Contrasting phylogeography in three endemic Hawaiian limpets (Cellana spp.) with similar life histories

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Abstract

The marine environment offers few obvious barriers to dispersal for broadcast-spawning species, yet population genetic structure can occur on a scale much smaller than the theoretical limits of larval dispersal. Comparative phylogeographical studies of sympatric sister species can illuminate how differences in life history, behaviour, and habitat affinity influence population partitioning. Here we use a mitochondrial DNA marker (612 bp of cytochrome c oxidase subunit I) to investigate population structure of three endemic Hawaiian broadcast-spawning limpets (Cellana spp.) with planktonic larvae that are competent to settle within 4 days. All three species exhibit significant population structure and isolation by distance, but the spatial scales of partitioning differ among the species. Cellana talcosa (n = 105) exhibits strong population structure between Kauai and the other main Hawaiian Islands (MHI) where the maximum channel width is 117 km, and no shared haplotypes were observed (ΦCT = 0.30, P < 0.001). In contrast, populations of Cellana exarata (n = 149) and Cellana sandwicensis (n = 109) exhibit weaker population structure within the MHI (ΦST = 0.03–0.04, P < 0.05), and between the MHI and the Northwestern Hawaiian Islands (ΦST = 0.03–0.09, P < 0.01), where the maximum channel width is 260 km. Biogeographical range and microhabitat use were correlated with estimates of dispersal, while phylogenetic affiliation and minimum pelagic larval duration were poor predictors of population partitioning. Despite similar life histories, these closely related limpets have contrasting patterns of population structure, illustrating the danger of relying on model species in management initiatives to predict population structure and dispersal in the context of marine protected area delineation.

Keywords: COI, fisheries management, marine protected areas, model taxa, mitochondrial DNA, pelagic larval dispersal

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Introduction

Recent meta-analyses support the long-standing view that dispersal potential of marine species is at least one to two orders of magnitude greater than terrestrial and freshwater organisms (Kinlan & Gaines 2003; Kinlan et al. 2005). Greater connectivity of sedentary marine organisms is routinely attributed to the dispersal potential of pelagic larvae and the scarcity of physical barriers among marine habitats (Mayr 1954; reviewed in Palumbi 1994; Shulman 1998). Biogeographical barriers between marine populations include obvious geographical features such as land masses, i.e. the Isthmus of Panama (Bermingham & Lessios 1993), but also more subtle factors such as currents and oceanographic regimes (Dawson 2001; Barber et al. 2002; Sotka et al. 2004). Indeed, there is a growing list of marine taxa that do not realize their apparent dispersal potential (Burton & Feldman 1981; Knowlton & Keller 1986; Shanks et al. 2003; Jones et al. 2005; Severance & Karl 2006).

Concordant genetic breaks in the distributions of broadcast-spawners have confirmed biogeographical barriers that were originally proposed based on species distributions. The demonstrated barriers include the
California transition zone (Briggs 1974; Dawson 2001), the Florida transition zone between the Gulf of Mexico and the Atlantic Ocean (Reeb & Avise 1990; Avise 1992), the Indonesian channels between the Indian and the Pacific Oceans (Benzie 1999; Barber et al. 2000), the Mona Passage between the East and West Caribbean Sea (Colin 1975; Taylor & Hellberg 2003, 2006; Baums et al. 2006), and the Cook Straight between the North and South islands of New Zealand (Smith 1988; Apte & Gardner 2002; Goldstien et al. 2006a).

In each of the aforementioned cases, without detailed knowledge of currents, temperature gradients, and/or sea level change, the causes of these genetic breaks would not be predicted, a priori. Population partitions at the Florida transition zone and Indian/Pacific boundary are believed to be influenced by emergent land barriers during low sea level stands and subsequent vicariant divergence. The California transition zone, Florida transition zone, and Cook Strait are accompanied by latitudinal changes in the marine climate which may influence distributions via a myriad of pathways (Wares 2001; Sotka & Hay 2002; Sotka et al. 2004). All of these barriers are maintained, at least in part, by oceanic currents (Avise 1992; Benzie 1999; Dawson 2001; Sotka et al. 2004; Baums et al. 2006). The best example of this to date is the Mona Passage, where coupled biological–physical oceanographic models predict highly restricted larval dispersal across a channel that corresponds with a population genetic break (Baums et al. 2005, 2006; Galindo et al. 2006).

Despite the success of such bio-oceanographic models and the identification of concordant patterns of population structure, the geographical locations of genetic breaks often differ among taxa. Patterns of population structure have also been associated with habitat affiliation, phylogeny, and life history. Marko (2004) and Rocha et al. (2002) found that habitat affiliation was the best predictor of differential patterns of population structure in two species of thaid gastropods (*Nucella* spp.) and three species of Atlantic surgeon fishes (*Acanthurus* spp.), respectively. The degree of genetic similarity is predictive of population structure in a group of three limpets in New Zealand, where the sister species *Cellana flavia* and *Cellana radians* exhibit similar levels of partitioning relative to the more divergent *Cellana ornata* across Cook Strait (Goldstien et al. 2006a, b). Life history, specifically pelagic larval duration, is a predictor of realized dispersal and population genetic structuring (Shanks et al. 2003; Paulay & Meyer 2006), although there are notable exceptions (reviewed in Gooch 1975; Hedgcock 1986; Palumbi 1994; Bohonak 1999).

The ability to predict the location of genetic breaks across taxa applies directly to the implementation of marine protected areas (MPAs). Effective MPAs must not only sustain target species within their boundaries, but also serve as reproductive reservoirs that supply recruits to unprotected areas (Roberts et al. 2001). Thus, the positioning of MPAs is critical, and their success is maximized when guided by accurate information about the patterns of connectivity among populations (Crowder et al. 2000; Dawson et al. 2006; Steneck et al. 2006), which can be ascertained with molecular techniques (Grosberg & Cunningham 2001; Palumbi 2003). When direct tagging is infeasible, molecular genetic approaches are one of the few options for documenting patterns of connectivity and designing effective MPA networks (Swearer et al. 2002).

The Hawaiian Archipelago (Fig. 1) is recognized as an excellent system for the study of terrestrial speciation and evolution (Hillebrand 1888; Wagner & Funk 1995). Less appreciated are marine population processes which operate across a larger geographical expanse of high and low islands, atolls, and submerged reefs (e.g. Rivera et al. 2004; Andrews et al. 2006; Craig et al. 2007). The objectives of this study are to illuminate the traits that shape population structure, and ultimately to resolve and define management units for the three endemic Hawaiian limpets (*Cellana exarata*, *Cellana sandwicensis*, and *Cellana talcosa*), known locally as opishi. The opishi are closely related sister taxa.
Management concerns for the opihis are compelling. The opihis are a prominent component of Hawaiian culinary culture, and are harvested commercially, recreationally, and for subsistence. Between 1900 and 1944, the commercial harvest of opihis decreased by an order of magnitude, to a present day average of ~6300 kg annually (Jordan & Evermann 1902, 1905; Hawaii Department of Land & Natural Resources 2005). MPAs are integral to a management initiative intended to reverse the decline of opihis, as well as other marine taxa in Hawaii (Halpern & Warner 2006; Roberts et al. 2003).

The study of sympatric sister species provides an appropriate context for comparative phylogeographical studies (see Collin 2001; Dawson et al. 2002; Paulay & Meyer 2006). Here we conduct range-wide surveys of all three species using 612 bp of cytochrome c oxidase subunit I (COI) to evaluate migration rates and patterns of population partitioning. Given the approximately linear arrangement of islands (Fig. 1), genetic differentiation should be correlated with geographical distances among sampling sites. Modest genetic structure and clinal patterns are expected under an island-hopping model with recruitment patterns characterized by isolation by distance (IBD) (Wright 1943). Using the Hawaiian Cellana, we evaluate the utility of representative ‘model’ species in predicting connectivity within and among communities, an approach that is pertinent to the design of MPA networks. In particular, we investigate patterns of population genetic structure in the context of four criteria:

1. Habitat model: the intertidal *Cellana exarata* and *C. sandwicensis* will have concordant population structure relative to the subtidal *C. talcosa*. (See Materials and methods for details).
2. Biogeographical model: the wide-ranging *Cellana exarata* and *C. sandwicensis* will have less pronounced population structure than the range restricted *C. talcosa*.
3. Phylogenetic model: the sister species *C. sandwicensis* and *C. talcosa* will have concordant population structure relative to the basal *C. exarata*.
4. Larval life history model: all three species will have uniform levels of population structure based on their similar larval life histories.

**Materials and methods**

**Sampling sites**

All sampling took place within the Hawaiian Archipelago (Fig. 1), which is centrally located in the tropical Pacific Ocean, ~3800 km from the nearest continent or high island. Within the main Hawaiian Islands (MHI), there are eight islands separated by oceanic channels of 11–160 km (Fig. 1). In the Northwestern Hawaiian Islands (NWHI), which is separated from the MHI by a 240-km channel, there are nine additional islands and a number of shallow, submerged reefs extending ~2400 km from the Big Island of Hawaii, with a maximum channel width of 380 km. Despite the broad geographical scale of the Hawaiian Archipelago, it spans less than 10° of latitude, which confers a more uniform climate than most continental margins. There are three primary currents in the Hawaiian Archipelago, the North Hawaiian Ridge Current which flows to the northwest along the island chain (Qiu et al. 1997), the Hawaiian Lee Countercurrent and the Subtropical Counter-current which both generally flow from west to east (Kobashi & Kawamura 2002). Theoretically, larvae should be able to get everywhere in archipelago on these currents. However, currents flow southwesterly through the channels, perpendicular to the island chain, and every channel between the islands holds the potential to constrict gene flow for species restricted to shallow coastal habitats. Based on Hawaiian geography, one would expect a simple population genetic pattern of IBD along the linear transect of island habitats.

**Study organisms**

Limpets in the genus *Cellana* are shallow water gastropods with moderate dispersal potential, although a number of species have broad distributions, occupying vast areas of the Asian, Indonesian, Indian, Australian, African coasts, as well as remote Indo-Pacific archipelagos (Powell 1973). Three endemic Hawaiian limpets (*C. exarata*, *C. sandwicensis*, and *C. talcosa*) inhabit the high intertidal, low intertidal, and shallow subtidal zones on wave-exposed rocky shores, respectively (Kay & Magruder 1977; C.E.B. unpublished data). Based on habitat affiliation, we expect the two intertidal species, *C. exarata* and *C. sandwicensis*, to have concordant population structure relative to the subtidal *C. talcosa*.

*Cellana exarata* and *C. sandwicensis* occur on every basaltic island, from the island of Hawaii (19°00′N, 155°40′W) to Puhahonu (25°01′N, 167°59′W), while *C. talcosa* is restricted to the MHI, from Hawaii to Niihau (22°00′N, 160°05′W) (Fig. 1). Based on biogeographical distribution, we expect that *C. exarata* and *C. sandwicensis* should exhibit similar patterns of population partitioning. If restricted range indicates restricted dispersal ability, *C. talcosa* should be characterized by the lowest dispersal and greatest corresponding population structure (Thorson 1950; Gilman 2006; Paulay & Meyer 2006).

In terms of larval behaviour, *Cellana exarata* and *C. sandwicensis* are competent to settle within 3 to 4 days of fertilization...
in laboratory cultures (Corpuz 1981; 1983; C.E.B. unpublished data), but Corpuz (1983) noted that C. exarata could delay settlement and remain in the pelagic veliger stage for at least 18 days. We and others have cultured the third species (C. talcosa) under similar laboratory conditions, and its development mirrored that of the other two species (C.E.B. unpublished data, Sarver unpublished data). Based on our limited knowledge of larval duration and behaviour, all three species are expected to exhibit similar levels of dispersal and population structure.

Sequence divergence in 521 bp of the ribosomal subunit 16S is 1.2% between C. sandwicensis and C. talcosa and 2.2% between C. exarata and the aforementioned sister species (Reeb 1995; C.E.B. unpublished data). Because the three species of opihi are closely related, phylogenetically, they are predicted to exhibit similar levels of population partitioning. An alternate prediction, based on phylogenetic order of the taxa, is that C. sandwicensis and C. talcosa will exhibit concordant population structures relative to C. exarata.

**Sampling**

The three species of Hawaiian Cellana were sampled between 2003 and 2005 at eight sites on six islands (Fig. 1). To simplify sites labels, we have numbered the islands from one to six and sites within an island were designated as either a or b. Thus, the sampling sites in the MHI include (southeast to northwest): Halape, Hawaii (1a); Kalaemano, Hawaii (1b); Kaluapapa, Molokai (2); Poipu, Kauai (3a); and Princeville, Kauai (3b). The sampling sites in the NWHI include Nihoa (4), Mokumanamana (5), and the La Perouse Pinnacles at Mokupapapa (6).

Whole animals were collected, or a small piece of tissue (~10 mg) was removed from the mantle using a sterile razor blade. Tissue specimens were immediately frozen or preserved in 95% ethanol. The NWHI posed a particular challenge to collections because of their remoteness, the consequent inability of the authors to be present for sample collection, and the paucity of sampling opportunities. Ophi exist in the most hydrodynamically extreme habitat in the Hawaiian Archipelago, where the mean significant wave height is two to three-fold greater than the diurnal tidal range (C.E.B. unpublished data). As a result of its lower position on the shoreline, C. sandwicensis is more hazardous to collect than C. exarata, and we have fewer samples. Sample sizes per population ranged from $n = 11$ to $n = 36$ (Table 1).

**PCR and sequencing**

Genomic DNA was extracted from the tissue samples using QIAGEN DNeasy Animal Tissue Kits. One mitochondrial DNA locus, COI 612 bp, was amplified using polymerase chain reaction (PCR). We used the COI primers LCO1490:

Table 1: Sample size, total number of haplotypes, number of unique haplotypes to a sampling site (Locality haplotypes), haplotype diversity, and nucleotide diversity in COI for each species. Cs is Cellana sandwicensis, Ct is Cellana talcosa, and Ce is Cellana exarata.

<table>
<thead>
<tr>
<th>Region</th>
<th>Island</th>
<th>Site</th>
<th>Specimens (N)</th>
<th>Total no. of haplotypes</th>
<th>Locality haplotypes</th>
<th>Haplotype diversity ($h$)</th>
<th>Nucleotide diversity ($\pi$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>MHI</td>
<td>HI</td>
<td>1a</td>
<td>20</td>
<td>22</td>
<td>20</td>
<td>0.99 ± 0.02</td>
<td>8.2 ± 10^-3 ± 3 × 10^-3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1b</td>
<td>21</td>
<td>20</td>
<td>23</td>
<td>0.92 ± 0.04</td>
<td>5.9 ± 10^-3 ± 3 × 10^-3</td>
</tr>
<tr>
<td></td>
<td>MO</td>
<td>2</td>
<td>18</td>
<td>21</td>
<td>20</td>
<td>0.99 ± 0.04</td>
<td>5.9 ± 10^-3 ± 3 × 10^-3</td>
</tr>
<tr>
<td></td>
<td>KA</td>
<td>3a</td>
<td>18</td>
<td>20</td>
<td>20</td>
<td>0.99 ± 0.04</td>
<td>5.9 ± 10^-3 ± 3 × 10^-3</td>
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<tr>
<td></td>
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<td>3b</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>0.99 ± 0.04</td>
<td>5.9 ± 10^-3 ± 3 × 10^-3</td>
</tr>
<tr>
<td>NWHI</td>
<td>NH</td>
<td>4</td>
<td>11</td>
<td>18</td>
<td>21</td>
<td>0.92 ± 0.04</td>
<td>5.9 ± 10^-3 ± 3 × 10^-3</td>
</tr>
<tr>
<td></td>
<td>MM</td>
<td>5</td>
<td>23</td>
<td>18</td>
<td>13</td>
<td>0.98 ± 0.08</td>
<td>5.9 ± 10^-3 ± 3 × 10^-3</td>
</tr>
<tr>
<td></td>
<td>MP</td>
<td>6</td>
<td>36</td>
<td>8</td>
<td>7</td>
<td>0.98 ± 0.08</td>
<td>5.9 ± 10^-3 ± 3 × 10^-3</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td>150</td>
<td>109</td>
<td>105</td>
<td>0.90 ± 0.02</td>
<td>6 ± 10^-3 ± 3 × 10^-3</td>
</tr>
</tbody>
</table>
Carlo (MHMCMC) search strategy was implemented. A Bayesian Metropolis Hastings Markov chain Monte Carlo (MHMCMC) model was used to estimate migration rate and other parameters. The model was run for one cycle with a 4-min, 95 °C denaturation step, a 1-min 30 s, 48 °C annealing step, and a 2-min, 72 °C elongation step on a Bio-Rad thermocycler. Thirty-four additional cycles were run with the following parameters: 30 s at 94 °C, 30 s at 48 °C, and 45 s at 72 °C, concluding with a final 10-min elongation step at 72 °C. PCR products were cleaned by adding 1.6 µL of exonuclease 1 and 1.6 µL of shrimp alkaline phosphatase (Exo-SAP) to 18 µL of PCR product and incubating at 37 °C for 30 min and 80 °C for 10 min. Purified DNA fragments were sequenced by the commercial service Macrogen and the Hawaii Institute of Marine Biology EPSCoR Sequencing Facility. There were no indels or broken reading frames, and the DNA sequences were aligned by eye.

Data analysis

Analysis of molecular variance (AMOVA) was used for hierarchical analysis of partitioning of COI diversity within and among populations, as well as within and among groups of populations using ARLEQUIN 3.01 (Excoffier et al. 2005). Population pairwise ΦST values, Nei's average pairwise genetic distance (Nei & Li 1979), and exact tests of population differentiation (Raymond & Rousset 1995) were also computed with ARLEQUIN.

Tests based on the infinite-alleles (Ewens 1972; Watterson 1978; Slatkin 1996) and infinite-sites models (Tajima 1989; Fu 1997) were used to test for significant deviations in allele frequencies from neutral expectations, as implemented in ARLEQUIN. Because many population genetic estimates are relatively insensitive to weak selection (see Slatkin & Barton 1989), loci which do not fail these tests are expected to provide reliable inferences about population structure (Hutchison & Templeton 1999).

Coalescent-based calculations of migration rate among populations (Nm) and the population mutation parameter (θ) were conducted with LAMARC 2.02 (Kuhner 2006). LAMARC was chosen over IM for this analysis because LAMARC is not limited by population number, while IM is restricted to two populations (Hey & Nielsen 2004). The calculations performed by ARLEQUIN are based on island model assumptions which are rarely met in natural populations (Whitlock & McCauley 1999). In contrast, LAMARC does not rely on the same population assumptions. A Bayesian Metropolis Hastings Markov chain Monte Carlo (MHMCMC) search strategy was implemented where one final Markov chain was executed with 60,000 samples, a final sampling interval of 40, and 2000 samples to discard. Three simultaneous searches with heating were enabled at temperatures of 1, 1.1, and 1.3. The upper and lower Bayesian priors were set to their maximum and minimum possible values, respectively. MODELTST 3.7 (Posada & Crandall 1998) was used to determine that a TrN base-substitution model (Tamura & Nei 1993) was most appropriate for each of the three species investigated. The posterior probability distributions were examined to determine the validity of each estimated parameter.

rsrs 13.0 was used to conduct ordinary least squares regressions to assess the association between pairwise genetic and geographical distance matrices–IBD. In certain cases, data were transformed or quadratic explanatory terms were added to the model to satisfy all assumptions of ordinary least squares regression. For example, fitting a straight line through a curved set of data will produce a patterned, nonhomogenous spread of the residuals when plotted against the fits, thereby invalidating the least squares regression model and the associated statistics (Neter et al. 1996). We did not use reduced major axis regression (Hellberg 1994) because the population samples were collected at point locations (<< 50 m of coastline) and populations were separated by a minimum of 63 km. Therefore, there is little variance in our measurements of distance relative to that of F-statistics (Nei et al. 1977), and ordinary least squares regression is the most appropriate analysis.

Two measures of geographical distance were used: the minimum travel distance between sites for pelagic larvae, and the cumulative minimum distance between islands. In the first geographical distance measure, no distinction is made between the distance travelled along a contiguous coastline and across the channels between islands. The second geographical distance measure assumes that islands are stepping-stones (sensu Kimura 1953), where distance along contiguous coastlines is ignored, and only the minimum cumulative open-water distance between islands is considered.

Results

Totals of 150 Cellana exarata, 109 Cellana sandwicensis, and 105 Cellana talcosa were sampled in this study (Table 1). Unique haplotypes were submitted to GenBank (Accession nos EF620934-EF621301).

Parsimony networks and population summary statistics

In all three species, we observed a large number of closely related haplotypes and high haplotype diversities (Table 1). Eighty-three per cent of the haplotypes were restricted to related haplotypes and high haplotype diversities (Table 1). In all three species, we observed a large number of closely related haplotypes and high haplotype diversities (Table 1). Eighty-three per cent of the haplotypes were restricted to one sampling site (hereafter referred to as locality haplotypes). In the total pooled samples, C. sandwicensis exhibited the highest haplotype diversity ($h = 0.96$),
followed by *C. talcosa* (*h* = 0.90), and *C. exarata* (*h* = 0.75). Nucleotide diversities tended to be low (π = 0–0.008) and were positively correlated with haplotype diversity in the three species.

Parsimony networks for each Hawaiian *Cellana* species exhibited strikingly different patterns, despite having similar numbers of haplotypes (Fig. 2, Table 1). *C. sandwicensis* exhibited the lowest association between haplotype identity and geographical location. Three of the five most common *C. sandwicensis* haplotypes are shared between the NWHI (sites 4–6) and the MHI (sites 1–3). Even low frequency haplotypes were shared between islands and between the NWHI and MHI. Forty-nine of the 59 haplotypes were restricted to a locality, but 45 of these 49 were singletons and were only sampled at one site, by definition.

*Cellana exarata* exhibited an intermediate level of association between haplotype and geographical location (Fig. 2, Table 1). The parsimony network of *C. exarata* was defined by a single dominant haplotype (*n* = 74) observed at every site, and three haplotypes that were common in the MHI (*n* = 4). Most haplotypes diverge from the dominant haplotype by only one to three mutations. MHI sites exhibit higher diversity and a greater number of unique haplotypes than NWHI sites. Only one haplotype was observed between the NWHI (4–6) and MHI sites (1–3), indicating that successful migration events between these regions are rare. The most striking spatial pattern is the detection of only one haplotype at site 5, while the flanking sites on Molokapapa (6, northwest), Nihoa (4) and Kauai (3a, southeast) had nine, two, and 11 sampled haplotypes, respectively. Overall, 43 of 52 haplotypes were restricted to a locality (41 singletons).

*Cellana talcosa* had the strongest association between haplotype and geographical location, most notably with fixed differences among haplotypes sampled on Kauai (sites 3a, b) and the other MHI sampled (sites 1–2, Fig. 2, Table 1). Six haplotypes were observed on Kauai, which were each distinguished by one to four mutations from haplotypes sampled elsewhere in the MHI. In contrast, 18 haplotypes were identified at site 2 on Molokai, and 29 haplotypes were identified at sites 1a, b on the Island of Hawaii. Four haplotypes were observed on both islands, indicating greater connectivity between Molokai and Hawaii than between either of these sites and Kauai. Overall, 40 of 49 haplotypes were restricted to a locality (39 singletons).

**Analysis of molecular variance**

The sampling sites were grouped by region and site for an AMOVA of the COI gene (Table 2). The regions were defined as the NWHI (sites 4–6) and the MHI (sites 1–3)
for *C. exarata* and *C. sandwicensis*, and the regions were defined as Kauai and the other MHI for *C. talcosa*, which is not known to occur in the NWHI.

In *C. exarata*, no significant effect of region was detected ($\Phi_{CT} = 0.02, P = 0.06$, Table 2a), but the effect of site nested within region was significant ($\Phi_{SC} = 0.02, P = 0.04$). The combined effect of site within region and region, i.e. the overall population genetic structuring, was highly significant ($\Phi_{ST} = 0.04, P < 0.01$).

In *C. sandwicensis*, genetic variation was significantly partitioned between regions ($\Phi_{CT} = 0.07, P < 0.01$, Table 2b) but not among the sites nested within the regions ($\Phi_{SC} = 0.01, P = 0.18$). The overall population genetic structuring was significant ($\Phi_{ST} = 0.08, P < 0.01$).

A large portion of the genetic variation in *C. talcosa* was partitioned between the regions ($\Phi_{CT} = 0.30, P < 0.01$, Table 2c), but there was no indication of partitioning among the sites nested within the regions ($\Phi_{SC} = 0.001, P = 0.45$). The overall population genetic structuring was highly significant ($\Phi_{ST} = 0.30, P < 0.01$).

### Migration–gene flow estimates

In general, the lowest effective migration rates ($N_{e}M$) were associated with the largest oceanic gaps between sites. The migration rates of *C. exarata* and *C. sandwicensis* were lowest between the MHI and the NWHI, while the migration rate of *C. talcosa* was lowest between Kauai (sites 3a, b) and the other MHI (sites 1–2, Table 3). Given the haplotype frequency distribution (Table 1, Fig. 2), effective migration estimates should be less than one per generation (Slatkin

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>SS</th>
<th>MS</th>
<th>Var comp</th>
<th>% var</th>
<th>$\Phi_{CT}$</th>
<th>$\Phi_{SC}$</th>
<th>Sig</th>
<th>$\Phi_{ST}$</th>
<th>Sig</th>
</tr>
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<tbody>
<tr>
<td><strong>A. C. exarata</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Region</td>
<td>1</td>
<td>2.27</td>
<td>2.27</td>
<td>0.015</td>
<td>1.90</td>
<td>0.019</td>
<td>0.057</td>
<td>0.036</td>
<td><strong>0.001</strong></td>
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</tr>
<tr>
<td>Site (region)</td>
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<td>5.33</td>
<td>1.07</td>
<td>0.014</td>
<td>1.73</td>
<td>0.017</td>
<td><strong>0.041</strong></td>
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</tr>
<tr>
<td>Within site</td>
<td>143</td>
<td>111.65</td>
<td>0.78</td>
<td>0.781</td>
<td>96.37</td>
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<tr>
<td><strong>B. C. sandwicensis</strong></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Region</td>
<td>1</td>
<td>6.90</td>
<td>6.90</td>
<td>0.125</td>
<td>6.86</td>
<td>0.069</td>
<td><strong>0.001</strong></td>
<td>0.078</td>
<td><strong>0.001</strong></td>
<td></td>
</tr>
<tr>
<td>Site (region)</td>
<td>4</td>
<td>7.99</td>
<td>2.00</td>
<td>0.018</td>
<td>0.97</td>
<td>0.010</td>
<td>0.179</td>
<td></td>
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</tr>
<tr>
<td>Within site</td>
<td>103</td>
<td>172.50</td>
<td>1.67</td>
<td>1.675</td>
<td>92.17</td>
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<tr>
<td>Total</td>
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<td>187.39</td>
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*MH*, Main Hawaiian Islands; *NWHI*, Northwestern Hawaiian Islands; *HI*, Island of Hawaii; *MO*, Molokai; *KA*, Kauai; *MM*, Mokumanamana; *MP*, Mokupapapa.
from the NWHI and between the NWHI and the MHI range are close to this expectation, where migration rates within the other MHI. The Bayesian estimates of migration rate NeM for C. exarata and C. sandwicensis, and for C. talcosa. Factors that explain a significant amount of variance (α = 0.05), given the previous factors entered in the model are indicated by bold font.

Within islands, estimates of dispersal were consistently high for both the big island of Hawaii (sites 1a, b) and Kauai (sites 3a, b), with all three species characterized by estimated migration rates NeM > 8.

Isolation by distance

Pairwise ΦST values were regressed against the cumulative stepping-stone distance and the larval travel distance to assess conformation to an IBD model (Fig. 3, Table 4). Stepping-stone distance between sites explained a significant and substantial proportion of the population differentiation (ΦST) for C. exarata (R2 = 0.56, P = 0.05), C. sandwicensis (R2 = 0.76, P = 0.01), and C. talcosa (R2 = 0.87, P < 0.01). The relationship between ΦST and stepping-stone distance was quadratic for C. exarata and C. sandwicensis, but linear for C. talcosa. Stepwise multiple regression indicated that the number of steps (channel crossings) between sites explained an additional 11% of the variance in ΦST, given the stepping-stone distance for C. talcosa (AR2 = 0.11, P = 0.02), but not for C. exarata or C. sandwicensis. Notably, larval travel distance (see Materials and methods) was not significantly related to pairwise ΦST.

The estimated migration rates from lамarc for each Cellana spp. were plotted against the cumulative stepping-stone distance (Fig. 4). While most regressions of migration rate vs. distance are linear on a log-log scale, there was an asymptotic relationship between stepping-stone distance and the simulated migration rate of C. talcosa. Consequently,

Table 4 Stepwise regression results for each species of Cellana. The dependent variable was the pairwise population ΦST, and the independent factors were cumulative stepping-stone distance between sites (SSD), the number of steps between sites (S), and the minimum larval travel distance between sites (LTD). The independent factors were added in the order shown. In order to meet the assumptions of the model, independent factors were quadratic for C. exarata and C. sandwicensis, and linear for C. talcosa.

<table>
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Discussion

The endemic Hawaiian *Cellana* spp. are sympatric species in a monophyletic group, with similar life histories. In this range-wide survey, we were interested in illuminating aspects of marine phylogeography among these species for management purposes, in the context of the common assumption that a single representative or model species can be used as a proxy to estimate dispersal among marine communities. Would surveying one species give us the proper foundations for management of all three? With distinct differences in population structure, the opili say ‘no’.

Population genetic diversity and structure

All three species are characterized by high haplotype diversity and low nucleotide diversity. However, the distribution of genetic diversity differed significantly among sites for the three species. Haplotype diversity was high for all three species on Hawaii and Molokai (MHI), the areas of greatest population size, based on available habitat. Orienting along a southeast to northwest axis, the haplotype diversity of *Cellana talcosa* and *Cellana exarata* dropped significantly (although *C. exarata* diversity increased from site 5 to site 6). In contrast, *Cellana sandwicensis* exhibited no decline in genetic diversity throughout this range.

Significant population partitioning was detected in all three species of Hawaiian limpets with AMOVA, but regional patterns of differentiation were not consistent among species. Pairwise *Φ* s values did reveal one common feature: gene-flow restrictions between northwestern and southeastern populations. For *C. exarata* and *C. sandwicensis*, a minor restriction was identified between the NWHI and MHI, and for *C. talcosa* a major restriction was identified between Kauai (northwest end of distribution) and remaining MHI samples.

Channels appear to be significant barriers to gene flow. However, channel width did not uniformly predict dispersal restrictions. The 255-km channel separating the NWHI from the MHI seems to be a significant barrier to gene flow for all Hawaiian *Cellana*. However, NWHI sites separated by 210–260 km were not significantly partitioned. This may be due, in part, to limited statistical power in the NWHI samples: small sample sizes in *C. sandwicensis* and depauperate haplotype diversity in *C. exarata*. Alternatively, the currents between Kauai (MHI) and Nihoa (NWHI) may be more restrictive to larval transport than those between the NWHI sites.

Within the MHI, significant population partitioning was detected between *C. sandwicensis* populations separated by 426 km (sites 1b, 3a) and between *C. exarata* and *C. talcosa* populations separated by 270 km (sites 2, 3a). If we assume that the channels between the islands are the primary
barriers to gene flow, then *C. exarata* and *C. talcosa* exhibited significant population structure when separated by 159 km of water and one island (Molokai–Kauai), and *C. sandwicensis* exhibited significant partitioning when separated by 218 km of water and three islands (Hawaii–Kauai).

**Geography and isolation by distance**

Evidence of IBD was observed in all three opihi based on regressions of pairwise population $\Phi_{ST}$ and Bayesian MHMCMC migration rate against geographical distance. The slopes for the range-restricted *C. talcosa* were consistently much steeper than those for *C. exarata* or *C. sandwicensis*, indicating lower gene flow. In the regression of $\Phi_{ST}$ against distance, *C. exarata* and *C. sandwicensis* exhibited shallow but significant quadratic relationships while *C. talcosa* exhibited a steep linear relationship (Fig. 3) where isolation increases with distance. For *C. exarata* and *C. sandwicensis*, $\Phi_{ST}$ values may asymptote due to the dispersal potential of the organisms, the finite range of opihi habitats (~1300 km) and their spatial arrangement.

Previous studies of marine population structure have emphasized the importance of stepping-stone habitats in maintaining connectivity among marine populations (Riginos & Nachman 2001; Barber et al. 2002). IBD regressions indicated that the ‘stepping-stone distance’ among islands was a better predictor of isolation than the distance between collection sites, i.e. minimum larval travel distance. Additionally, significant structure was not detected between populations sampled on the same islands. These data indicate that there is high connectivity along coastlines within an island and comparatively low connectivity between adjacent islands. In Bayesian estimates of migration, the slopes were approximately –1 for *C. sandwicensis* and *C. exarata*, suggesting a one-dimensional stepping-stone arrangement of populations (Slatkin & Maddison 1989; Slatkin 1991; Hellberg 1994), as expected based on the generally linear arrangement of islands in the Hawaiian Archipelago. With a slope ranging from approximately –4 to –6, *C. talcosa* exhibits a nonlinear IBD response and does not conform to theoretical expectations of either a one or two-dimensional stepping-stone model.

**Evaluation of model species criteria**

In the next four subsections, we evaluate hypotheses for predicting population structure in Hawaiian limpets. These correspond to habitat (intertidal-subtidal), biogeography (range size), phylogeny (sister species), and life history (larval duration).

**Habitat.** *C. exarata* and *C. sandwicensis* reside above the waterline, while *C. talcosa* resides subtidally. Based on habitat specialization and the fact that submergence is a spawning cue for the two intertidal species (Corpuz 1983), we would expect concordant structure in the two intertidal species. The data are consistent with this prediction. *C. talcosa* larvae may behave differently to enhance recruitment into their specialized shallow subtidal habitat, perhaps leading to an increased degree of larval retention (see Paris & Cowen 2004) and greater genetic structure.

**Biogeography and range size.** If restricted range is indicative of limited dispersal, then *C. talcosa* should have the most pronounced population structure (Thorson 1950; Gilman 2006; Paulay & Meyer 2006). Indeed, many endemic Hawaiian fishes are believed to be the product of restricted gene flow (reviewed in Hourigan & Reese 1987), a somewhat counterintuitive notion given the vast geographical leap required to colonize Hawaii. Yet a growing body of evidence indicates that extensive dispersers can maintain contact between Hawaiian populations and conspecifics elsewhere in the central West Pacific (Lessios et al. 2003; Craig et al. 2007; Schultz et al. 2007), reducing opportunities for speciation in isolation. In contrast, when a species with limited dispersal makes the rare leap to Hawaii, it does not maintain genetic connectivity with other Pacific habitats, and the isolated Hawaiian population is set upon an independent evolutionary trajectory. In the Hawaiian limpets, restricted range seems to be a good predictor of gene flow. Clearly, the most abrupt partitioning was observed in *C. talcosa*, where all six haplotypes detected on Kauai were endemic (Fig. 2), thereby indicating no recent gene flow. Hence, the species with the most restricted range shows clear evidence of the most restricted gene flow in concordance with predictions of the biogeographical model.

**Phylogeny.** Based strictly on phylogenetic criteria, the sister taxa *C. sandwicensis* and *C. talcosa* should exhibit similar patterns of population partitioning relative to *C. exarata*. Phylogeny can be a powerful predictor of concordance in population structure and other organismal traits (Bowen et al. 2006). However, contrary evidence exists (Rocha et al. 2002). In opihi, similarities in population connectivity are not predicted by phylogenetic relationships. The two sister species are at opposite ends of the continuum, ranked from high to low gene flow: *C. sandwicensis* ≥ *C. exarata* > *C. talcosa*. Consequently, our data do not support the idea that phylogenetic similarity is correlated with population genetic patterns.

**Larval life history.** Based on the available data regarding the minimum pelagic larval duration of the Hawaiian *Cellana*, one would expect similar levels of population partitioning among these species. However, our data clearly do not support this model. The simplest explanation...
for the observed difference in population structure between *C. talcosa* and the other opihis is a divergence in larval behaviour or duration (Scheltema 1988; Shulman 1998; Riginos & Victor 2001). Although the minimum larval duration is similar among the opihis, perhaps the maximum pelagic duration of *C. talcosa* larvae is shorter than the other two opihis species. Direct comparison of the larval biology of Hawaiian ophihis should help to elucidate the root cause of the differential population structure observed in this monophyletic lineage.

Overall, two hypotheses were supported and two were rejected, but none of these hypotheses are mutually exclusive. For example, we believe there is a likely correlation between habitat type and larval behaviour that could be considered part of the larval life history. Additionally, the Hawaiian *Cellana* spp. do not allow for differentiation between the restricted range model and the habitat model because of the correlation between habitat preference and biogeographical range. Nonetheless, phylogeny and pelagic larval duration were not supported as predictors of population structure, while biogeographical range and habitat were supported. There are also clear signatures of recent range expansion (*C. talcosa*, Kauai) and genetic bottlenecks (*C. exarata*, NWHI) reflecting the role of historical events in shaping contemporary population structure.

### Management Implications

The resolution of connectivity among communities is imperative for the delineation of MPA networks (Dawson et al. 2006; Steneck et al. 2006). While Hawaiian *Cellana* exhibit a diversity of population genetic patterns, they nonetheless show significant structure in all three species. These findings, coupled with habitat differences (C.E.B. unpublished data), demonstrate that a species-specific treatment adds significantly to our understanding and management of these taxa. Specifically, current management practice, where all opihis species are pooled into a single management unit should be abandoned and replaced by strategies that incorporate the differences in population connectivity among species.

There is long-standing controversy regarding whether the uninhabited NWHI (a recently designated Marine National Monument and the world’s largest MPA) is a source of larvae for the depleted fisheries of the MHI (Polovina et al. 1999; DeMartini & Friedlander 2004). In the case of opihis, the answer is no. There is significant partitioning between the NWHI and the MHI in both *C. exarata* (pairwise $\Phi_{ST} = 0.03–0.08$) and *C. sandwicensis* (pairwise $\Phi_{ST} = 0.01–0.08$) and estimates of dispersal (effective migrants per generation ≤ 2) are too low to augment the depleted MHI fishery. The patterns of population subdivision clearly indicate that the NWHI do not harbour source populations of opihis capable of seeding the MHI. Even within the MHI, a single MPA is unlikely to function as a source for other islands because all three opihis exhibit significant structure on this geographical scale.

### Conclusion

Population partitioning in the three species of Hawaiian *Cellana* was observed at finer spatial scales (< 200 km) than was expected for broadcast-spawning invertebrates with a pelagic larval phase. Barriers to gene flow do not include geologically ancient land masses (*sensu* Barber et al. 2002). Instead, deep open ocean channels and variable currents among islands (*sensu* Taylor & Hellberg 2003, 2006; Baums et al. 2006) act to restrict gene flow. Despite close phylogenetic affinity and similar life histories, the endemic Hawaiian *Cellana* exhibit distinctly different population structures. Among the four factors evaluated to explain patterns of connectivity, the habitat specificity and biogeography models best fit the data; while predictions based on phylogenetic affinity and larval life history did not match patterns of population partitioning. These contrasting population genetic signatures highlight the hazards of making sweeping predictions about population connectivity from alleged model organisms, even among closely related species with similar life histories.

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References


Hutchison DW, Templeton AR (1999) Correlation of pairwise


Chris Bird studies coastal molecular community ecology and believes in the sanctity of ‘ōpīhi. Brendan Holland is a gentleman with diverse molluscan interests. Brian Bowen studies the phylogeography of marine vertebrates but acknowledges lessons from the other ~32 phyla in the animal kingdom. Rob Toonen studies marine invertebrates but also acknowledges lessons from the chordata.

### Supplementary material

The following supplementary material is available for this article:

**Table S1** Pairwise population $\Phi_{ST}$ values, their significance, and the significance of exact tests of sample differentiation.

**Table S2** Proportional pairwise population migration rate estimates ($M$) for each Cellana spp.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-294X.2007.03385.x

(This link will take you to the article abstract).

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