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Extinction, colonization, and species occupancy in tidepool fishes

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Abstract Despite the increasing sophistication of ecological models with respect to the size and spatial arrangement of habitat, there is relatively little empirical documentation of how species dynamics change as a function of habitat size and the fraction of habitat occupied. In an assemblage of tidepool fishes, I used maximum-likelihood estimation to test whether models which included habitat size provided a better fit to empirical data on extinction and colonization probabilities than models that assumed constant probabilities over all habitats. I found species differences in how extinction and colonization probabilities scaled with habitat size (and hence local population size). However, there was little evidence for a relationship between extinction and colonization probabilities and the fraction of occupied tidepools, as assumed in simple metapopulation models. Instead, colonization and extinction were independent of the fraction of occupied tidepools, favoring a MacArthur-Wilson island-mainland model. When I incorporated declines in extinction probability with tidepool volume in a simple simulation model, I found that predicted occupancy could change greatly, especially when colonization was low. However, the predicted fraction of occupied patches in the simulation model changed little when I incorporated the range of values reported here for extinction and colonization and the rate at which they scale with habitat size. Quantifying extinction and colonization patterns of natural populations is fundamental to understanding how species are distributed spatially and whether metapopulation models of species occupancy provide explanatory power for field populations.

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Introduction

There is an increasing literature on how the distribution of habitat, both in size and spatial arrangement, can affect population abundance and occupancy patterns (Lovejoy et al. 1986; Quinn and Hastings 1987; Quinn and Robinson 1987; Harrison et al. 1988; Quinn et al. 1989; Hanski and Gyllenberg 1993; Hanski et al. 1995). For example, extinction rates and their dependence on population size, habitat size, and habitat distribution have received attention for their importance to conservation biology, especially in the area of reserve design. More generally, classical island biogeography theory (MacArthur and Wilson 1963, 1967) drew the attention of ecologists to the significance of immigration and extinction rates and habitat size for species diversity patterns. Within this context, islands have been broadly defined to include many insular habitat types such as discrete talus slopes (Smith 1974), mountain tops (Brown 1971, 1978), individual plants (Brown and Kodric-Brown 1977), and freshwater rockpools (Pajunen 1986; Bengtsson 1989).

The ideas embodied in island biogeography theory have also been applied to incidence function models, where a species presence is described as a probability distribution over a range of island areas (Diamond 1975; Gilpin and Diamond 1981; Peltonen and Hanski 1991; Hanski 1992). These models use a sequence of presence and absence data to estimate colonization and extinction probabilities, and examine how these probabilities change with insular habitat size and population size. Extinction has generally been estimated in two ways: as $1/T$ (called "risk of extinction") where T is the time to extinction (e.g., Pimm et al. 1988) or as the proportion of times that a species was absent, given it was present in the previous census (e.g., Diamond and May 1977). Recently, Clark and Rosenzweig (1994) and Rosenzweig and Clark (1994) developed a maximum-likelihood method for presence/absence data which they suggested avoids the distribution problems of $1/T$ (Pimm et al. 1988) and allows the accuracy of the estimate to be evaluated. The decline of extinction rates with habitat size or island area (A) has been modeled commonly as z^*A^{-x} where z and x are estimated parameters (Gilpin and Diamond 1976; Peltonen and Hanski 1991; Hanski 1992). Peltonen and Hanski (1991) and Hanski (1992) found that the rate at which extinction declined with island area (x) was species specific and had implications for how stochasticity affects population dynamics.

Evaluating rates of extinction and colonization are relevant not only to island biogeography models, but also to the developing literature on metapopulation models (e.g., Levins 1969, 1970; Hanski 1982; Gotelli 1991; Gilpin and Hanski 1991). The metapopulation model favored for a particular system is determined by whether extinction (or emigration) and colonization (or immigration) are dependent upon the fraction of patches occupied, where extinction and colonization probabilities are equivalent over all habitat patches. Levins (1969, 1970) modeled metapopulations with extinction probabilities that were independent and immigration probabilities dependent on the fraction of patches occupied. More recently, other models have been introduced that vary the dependence of extinction and colonization on the fraction of occupied patches. For organisms where new immigrants can come from outside the system and are decoupled from occupancy, Gotelli (1991) has suggested a "propagule rain" model may be appropriate. Models which include a propagule rain express immigration independently of regional occurrence. The few published examples of how extinction and colonization correlate with species occupancy patterns show a variety of results (Hanski 1982; Gotelli and Kelley 1993; Hanski and Gyllenberg 1993).

Metapopulation models have also been used to predict the equilibrium fraction of habitat occupied, with mixed results. A metapopulation model for river fishes predicted equilibrium species occupancy patterns that differed from those observed for at least two of three species analyzed (Gotelli and Kelley 1993). Using multispecies data sets, some authors have also compared the observed distribution frequency of all species with equilibrium occupancy patterns predicted by different metapopulation models (Hanski 1982; Gotelli and Simberloff 1987; Gaston and Lawton 1989; Collins and Glenn 1990, 1991; Gotelli and Kelley 1993; Hanski and Gyllenberg 1993).

I describe here how insular habitat structure affected species extinction and colonization probabilities and the distribution of three species of fishes among their tidepool habitats. From patterns of species occupancy in tidepools, I examined whether tidepool size was an important determinant of extinction and colonization probabilities, and whether these probabilities differed between species. I then assessed the relationship between the fraction of tidepools occupied at any time and the associated probabilities of extinction and colonization for all three species. Finally, I compared predicted and observed occupancy, both with and without tidepool size effects on probabilities of extinction and colonization.

Study system

Although the natural history of this system has been described elsewhere (Pfister 1995, 1996, 1997), I will briefly describe the features important to this study. The three species of sculpins studied here occupy tidepool habitat for their entire life, with the exception of the planktonic larval stage which may last up to 1 or 2 months (Washington et al. 1984). Once they have settled into a tidepool, they display site fidelity and can be repeatedly found in the same tidepool (Green 1971, 1973; Yoshiyama et al. 1992; Pfister 1995, 1996); in some cases, I have repeatedly recaptured individuals within the same pool for 2–3 years (unpublished data). Movement of marked fishes between adjacent tidepools was very low and tidepools only 1–2 m apart had distinct populations of marked individuals (Pfister 1995, 1996). In previous studies of this system, I have demonstrated experimentally that heterospecifics do not affect the colonization rate of any single species; instead, individual fishes respond to changes in the abundance of heterospecifics with modifications to growth and emigration rates (Pfister 1995). Although tidepools can vary substantially in the organisms that occupy the substrate (Dethier 1984), very few statistical relationships exist between the percent cover of a particular substrate type and the abundance or distribution of tidepool sculpin species (Pfister 1995). The only tidepool characteristic that consistently explained a significant amount of the variation in the abundance of tidepool fishes was tidepool volume, which was positively related to abundance of each of the three common species in the system (Pfister 1995). Thus, tidepools may be thought of as insular habitats for these fishes; that is, events on the scale of the tidepool may be important to the population within the pool, while linkage among tidepool populations occur via dispersal events over a potentially vast geographic area. Indeed, in the terminology of Hanski and Simberloff (1997), these tidepool fishes may be characterized as a metapopulation or a "set of local populations within some larger area, where typically migration from one local population to at least some other patches is possible." As with any plant or animal population with a dispersal stage during the early life cycle, there is potential for the young to disperse away from the local adult population. The degree to which individual young and adults are related is unknown in these species.

All censuses of tidepool sculpins were conducted on the outer coast of Washington state at Tatoosh Island, Shi Shi Beach and Mukkaw Bay (described in Pfister 1995, 1996). All sites have an extensive rocky intertidal habitat dotted with tidepools of varying sizes. The most common resident fish species in these tidepools included *Clinocottus embryum*, *C. globiceps*, and *Oligocottus maculosus*. Although *O. snyderi* was also present in some tidepools, it was not common enough to include in subsequent analyses. Tidepools can vary substantially in volume, and the tidepools used for these analyses ranged in volume over at least two orders of magnitude. I use habitat size interchangeably with tidepool volume in this study.

Materials and methods

Censuses of tidepool sculpins

I censused tidepool sculpins by draining a tidepool partially, mixing in a few drops of the anesthetic Quinaldine, and then dipnetting any fish that came swimming to the surface, while continually pouring water into crevices to flush out fishes. The fishes were transferred to a bucket with untainted seawater where they rapidly recovered from any ill effects of the Quinaldine. I then drained the remaining water from the pool, thoroughly searched the pool again, and refilled the pool with seawater. I recorded species identity, standard length (a measure from the head to the start of the caudal fin), and gender whenever possible before returning the fishes. From extensive mark-recapture studies with these fishes, it is clear that the census technique was thorough, since the same individuals were repeatedly recaptured (Pfister 1995, 1996).

I estimated the volume of each tidepool using a colorimetric technique. I added a known volume of Schilling blue food coloring (McCormick, Hunt Valley, Md.) into each tidepool and mixed completely. I took a water sample from the pool and read the absorbance at 640 nm with a Spectronic 20 (Bausch and Lomb). Pool volume was then estimated from a standard curve prepared from the same stock of blue food coloring.

Extinction, colonization, and the size of habitat patches

I examined how extinction and colonization probabilities scaled with habitat size using censuses from 29 tidepools, asking whether models which included tidepool volume better fit extinction and colonization data. Eighteen tidepools on Tatoosh Island, 5 tidepools at Mukkaw Bay, and 6 tidepools at Shi Shi Beach were included. All tidepools were censused at least 5 consecutive times (range: 5–28 consecutive censuses, mean: 10.7 censuses per tidepool) at three sites. In general, censuses were separated by 1 month, although several censuses ranged from 0.5 to 2.5 months due to weather constraints. All censuses were taken between 1991 and 1993 and included the spring and summer months when recruitment of young fishes occurs (Pfister 1996). The record for each tidepool can be thought of as a series of presence/absence data. I defined colonization and extinction to be conditional probabilities and assumed an underlying binomial distribution. With this specified error structure, I was able to use maximum-likelihood methods to determine whether tidepool volume improved the fit of colonization and extinction models to the data.

Clark and Rosenzweig (1994) also discuss a maximum-likelihood method for dealing with presence/absence data, and contrast regular and sporadic census data. Their formulation is slightly different to mine, since they introduce a third estimator (the "disappearance probability") where the probability of extinction is followed during the same interval by a failure to reimmigrate (see also Rosenzweig and Clark 1994). I have ignored this third parameter because my censuses were relatively numerous and the intervals were relatively short (1 month), and because the "disappearance probability" parameter can exceed 1.0, making interpretation difficult. Below I outline the models that I compared, starting with the most simple and proceeding to the most complex.

In the simplest scenario, extinction (E) and colonization (C) are constants, unrelated to habitat size (tidepool volume):

$$E_i = \Theta_i \tag{1}$$

and

$$C_i = \varphi_i \tag{2}$$

for all i species. Alternatively, extinction and colonization could be some function of tidepool volume. I modelled the probability of extinction using an exponential model with a concave decrease decrease in extinction as tidepool size increased:

$$E_i = \Theta_i \exp(-\Omega_i V_n), \tag{3}$$

where Θ_i is a constant, Ω_i scales extinction to tidepool size, and V_n is volume in liters for each tidepool n. Equation 3 results in an extinction probability that declines with increasing habitat (or population) size consistent with demographic theory, while Θ_i and Ω_i bring flexibility to the maximum value of extinction at the smallest tidepool size and the steepness with which extinction probability declines with tidepool volume, respectively. A model used previously for scaling extinction with island area equates extinction to z^*A^{-x} (Gilpin and Diamond 1976, 1981; Peltonen and Hanski 1991; Hanski 1992), where z and x are estimated parameters. I also tested the fit of my data to this model, but found that it provided a poorer fit to the data and did not permit the same flexibility in the shape of the relationship between extinction probability and tidepool volume as Eq. 3.

I then included effects of tidepool size on models of colonization probabilities in two ways. First, I modelled an exponential increase in colonization probability with volume:

$$C_i = \varphi_i \exp(\phi_i V_n), \tag{4}$$

where φ_i is a constant, and ϕ_i scales colonization to tidepool size. However, since colonization may be constrained by the number of individuals in an area that can colonize, a more realistic model for colonization might be one where the colonization probability increases with tidepool size to an asymptote. Thus, increasing the size of a tidepool above a certain volume (or increasing the population size over a certain value) does not increase the colonization probability:

$$C_i = \varphi_i[1 - \exp(-\phi_i V_n)] \tag{5}$$

Although values for E_i and C_i could be 0 or 1.0, I added 0.01 to all 0 values and subtracted 0.01 from all 1.0 values in order to find solutions to the models.

I assumed extinction and colonization were binomial processes, and defined a likelihood function for extinction of each i species in each n tidepool to be:

$$L(E)_{i_n} = (E_{i_n})^{\alpha} \cdot (1 - E_{i_n})^{\beta} \tag{6}$$

where α is the number of times a species that was present went extinct and β is the number of times a species was present but did not go extinct. Similarly, I defined a likelihood function for colonization to be:

$$L(C)_{i_n} = (C_{i_n})^{\delta} \cdot (1 - C_{i_n})^{\varepsilon}, \tag{7}$$

where δ is the number of times a species was absent and a colonization event occurred and ε is the number of times a species was absent and no colonization event occurred. E_{i_n} and C_{i_n} are estimates based on whatever model was used. The negative log likelihood functions for extinction and colonization then become:

$$\boldsymbol{L}(E)_{i_n} = -[\alpha \cdot \log(E_{i_n}) + \beta \cdot \log(1 - E_{i_n})] \tag{8}$$

and

$$\boldsymbol{L}(C)_{i_n} = -[\delta \cdot \log(C_{i_n}) + \varepsilon \cdot \log(1 - C_{i_n})] \tag{9}$$

All parameter estimation and likelihood analyses were done in SYSTAT (Wilkinson 1989) using alternative forms of Eqs. 1–5 as models and Eq. 8 or 9 as negative log likelihood functions.

I tested whether the models where volume was a constant (Eqs. 1, 2) fit the data better than the models dependent on tidepool volume (Eqs. 3–5) with a likelihood ratio test (LRT). LRTs are appropriate for models which differ in the number of parameters they use, where the negative log likelihood value of the more simple model is subtracted from the negative log likelihood value of the more complex model. The resulting statistic, $[-2(\boldsymbol{L}_1 - \boldsymbol{L}_2)]$ is χ^2 distributed, where the total degrees of freedom is the difference in the degrees of freedom between the two models (Hilborn and Mangel 1997). Since I used two different functions to examine how colonization probabilities might depend on volume (Eqs. 6, 7), I compared these models with an Akaike information criterion (AIC), where $\mathrm{AIC} = -2\boldsymbol{L} + 2q$, where q is the number of parameters. The model with the lowest AIC is considered the best fit to the data and complex models with more parameters are "penalized." A thorough discussion of the use of AIC in model selection is provided in Lebreton et al. (1992).

Extinction, colonization, and species occupancy patterns

Of the 29 tidepool censuses included above, 9 are tidepools on Tatoosh Island that I censused approximately every month from February 1991 until September 1993. For each census date I estimated the fraction of tidepools occupied by each species (pt_i), the extinction probability (ext_{t_i}), and the colonization probability (col_{t_i}) for each species i at each time t (Levins 1969; Gotelli 1991). For these analyses, the extinction probability was the number of instances where tidepools with species i at time t were missing species i at time $t+1$. Similarly, the colonization probability was simply the number of tidepools which previously did not contain species i at time t which were found to contain species i at time $t+1$. Thus, ext_{t_i} and col_{t_i} provide a spatial estimate of extinction and colonization for each t.

Metapopulation models are distinguished based upon whether colonization and extinction are dependent upon the fraction of habitat patches occupied (Gotelli 1991). Thus, I estimated Spearman correlation coefficients between col_{t_i}, ext_{t_i}, and pt_i for all i species to determine the best model to predict equilibrial occupancy ($\hat{p}$) based on maximum likelihood estimates of extinction and colonization. I estimated 95% confidence intervals for each species $\hat{p}$ using a Monte Carlo bootstrapping procedure. I drew randomly from a normal distribution estimated from the mean and standard errors for extinction and colonization in the 29 tidepools. I repeated this procedure 2000 times, examining the distribution of each $\hat{p}$ and estimating the 95% confidence intervals on each p. I compared statistically the $\hat{p}$ estimates with the observed distribution of occupancy (pt_i) from the 9 tidepools with long-term censuses using a Kolmogorov-Smirnov test for equality of distributions.

One of the principal reasons $\hat{p}$ could deviate from observed p values is the lack of equivalency in extinction and colonization probabilities among tidepools. I explored how habitat size affected occupancy by considering how the rate at which extinction declines with volume affected $\hat{p}$. I simulated different declines in extinction with tidepool volume by changing Ω in Eq. 3 for a hypothetical set of 10 tidepools with incremental increases in volume from 10 to 1000 l. I computed a mean $\hat{p}$ using extinction probabilities that declined with volume (Eq. 3 with differing values for Ω) and constant probabilities of colonization; I held Θ constant.

Results

Extinction, colonization and the size of habitat patches

The distributions of extinction and colonization probabilities by tidepool volume that provided the raw data for maximum-likelihood estimation are shown in Fig. 1a, b. Whether the model for extinction which included tidepool size (Eq. 3) best fit extinction patterns in the field depended upon the species considered. Models which included tidepool size fit extinction patterns for *O. maculosus* and *C. globiceps* (but not *C. embryum*) significantly better than one that assumed constant probabilities over all tidepools (Table 1). Thus, extinction probabilities of *O. maculosus* and *C. globiceps* both declined with increasing tidepool volume.

The results for colonization were equally dependent upon which species was considered (Table 2). The model which assumed constant colonization probabilities over all tidepool sizes provided the best fit to colonization patterns of *O. maculosus* and *C. globiceps*, but not *C. embryum* (Table 2). Thus, colonization probabilities in all but *C. embryum* were independent of tidepool size. In contrast, the model which best fit the colonization data for *C. embryum* was where colonization increased as tidepool size increased (Eq. 5).

Extinction, colonization, and species occupancy patterns

The distribution of pt_i, or the observed fraction of tidepools occupied, differed significantly between species (Table 3, $P < 0.001$, $F_{2,74} = 68.64$, ANOVA and Tukey's multiple-comparison test with arcsine-square

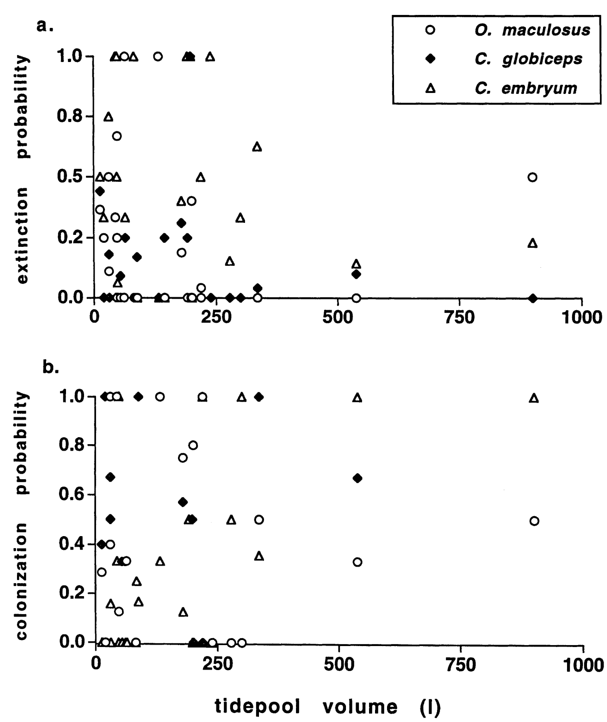

Fig. 1 Probabilities of extinction (**a**) and colonization (**b**) for each species and for each of 29 tidepools as a function of tidepool volume (in liters). Each point represents a tidepool mean based on a sequence of censuses ranging from 5 to 27 per tidepool

Table 1 Results of log likelihood estimates of extinction probabilities of each species. Parameter estimates (95% confidence intervals) and negative log likelihood values (***L***) are given for both Eq. 1 where extinction is a constant and Eq. 3 where extinction probabilities decline with tidepool size. Significant likelihood ratio test (*LRT*) results indicate that Eq. 3, where tidepool size is incorporated, gave a better fit to the data

	Eq. 1		Eq. 3		
O. maculosus	$\Theta = 0.123$ (0.077, 0.169) $\boldsymbol{L} = -73.65$	LRT = 7.52, $0.005 < P < 0.01$	$\Theta = 0.203$ (0.109, 0.298)	$\boldsymbol{L} = -69.89$	$\Omega = 0.003$ (0.0001, 0.005)
C. globiceps	$\Theta = 0.097$ (0.058, 0.136) $\boldsymbol{L} = -69.90$	LRT = 3.98, $0.05 < P < 0.025$	$\Theta = 0.145$ (0.070, 0.219)	$\boldsymbol{L} = -67.91$	$\Omega = 0.002$ (0.0001, 0.004)
C. embryum	$\Theta = 0.287$ (0.203, 0.370) $\boldsymbol{L} = -67.47$	LRT = 1.24, $0.50 < P < 0.25$	$\Theta = 0.346$ (0.246, 0.446)	$\boldsymbol{L} = -66.85$	$\Omega = 0.0006$ (0.0006, 0.0006)

Table 2 Results of log likelihood estimates of colonization probabilities for individuals of each species. Parameter estimates (95% confidence intervals) and negative log likelihood values (***L***) are given for both Eq. 2 where colonization is a constant and Eqs. 4 and 5 where colonization probabilities increase exponentially with tidepool size, becoming asymptotic in the latter. The likelihood ratio tests (*LRT*) compare Eq. 4 to Eq. 2 and Eq. 5 to Eq. 2. The Akaike information criterion (*AIC*) allows for comparison between Eq. 4 and 5

Eq. 2	Eq. 4			Eq. 5		
O. maculosus						
$\varphi = 0.330$ (0.218, 0.442) $\boldsymbol{L} = -42.85$	$\varphi = 0.269$ (0.202, 0.336)	$\boldsymbol{L} = -41.97$ LRT = 1.76, $0.25 > P > 0.10$ AIC = 87.94	$\phi = -0.001$ (−0.001, −0.001)	$\varphi = 0.337$ (0.213, 0.460)	$\boldsymbol{L} = -42.80$ LRT = 0.10, $0.90 > P > 0.75$ AIC = 89.60	$\phi = 0.136$ (−0.338, 0.610)
C. globiceps						
$\varphi = 0.421$ (0.274, 0.557) $\boldsymbol{L} = -34.42$	$\varphi = 0.405$ (0.274, 0.535)	$\boldsymbol{L} = -34.40$ LRT = 0.4, $0.75 > P > 0.\ 50$ AIC = 72.80	$\phi = -0.0003$ (−0.0003, −0.0003)	$\varphi = 0.423$ (0.278, 0.567)	$\boldsymbol{L} = -34.42$ LRT = 0 AIC = 72.84	$\phi = 0.293$ (−1.616, 2.203)
C. embryum						
$\varphi = 0.167$ (0.107, 0.226) $\boldsymbol{L} = 68.34$	$\varphi = 0.098$ (0.098, 0.098)	$\boldsymbol{L} = 56.42$ LRT = 23.84, $P < 0.001$ AIC = 116.84	$\phi = -0.003$ (−0.003, −0.003)	$\varphi = 3.698$ (3.548, 3.849)	$\boldsymbol{L} = 54.20$ LRT = 28.28, $P < 0.001$ AIC = 112.40	$\phi = 0.0003$ (0.0003, 0.0003)

Table 3 Tidepool occupancy (p), extinction (ext_t) and colonization (col_t) probabilities in 9 tidepools over 27 months

Species	Mean (± SD) observed occupancy (p)	Spearman correlation coefficients between p and	
		colonization probability	extinction probability
O. maculosus	0.75 ± 0.14	−0.300, $n = 23$	0.152, $n = 24$
C. globiceps	0.85 ± 0.12	0.098, $n = 17$	0.150, $n = 24$
C. embryum	0.42 ± 0.14	−0.681*, $n = 24$	0.017, $n = 24$

* $P < 0.001$

root-transformed data). *C. globiceps* occupied the highest fraction of tidepools, *O. maculosus* followed, and *C. embryum* occupied the lowest mean number of tidepools. Extinction probabilities (ext_t) for all species were unrelated to p_t Table (3). Colonization probabilities (col_t) were also unrelated to p_t for *O. maculosus* and *C. globiceps* (Table 3). Only *C. embryum* colonization probabilities showed a relationship with p (Table 3); *C. embryum* colonization probabilities declined as the fractions of tidepools already occupied by *C. embryum* increased. Observed occupancy for each species appeared to be unimodal (Fig. 2).

Extinction and colonization unrelated to occupancy is consistent with a metapopulation model proposed by Gotelli (1991) and Hanski and Gilpin (1991), which also predicts a unimodal $\hat{p}$.

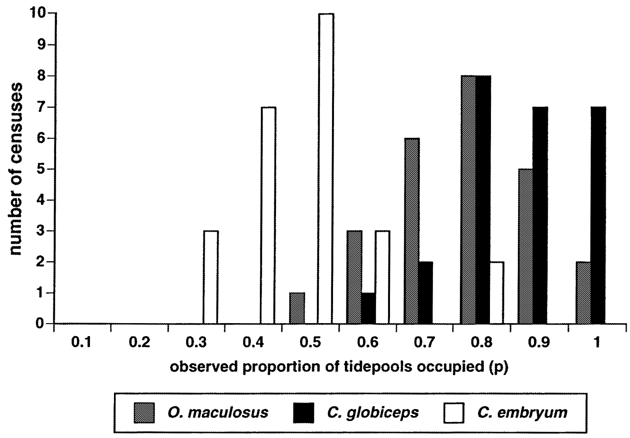

Fig. 2 The proportion of tidepools occupied for each species based on 9 tidepools censused over 25 approximately monthly intervals on Tatoosh Island

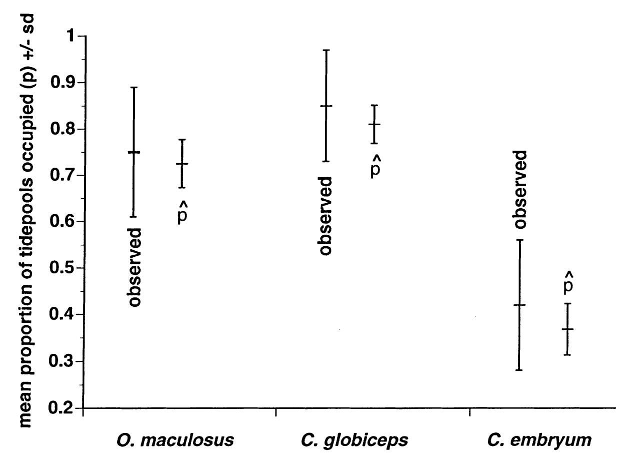

Fig. 3 The observed mean fraction of tidepools occupied (p) and the estimated equilibrium fraction of tidepools occupied ($\hat{p}$). *Horizontal hatches* represent the mean, *bars* are the SD. For each species, $\hat{p}$ estimates did not differ significantly from the observed distribution of p with a Kolmogorov-Smirnov test

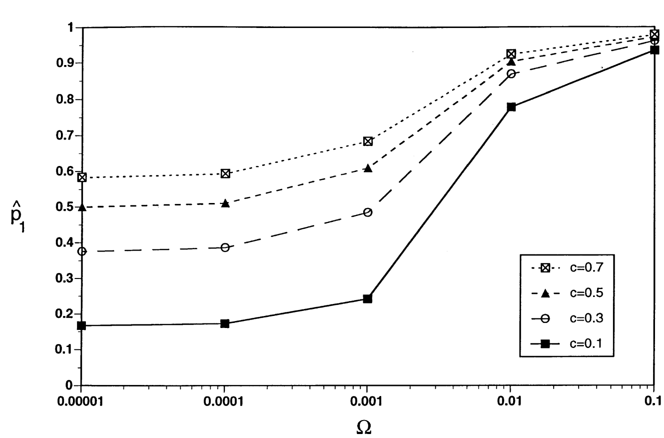

Fig. 4 The relationship between a decline in extinction probability with tidepool volume (an increasing Ω from Eq. 3 and the predicted mean occupancy rate, $\hat{p}$. *Lines* represent different values for colonization (c). The results are based on simulations using 10 tidepools with incremental increases in volume from 10 to 1000 l; Θ was held constant at 0.5

When I bootstrapped confidence intervals for $\hat{p}$ using extinction and colonization estimates drawn from a normal distribution, $\hat{p}$ closely matched the observed p based on censuses through time for 9 tidepools (Fig. 3). The observed and expected distributions for each of the three species were statistically indistinguishable (Fig. 3; Kolmogorov-Smirnov two-sample tests; Sokal and Rohlf 1981).

I simulated different declines in extinction with tidepool volume by changing Ω in Eq. 3 for a hypothetical set of 10 tidepools with incremental increases in volume from 10 to 1000 l. As extinction declined more rapidly with tidepool volume (by increasing Ω), mean estimates of $\hat{p}$ changed markedly (Fig. 4), especially when colonization probabilities were low. However, given the estimates of Ω and colonization probability (φ) in these three species of fishes (Table 1, 2), variation in these estimates should cause little change in $\hat{p}$.

Discussion

Species-specific responses to insular habitats

A principal concern about habitat fragmentation is whether small habitat fragments simply contain a random sample of what is in larger habitat areas. Thus, for both natural and artificial insular habitats, we want to know whether there are processes that scale with habitat size. The increase in species diversity with an increase in island or insular habitat area is well documented empirically (Preston 1960; MacArthur and Wilson 1963, 1967; Browne 1981; Nilsson and Nilsson 1982; Toft and Schoener 1983). However, less is known about how population processes scale with habitat and population size. In the system described here, habitat size (tidepool volume) correlates positively with population size (Pfister 1995). Hence, processes that scale with tidepool size also scale with population size.

There is increasing empirical support for the hypothesis that species respond differentially to processes that scale with habitat size (Diamond 1975; Gilpin and Diamond 1981; Taylor 1991; Peltonen and Hanski 1991; Hanski 1992; Hanski et al. 1995), and that these patterns can be attributed to differential rates of extinction and colonization (Tracy and George 1992; Peltonen and Hanski 1992; Hanski 1992; Hanski et al. 1995). In this study, the rate at which extinction changes as a function of tidepool size differed between species (Table 1). *O. maculosus* had the steepest decline in extinction rate with tidepool volume or population size (or the largest value of Ω in Table 1), followed by *C. globiceps*. *C. embryum*, in contrast, showed no significant decline in extinction probability with tidepool size.

C. globiceps had the greatest probability of colonization, which is a reflection of the relatively high incidence of recruitment of this species relative to the other two species (Pfister 1996, 1997). Thus, it appears that *C. globiceps* achieves the highest occupancy over all tidepools through a combination of both increased colonization and decreased extinction relative to other members of this guild. Only the *C. embryum* colonization probability was related to tidepool size, increasing as tidepool size increased (Table 2).

Interestingly, for the two most widespread and abundant species in this system (*O. maculosus* and *C. globiceps*), there appears to be a competition/colonization trade-off such as those invoked for multi-species metapopulation models (Nee and May 1992; Tilman 1994; Kareiva and Wennergren 1995). *O. maculosus* is a superior competitor (Pfister 1995) while *C. globiceps* enjoys higher colonization probabilities and a higher occupancy across habitats (Table 3). Ideally, the application of metapopulation models in a multi-species assemblage such as this might include parameter estimation for each species in the context of long-term experimental removals of heterospecifics. Although these data are not available, previous short-term experimental manipulations (2–3 months) with these fishes suggest that colonization rates are unchanged by heterospecific competitors, while extinction rates may be increased by competitors, due to increased individual emigration (Pfister 1995).

Species occupancy patterns and their relation to metapopulation dynamics

Incidence function models assume that species occupancy patterns are independent of the fraction of occupied habitat (Diamond 1975; Gilpin and Diamond 1981), whereas metapopulation models are dependent upon how immigration (or colonization) and extinction are related to local population abundance and regional distribution (Gotelli 1991). The metapopulation model that best fit the data described here was one in which both colonization and extinction were independent of local occupancy (Gotelli 1991; Hanski and Gilpin 1991) which results in a $\hat{p}$ that is equivalent to the incidence function used by Diamond (1975) and Gilpin and Diamond (1981). In the terms used previously for metapopulation models, this indicates a population with a "propagule rain" but without a "rescue effect" (Gotelli 1991). In other words, colonization stays constant even at relatively low occupancy due to a supply of colonists from outside the study system, while extinction probabilities do not decline as occupancy increases. The natural history of these fishes is consistent with a "propagule rain." New recruits seasonally colonize these tidepools from the plankton, often in variable numbers that appear unrelated to adult density patterns (Pfister 1995, 1996).

An important issue is whether this study spanned a long enough time period to detect metapopulation dynamics. Although metapopulation dynamics may take decades to detect (Harrison 1994), a critical consideration is whether one can detect metapopulation dynamics over the lifespan of the organism. For the fishes studied here, the 3-year duration of the study encompasses the lifespan of the majority of individuals in the population (Pfister 1996) and should be a sufficient to detect whether extinction and colonization are related to occupancy. Another consideration is whether 1-month intervals are the best for capturing extinction and colonization dynamics. Certainly, turnover occurred during this interval and monthly censuses allowed me to include the seasonal variability in this system.

One of the principal assumptions of most metapopulation models is the equivalency of rates among habitat patches. However, empirical studies have shown how populations in the field violate this assumption, often occurring as 'source-sink' populations (sensu Pulliam 1988) or 'mainland-island' populations (Harrison et al. 1987; Harrison 1991). For two of the fish species examined here, extinction probabilities are not equivalent over all habitat sizes, declining instead as tidepool size and population size increase (Table 1). When I explored how alterations in the rate at which extinction declines with volume with differing values for colonization, I found that $\hat{p}$ can change greatly, especially when colonization probabilities are low (Fig. 4). However, colonization estimates and the rate of change in extinction for each species in this system (from Tables 1 and 2, respectively) fall in a region of the graph where we would expect variance in these probabilities to alter $\hat{p}$ relatively little. Clearly, the effects of patch differences on equilibrium occupancy patterns will depend upon how variation in extinction and colonization are incorporated into metapopulation models. Although there are ample opportunities for theoretical explorations, there is also a dire need for empirical examples of how habitat heterogeneity affects the dynamics of occupancy and the rates of migration.

The metapopulation concept and the distribution of field populations

Since Levins (1969, 1970) introduced quantitatively the metapopulation concept, there have been many discussions (e.g., Gilpin and Hanski 1991) and some empirical efforts to determine whether field populations conform to the simple assumptions and predictions of the Levins and related models. Although some species appear to have dynamics driven by extinction and colonization, upon closer inspection their conformance to the models breaks down (Harrison et al. 1988, 1995; Gotelli and Kelley 1993; but see Hanski et al. 1995), causing some to suggest that the models may have limited applicability (Harrison 1994; Harrison et al. 1995). However, despite the increasing empirical literature on how local population dynamics are impacted by local population size (e.g., Spight 1974; Kareiva 1985; Schoener and Spiller 1987; Paine 1988), the proposed metapopulation models still suffer from a dearth of empirical information on how colonization and extinction change with local abundance and regional occupancy, and whether habitat patches are functionally equivalent. Often, occupancy patterns are reported and underlying probabilities of colonization and extinction are assumed (Hanski 1982; Gotelli and Simberloff 1987; Gaston and Lawton 1989; Collins and Glenn 1990, 1991). Assessing the determinants of extinction and colonization probabilities and whether they are related to the number of occupied patches requires extensive spatio-temporal information, a characteristic of only several data sets to date (Gotelli and Kelley 1993; Hanski et al. 1994, 1995; this study). The utility of the metapopulation concept in ecology requires greater emphasis on quantifying the role of extinction and colonization in determining species occupancy patterns.

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