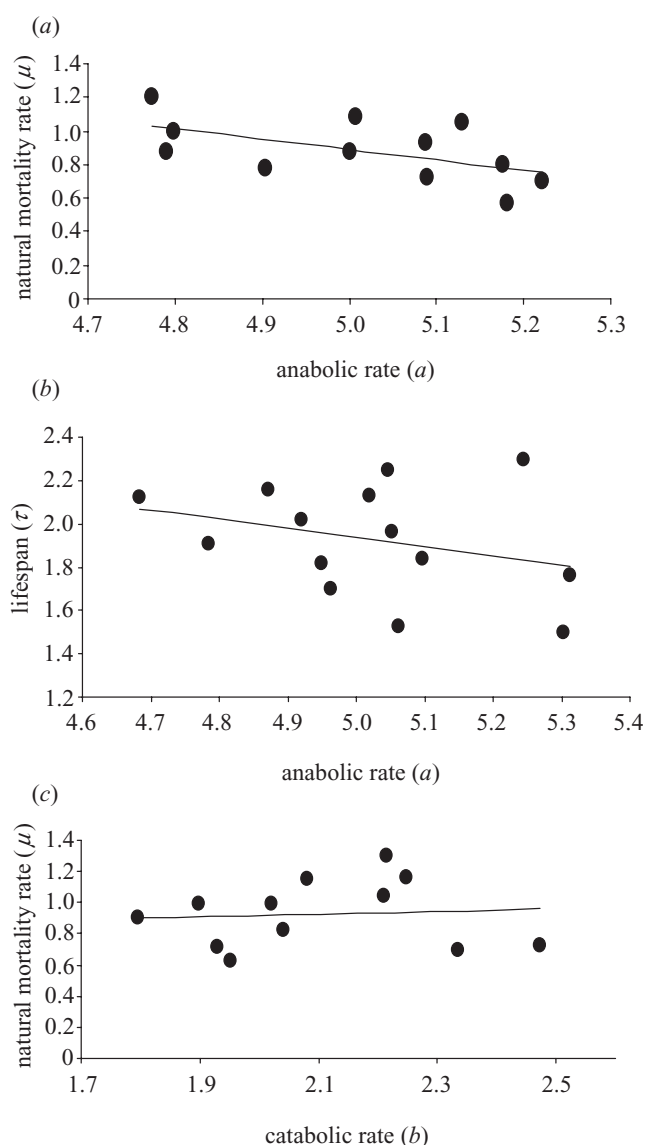
(*a*)

(*b*)

(*c*)

Figure 5. Life-history invariants for (*a*) anabolic rate and natural mortality (trend line explains 66% of the variation), (*b*) anabolic rate and lifespan mortality (trend line explains 9% of the variation) and (*c*) catabolic rate and natural mortality (trend line explains 0.5% of the variation).

predicted between catabolic rate (*b*) and natural mortality rate (μ) (figure 5*c*; Beverton & Holt 1959; Charnov 1993).

4. DISCUSSION

We have shown that species diversity can be explained in terms of life-history trait trade-offs. We have questioned, what is the adaptive significance of variation in lifespan (τ) and natural mortality rate (μ), how does it impact upon future reproductive success, and what are the consequences of these life-history trait trade-offs for species diversification? We have demonstrated that provided there is sufficient variation in the life-history traits to mitigate the effects of interspecific competition then increases in future reproductive success can be favoured. Further, we have illustrated several implications in understanding the evolutionary ecology of longevity. First, long-term population growth rate provides information on the evolutionary stable states in these simple assemblages. Second,

the ESS can be characterized in terms of the span around the focus point (either a minimum or a maximum point). This provides information of the potential for diversification and evolution about these ESS points. Third, mutation and selection can lead to a finite number of species coexisting with different longevity strategies. Fourth, mutation and selection on multiple traits can lead to positive or negative patterns in life-history invariants.

In particular, the predicted fitness surface shows an evolutionary maximum separated by an evolutionary minimum and support for the non-trivial ESS points are well approximated by the support function (a second-order Taylor expansion of fitness). This analysis suggests that different strategies about these points have equivalent fitness and as such might coexist (Mangel 1991; Mangel & Stamps 2001). Disruptive selection away from these points can occur leading to evolutionary branching and the potential for species coexistence.

(a) *Niche differentiation*

Evolution constrains the patterns of ecological diversification. In contrast to other life-history trait competition trade-off models (e.g. Horn & MacArthur 1972; Tilman 1994) where fugitive species can always invade and coexist in assemblages, we predict that only a finite number of species are observed to coexist. The observed patterns of species coexistence occur as the continuously varying selection regime (of natural mortality rate or lifespan) acts through interspecific competition. Such selection regimes have also been invoked in the persistence of single monomorphic and polymorphic populations (as bet-hedging strategies) under randomly fluctuating environments. Although it has been demonstrated that a set of distinct strategies can be promoted (rather than the continuous spread of strategies) this conclusion is strictly contingent on the degree of environmental variability (Sasaki & Ellner 1995). Here, by contrast, we have shown that even in the absence of temporally fluctuating environments a distinct set of strategies can emerge through differences in species' life-history characteristics.

One clear prediction of our theory is that species should be separated by some degree of limiting similarity depending on the breadth of the interspecific competition. Broad competition effects (larger σ_x) favour less diversification. However, transient dynamics might allow species with very similar life histories to coexist over ecological time. We emphasize that describing the patterns of diversification in terms of limiting similarity may easily neglect or obscure the potential importance of transient effects (Hastings 2004) in structuring multispecies assemblages.

(b) *Rate of living theory and life-history patterns*

One hypothesis for the differential patterns of longevity between species and the importance of longevity on assemblage structure is the rate-of-living hypothesis which states that high metabolic rates are positively correlated with increased cellular damage through reactive oxidative processes (Pearl 1928; Finch 1990; Partridge & Gems 2002) and this can lead to shortened lifespans. Predictions from our study suggest that such patterns may not necessarily be reflected in life-history trait correlations. We have illustrated that life-history trait correlations with anabolic rate or catabolic rate show contrasting but interpretable

patterns. Species that require more resources are predicted to have shorter lifespans (figure 5). Thus, a negative correlation would be expected between the life-history trait and anabolic rate. However, additional nonlinear costs through the effects of size or biomass (driven by the rate of change of mass; equation (2.1)) on anabolic resource uptake rate may be important determinants of the correlative patterns with longevity (West *et al.* 2001; Promislow & Haselkorn 2002). Furthermore, we suggest that species that are relatively long-lived might have more opportunity to obtain resources, hence it might be expected that a negative correlation could arise between mortality rate and anabolic rate (figure 5). By contrast, however, if there are no costs (through size or mass) on resource use (e.g. on catabolic rate (b)), then the increased rate of mortality might be positively correlated with resource use (figure 5) consistent with the theory on the rate of living or calorific restriction (Pearl 1928; Finch 1990; Rogina *et al.* 2002).

(c) *Tests and implications*

We have coupled ecological and evolutionary processes to understand both the longevity and the diversity of species assemblages. Our models were motivated by the high levels of diversity in the rockfish assemblage of the north Pacific and the degree of variation observed in the patterns of rockfish ageing. Understanding life-history patterns of longevity, growth and age at maturity are crucial in the management and conservation of the rockfishes. Moreover, expressed in terms of how different longevity strategies affect competitive ability, we have asked how such life-history trait trade-offs might have shaped species diversification events. The rockfishes show a high degree of endemism centred around southern California waters (Love *et al.* 2002). Comparative evolutionary approaches of how ageing and maturity are explained in terms of life histories would allow the ultimate (evolutionary) mechanisms of diversification to be determined. The availability of rockfish phylogenies (Johns & Avise 1998), life histories (Love *et al.* 2002) and oceanographic characteristics of the north Pacific (Karl *et al.* 2001) allows the predictions identified in this current study to be rigorously tested. Understanding these mechanisms of diversification and speciation in terms of characteristics of lifespan remains available for future development. Although speciation may depend on environmental productivity (Doebeli & Dieckmann 2003), the form of the competition function (Kisdi 1999) or broad phylogenetic relationships (Barraclough & Nee 2001; Losos & Glor 2003), it is likely that, as originally highlighted by Levins & Culver (1971), species-specific traits (such as longevity), through their effects on future reproductive success and competitive ability, are important determinants of species diversity and diversification.

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