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Sea snakes rarely venture far from home

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Abstract

The extent to which populations are connected by dispersal influences all aspects of their biology and informs the spatial scale of optimal conservation strategies. Obtaining direct estimates of dispersal is challenging, particularly in marine systems, with studies typically relying on indirect approaches to evaluate connectivity. To overcome this challenge, we combine information from an eight-year mark-recapture study with high-resolution genetic data to demonstrate extremely low dispersal and restricted gene flow at small spatial scales for a large, potentially mobile marine vertebrate, the turtleheaded sea snake (*Emydocephalus annulatus*). Our mark-recapture study indicated that adjacent bays in New Caledonia (<1.15 km apart) contain virtually separate sea snake populations. Sea snakes could easily swim between bays but rarely do so. Of 817 recaptures of marked snakes, only two snakes had moved between bays. We genotyped 136 snakes for 11 polymorphic microsatellite loci and found statistically significant genetic divergence between the two bays ($F_{ST} = 0.008$, $P < 0.01$). Bayesian clustering analyses detected low mixed ancestry within bays and genetic relatedness coefficients were higher, on average, within than between bays. Our results indicate that turtleheaded sea snakes rarely venture far from home, which has strong implications for their ecology, evolution, and conservation.

Introduction

All widespread species exhibit some degree of population structure, often with higher levels of genetic exchange among individuals that live in the same area, than between individuals that live further apart. Such subdivisions can create a series of more-or-less separate local populations linked by relatively low rates of gene flow (Hanski 1999). Subdivision of a widespread taxon into discrete populations, that function as separate ecological units, has important implications. At an evolutionary level, low dispersal rates among subpopulations enable local adaptations to accumulate. At an ecological level, philopatry of predators means that the prey resources within a single area need to be sufficient, year-round, to sustain that predator population. In terms of management, philopatry means that any perturbation to a local system will have primarily local consequences, but that recovery may be delayed because of low immigration of conspecifics from other areas.

In terms of conservation priorities, the spatial heterogeneity in major traits permitted by philopatry may result in much of the critical genetic variation within a species occurring among rather than within populations, such that the loss of any single population could reduce genetic diversity in the taxon overall (Hanski 1999).

Although adult philopatry has important implications for population connectivity, dispersal by propagules or juveniles often affords high levels of connectivity even when adults are sedentary (e.g., plants and many benthic marine invertebrates and demersal vertebrates). Indeed, dispersal by propagules is so important in the marine environment that the paradigm of larval dispersal dominates marine connectivity research (Cowen and Sponaugle 2009; Jones et al. 2009; Weersing and Toonen 2009), particularly in relation to fisheries management and the design of effective marine protected areas (McCook et al. 2009). However, the considerable diversity of life-history strategies among marine

species (e.g., from oviparous to viviparous) means marine connectivity studies must also consider taxa that do not fit the larval dispersal paradigm. In addition, average year-round movement patterns of adults are not necessarily good predictors of demographic connectivity if they are uncoupled from breeding events, such as migrations to breeding sites (e.g., nesting sites of marine turtles [Avise 2007]). In order to understand demographic population connectivity of mobile species, we need empirical data about movement patterns of adults (and juveniles) combined with spatial information about mating success and reproduction. However, spatially explicit data about movement patterns and reproductive success are notoriously difficult to obtain in the marine environment. As such, researchers typically rely on indirect methods, such as population genetics or oceanographic modeling, to infer the degree of demographic isolation versus connectivity among populations (Jones et al. 2009).

Although sea snakes are diverse and abundant in tropical coral-reef systems, the ecology of these animals has attracted little detailed research. These large and powerful animals have the potential for long distance dispersal (Brischoux et al. 2007); however, estimates of dispersal distances for sea snakes are scarce (Burns and Heatwole 1998; Heatwole 1999). All 70 species of true sea snakes (subfamily Hydrophiinae) give birth to live young (Heatwole 1999) and the sexes may differ in seasonal movement patterns, possibly related to winter mating events (Lynch 2000). The turtleheaded sea snake, *Emydocephalus annulatus*, is a member of the *Aipysurus* group of hydrophiine sea snakes (Voris 1977; Lukoschek and Keogh 2006). This relatively small (to 1 m total length) heavy-bodied species is found in shallow-water coral-reef habitats through the tropical Pacific, from the Philippines to the Great Barrier Reef (GBR), and from New Caledonia to northwestern Australia (Heatwole 1999). Throughout its range *E. annulatus* has a highly aggregated distribution at small spatial scales (individual reefs [Lukoschek et al. 2007a]) and a markedly disjunct distribution at larger spatial scales (Cogger 2000). The turtleheaded sea snake has a highly specialized diet, the eggs of demersal-spawning reef fishes (Voris 1966; Shine et al. 2004), yet can be locally abundant (Guinea and Whiting 2005). Disturbingly, turtleheaded sea snakes recently have disappeared from some of the locations where they were previously abundant (Guinea 2007).

Given the importance of philopatry and population connectivity for the ecology, evolution, conservation, and management of species, and in the light of growing conservation concerns for some reef-associated sea snake species from the *Aipysurus* group (IUCN 2011), we investigated philopatry and connectivity for the reef-associated turtleheaded sea snake, *E. annulatus* in New Caledonia. Our study is unusual in that it combines long-term mark-recapture data with genetic information from 11 high-resolution microsatellite markers to demonstrate strong philopatry of *E. annulatus* to their

"home" bays and significant genetic divergence between bays. Our findings indicate that the turtleheaded sea snake can be demographically isolated at very small spatial scales, raising concerns for the ability of reef-associated sea snake populations to recover following precipitous population declines or local extirpations.

Materials and Methods

Philopatry

In order to investigate movement patterns we conducted a long-term mark-recapture study of turtleheaded sea snakes in two adjacent bays (Anse Vata and Baie des Citrons) bordering the city of Noumea in New Caledonia (Fig. 1). Both study sites are $\sim$100 $\times$ 50 m extending from the shoreline across the reef-flat to the drop-off to deeper water ($>$2 m at low tide). The bays are separated by an intervening rocky headland, but the two study sites (which are separated by an aquatic path of 1.15 km) are connected by continuous shallow-water reef habitat (Fig. 1).

Every January from 2004 through 2011 we snorkeled the study areas to capture turtleheaded sea snakes. Captured snakes were taken to a nearby laboratory and uniquely marked using Trovan PIT tags (Identify UK Ltd., East Yorkshire, UK) implanted subcutaneously near the cloaca. A skin sample was taken for DNA and the snake was then released at its site of capture. In order evaluate seasonal stability of philopatry observed during the summer surveys (see Results) we conducted mid-winter mark-recapture surveys in July 2004 and 2011. In addition, to further explore the philopatry observed in the two main study sites, we captured snakes at a third site in January and July 2011. This site was also in Baie des Citrons but 550 m north of the main site, on the same beach (i.e., no intervening headland: Fig. 1). Shallow-water coral reefs, interspersed with sandy areas, stretch continuously between the two Baie des Citrons sites (Fig. 1).

Genetic estimates of population subdivision

In order to evaluate whether the observed adult philopatry resulted in restricted gene flow between the two bays, we genotyped 136 snakes (Baie des Citrons, $n = 61$; Anse Vata, $n = 75$) captured in 2006, 2007, and/or 2008 for 11 polymorphic microsatellite loci (two to 14 alleles per locus) developed for *E. annulatus* (see Lukoschek and Avise 2011) for details about primers, PCR conditions and microsatellite characteristics). Genomic DNA was extracted from skin samples using a modified organic protocol (Lukoschek and Keogh 2006). Observed and expected heterozygosities, deviations from Hardy–Weinberg equilibria (HWE), and exact tests of linkage disequilibrium (LD) between loci were calculated using GenePop Web Version 4.0.10 (Rousset 2008).

Figure 1. Map of study area showing the two main study sites in Anse Vata and Baie des Citrons and the second Baie des Citrons study site to the north (note small scale of map). Insert shows where bays are located in Noumea, New Caledonia. Photo of *Emydocephalus annulatus*, courtesy Nigel Marsh.

Significance levels were calculated using Markov chains run for 1,000,000 steps and were adjusted for multiple comparisons using sequential Bonferroni corrections (Rice 1989).

Pairwise F_{ST} and R_{ST} values were estimated between the two locations in Arlequin 3.5 (Excoffier and Lischer 2010). Stochastic temporal fluctuations in allele frequencies can overwhelm spatial patterns of genetic differentiation, so we first estimated pairwise F_{ST} values between snakes captured or recaptured in years 2006, 2007, and/or 2008. There was no evidence of temporal stochasticity in allele frequencies for either bay (F_{ST}; –0.006 to –0.016, $P > 0.98$ in all cases), so subsequent analyses were conducted with the three years combined. Given the high marker polymorphism (Table S1), we also calculated a standardized measure of genetic differentiation, G'_{ST} (Hedrick 2005), using the recoding approach (Meirmans 2006).

We used the Bayesian clustering algorithm implemented in STRUCTURE 2.3.2 (Pritchard et al. 2000), which identifies the affinities of individual multilocus genotypes to genetic populations (clusters), assuming HWE and linkage equilibrium within populations. We used two STRUCTURE models: the no-admixture model, which assumes that individuals are drawn discretely from one population or another and is recommended for low F_{ST} values (Pritchard et al. 2000), and the admixture model, which assumes individuals have mixed ancestry, with the admixture parameter (α) inferred from the data. For both models we used correlated allele frequencies among populations, with the allele frequency distribution parameter (λ) set to 1. We also allowed the algorithm to use the sampling location of each individual to assist with clustering (LOCPRIOR), as recommended in cases of weak population structure (Hubisz et al. 2009). For each value of K (number of clusters) from 1 to 6 we ran two long Markov Chain Monti Carlo (MCMC) runs (burn-in of 100,000 repetitions followed by 500,000 repetitions) and three shorter MCMC runs (burn-in of 50,000 repetitions followed by 250,000 repetitions) to ensure convergence on parameters and likelihood values. The most likely number of true populations (K) was

evaluated both by comparing Pr (X/K) values (the mean log likelihoods penalized by one-half of their variance [Pritchard et al. 2000]) and by evaluating the rate of change in the log probabilities of data between successive K values (ΔK) (Evanno et al. 2005).

Relatedness

We estimated mean within-group pairwise relatedness using three coefficients: the Queller and Goodnight index (r_{QG}; Queller and Goodnight 1989) and the Lynch and Ritland index (r_{LR}; Lynch and Ritland 1999), calculated using the software GENALEX version 6.4 (Peakall and Smouse 2006), and the Loiselle kinship coefficient (ρ_{ij}; Loiselle et al. 1995), calculated in GenoDive version 2.0b2 (Meirmans and van Tienderen 2004). The 95% confidence intervals around the means were estimated using 999 bootstrap pseudoreplicates. We also tested whether the mean relatedness within bays was significantly greater than expected using 999 permutations randomizing individuals into bays. Permutations for significance tests were conducted in GENALEX.

Results

Philopatry

During the eight years of annual midsummer (January) surveys we recaptured marked snakes on 649 occasions (>1500 captures overall, one to seven captures per snake, one to seven years between successive captures). Most of the resident snakes were caught within each 10-day study period; the estimated proportion of resident snakes caught each year (calculated from the rate at which the percent of unmarked snakes declined during successive dives) averaged 84.6% at Anse Vata and 89.5% at Baie des Citrons. A total of 251 snakes were marked at Baie des Citrons, and all recaptures were of Baie des Citron snakes. Similarly, 397 snakes were marked at Anse Vata and all recaptures except one were of Anse Vata snakes. The one exception was an adult male captured 12 January 2010 at Baie des Citrons and recaptured 4 January 2011 at Anse Vata.

The two mid-winter surveys (July 2004 and 2011) confirmed strong philopatry between as well as within seasons. During these surveys we captured a total of 209 snakes (122 from Anse Vata, 87 from Baie des Citrons), 95 of which were marked animals ($n = 55$ and 40, respectively). With just one exception, all recaptures occurred at the same site where the snakes had been initially marked in previous summer surveys. The exception was an adult male captured on 11 January 2006 and again on 8 January 2008 in Baie des Citrons, but captured on 25 July 2011 in Anse Vata. Moreover, 43 snakes newly marked during the July 2004 surveys (31 from Anse Vata, 12 from Baie des Citrons) were subsequently caught during January surveys in later years (total of 73 recaptures,

46 from Anse Vata, 27 from Baie des Citrons). In every case, the snake was in the same study site in summer as it had been in winter.

In January and July 2011 we captured 85 snakes in the northern Baie des Citrons site. All were unmarked snakes, despite the fact that we had marked and released 251 snakes at the main (southern) Baie des Citrons site over the preceding eight years, including 160 captures and recaptures over the preceding 20 days (10 days each survey period).

Genetic estimates of population subdivision

Numbers of alleles per locus ranged from two to 14 and were very similar in each location (Table S1). Expected and observed heterozygosities for eight of the 11 loci ranged from 0.44 to 0.89 and 0.51 to 0.91, respectively (Table S1), while the other three loci had heterozygosities of <0.10 in each location. Single-locus exact tests found departures from HWE in three of the 22 within-location tests (Table S1), although these were not significant after Bonferroni correction (initial $\alpha = 0.0045$). Nonetheless, the locus Ea478 was not in HWE in either location or across both locations and there was evidence of null alleles at this locus (Lukoschek and Avise 2011). To ensure that null alleles did not affect our result, all analyses also were conducted with Ea478 excluded. The results for 10 and 11 loci were virtually identical, so we reported only the results for 11 loci. Significant LD occurred in five of 110 tests within locations and three of 55 global tests but no test was significant after Bonferroni correction. Moreover, different pairs of loci were involved in LD in the two locations, indicating sampling artefacts rather than true physical linkage (Lukoschek and Avise 2011).

F-statistics revealed significant genetic differentiation between the two bays based on microsatellite allele frequencies ($F_{ST} = 0.008$, $P < 0.01$), but no significant differentiation when the number of mutational steps between alleles was taken into account ($R_{ST} = -0.005$, $P > 0.77$). G'_{ST} between the two bays was 0.022.

The Pr (X/K) values from STRUCTURE supported the existence of either one or two populations. The no-admixture model returned almost identical Pr (X/K) values for both one and two genetic clusters, although stronger support was indicated for one population by the admixture model (Table 1). Nonetheless, the estimated q values for both the admixture and no-admixture models assigned snakes from Anse Vata almost exclusively to one genetic cluster (admixture, mean $q = 0.95 \pm 0.01$ SE: no-admixture, mean $q = 0.98 \pm 0.01$ SE), whereas snakes from Baie des Citrons predominantly belonged to the second genetic cluster (admixture, mean $q = 0.61 \pm 0.02$ SE: no-admixture, mean $q = 0.60 \pm 0.04$ SE), albeit with evidence for mixed ancestry in this bay (Fig. 2). The largest ΔK value (rate of change in the log probabilities of data between successive K values, [Evanno et al. 2005])
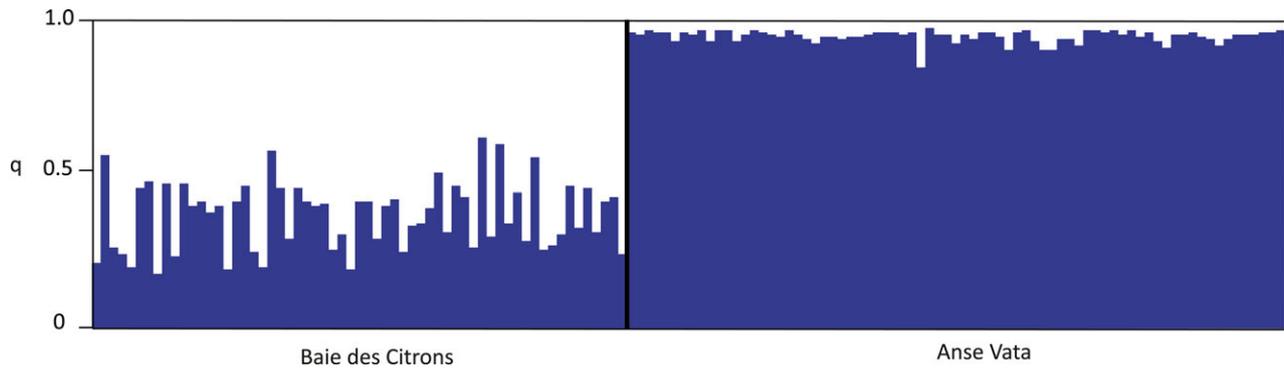
Figure 2. Bayesian clustering of *Emydocephalus annulatus* multilocus genotypes using the algorithm implemented in STRUCTURE 2.3.2, with the sampling location of each snake used to assist with clustering. The *Y*-axis (q) represents the proportion of each individual's multilocus genotype assigned to one of the two genetic clusters. Snakes are grouped according to the bay in which they were sampled (*X*-axis).

was for two genetic clusters (Table 1); however, because of the way ΔK is calculated (Evanno et al. 2005), it cannot be estimated for just one cluster.

Relatedness

In all cases, the mean relatedness coefficients within bays were positive and larger than mean relatedness coefficients between bays, which had negative values (Table 2). In addition, two of the three relatedness coefficients were significantly larger within bays than expected if snakes were randomly assigned to bays (r_{LR}: $P < 0.001$ and ρ_{ij}: $P < 0.05$ based on 999 permutations; for the third coefficient, r_{QG}: $P > 0.05$). On average, relatedness coefficients for snakes within Baie des Citrons were larger than for Anse Vata, but also more variable (Table 2).

Discussion

Our long-term mark-recapture data demonstrate that despite their potentially high vagility, sea snakes can exhibit very strong philopatry over very small spatial scales. This philopatry occurred during both summer and winter seasons, and

resulted in significant genetic divergence between adjacent populations. To our knowledge, these are the most extreme levels of philopatry and restricted gene flow recorded in any large vagile marine vertebrate species. Some elasmobranch species show female philopatry to breeding aggregations but there is also male-biased dispersal (Pardini et al. 2001), with little or no evidence of restricted gene flow for sharks or rays at nuclear markers over small to intermediate (Tillett et al. 2011) or even large spatial scales (Pardini et al. 2001). Similarly, marine turtles show strong female philopatry to nesting beaches but there is high male-mediated gene flow between rookeries (see Avise 2007 and references therein). Amphibious sea kraits (*Laticauda* spp.) show strong philopatry to home islands (Shetty and Shine 2002), and even to small areas within a single island (Brischoux et al. 2009), but travel long distances in the course of foraging (Brischoux et al. 2007) and often are recaptured on islands different from the one on which they were originally marked (up to 80 km away: X. Bonnet, pers. comm.). Presumably for this reason, there is no significant spatial structuring of mitochondrial

Table 1. STRUCTURE results for the no-admixture and admixture models for *K* values of 1 to 6. The Pr (*X/K*) and variance in Pr (*X/K*) are averaged over five runs (see text for more details).

	No-admixture model			Admixture model		
		Variance			Variance	
K	Pr (*X/K*)	Pr (*X/K*)	ΔK	Pr (*X/K*)	Pr (*X/K*)	ΔK
1	−3522.9	34.7		−3522.8	34.4	
2	−3527.6	195.5	0.809	−3555.8	223.6	0.785
3	−3691.5	606.3	0.228	−3769.1	709.5	0.267
4	−3789.6	828.7	0.103	−3615.9	322.5	0.236
5	−3802.8	900.5	0.024	−3891.5	926.0	0.157
6	−3837.6	979.4		−3787.2	694.7	

Table 2. Relatedness coefficients among *Emydocephalus annulatus* individuals within two adjacent New Caledonian bays and between bays, shown as mean (SE). Values in bold indicate that the coefficients were significantly larger than expected when snakes were randomly assigned to bays.

	r_{LR}	r_{QG}	r_{ij}
Baie des Citrons	**0.0055**	0.0011	**0.0113**
	(0.0038)	(0.0053)	**(0.0021)**
Anse Vata	**0.0001**	0.0009	**0.0047**
	(0.0030)	(0.0042)	**(0.0015)**
Between bays	−0.0179	−0.0185	−0.0012
	(0.0021)	(0.0031)	(0.0012)

r_{LR}: Lynch and Ritland index [30].
r_{QG}: Queller and Goodnight index [29].
r_{ij}: Loiselle kinship coefficient [32].

haplotypes or microsatellite alleles within *Laticauda laticaudata* or *Laticauda saintgironsi* species across the Noumea lagoon (Lane and Shine 2011); indeed, sea kraits show little genetic divergence over distances of hundreds of kilometers (Lane and Shine 2011), a dramatic contrast to our findings for *Emydocephalus*.

Previous studies have suggested that the degree of population connectivity depends upon species attributes, so that a small nonvagile habitat specialist in a heterogeneous landscape is more likely to exist as a series of discrete populations within habitat patches than is a more ecologically generalized and highly vagile organism in a more homogeneous landscape (Hanski 1999). Coral reefs are typically heterogeneous habitats, with patchiness occurring at several spatial scales. Most teleost fishes have a dispersive pelagic larval phase so are not relevant comparisons to our study species; however, there are exceptions. In particular, syngnathids give birth to live young (male pregnancy) and adults have low mobility, so might be expected to show similar fine-scale philopatry and population genetic structure. However, a mark-recapture study that tagged 5695 fishes from seven syngnathid species (three adjacent sites in Tampa Bay each 100 m diameter) only recorded 49 recaptures (Masonjones et al. 2010). Although this result may partly reflect large population sizes, the intensity of sampling (>20 sampling events over two years) also suggests considerable movement in and out of study areas at spatial scales comparable to ours. Moreover, contrary to expectation, there is no evidence of population genetic structure at small spatial scales comparable to our study (<2 km between sites) for several live-bearing syngnathid species (Mobley et al. 2010) or for the spiny damselfish, *Acanthochromis polyacanthus* (Miller-Sims et al. 2008), a small, site-attached reef-fish that defends its broods until they are fully developed, thereby effectively removing the dispersive larval stage. Genetic structure in these small reef fish without dispersive pelagic larvae only becomes apparent at larger spatial scales (Miller-Sims et al. 2008; Mobley et al. 2010). The only cases of comparable fine-scale genetic structure for any reef-associated vertebrate appears to be that reported for two small mouth-brooding reef-fish species: the Banggai cardinalfish, *Pterapogon kauderni* (Hoffman et al. 2005; significant microsatellite F_{ST} values [0.06–0.22] between three sites 2–5 km apart) and Doederlein's cardinalfish, *Apogon doederleini* (Gerlach et al. 2007; significant microsatellite F_{ST} values [0.013–0.026] between three reefs 2–6 km apart).

Habitat specialization can result in dispersal barriers and restricted gene flow despite high dispersal potential. For example, deep-water channels between reefs were found to be strong dispersal barriers for the reef-associated sea snake, *Aipysurus Laevis* (Lukoschek et al. 2007b). However, the case with *Emydocephalus* is different, in that our study sites were in close proximity and not separated by any obvious break in reef habitat (Fig. 1). At maximum swimming speeds (ap-

proximately 30 m/min; Shine, unpublished data), a snake could travel from one site to the other in 38 min. At the more leisurely rates of mate-searching males (2.5–4 m/min) and foraging snakes (<2 m/min; Shine et al. 2004), the trip would take five to 10 h. Although the two bays that we sampled were connected by suitable shallow reef habitat (where *E. annulatus* is frequently seen) extending around the rocky headland, we recorded only two cases (out of >700 recaptures) of an individual snake moving from one bay to the other. We note one caveat: our mark-recapture data were taken mostly in midsummer (when sea snakes are gravid) and winter (when the snakes mate). Thus, neonates might disperse soon after they are born (March–April), before we caught them for the first time. We doubt this possibility. First, neonatal snakes (including sea snakes) typically are secretive and sedentary (Zimmerman and Shohet 1994), and have lower locomotor abilities than adult conspecifics (Shine et al. 2003a). Second, in July 2004 we captured three juveniles (<42 cm Snout Vent Length) and all were subsequently recaptured at their original capture site. Nonetheless, we cannot exclude the possibility of occasional dispersal by neonates, which could contribute to the mixed ancestry of some individuals from the Baie des Citrons (Fig. 2) and the small F_{ST} value.

Recent colonization offers another explanation for the weak (but significant) genetic structure we detected, despite the strong philopatry of *E. annulatus* in New Caledonia. Characterization of 11 microsatellite loci used for this study indicated that New Caledonia has a small subset of the allelic diversity found in this species (Lukoschek and Avise 2011), with lower allelic diversities and heterozygosities at these 11 loci than at most other locations sampled (Lukoschek, unpublished data). A recent study demonstrated that *A. laevis* underwent west to east range expansion during the late Pleistocene, from Timor Sea reefs to the Gulf of Carpentaria and GBR (and potentially, New Caledonia; Lukoschek et al. 2007b). The much higher genetic diversities for *E. annulatus* on Timor Sea reefs (for nuclear and mitochondrial DNA) than New Caledonia and the southern GBR (Lukoschek, unpublished data), combined with the similar geographical ranges of *A. laevis* and *E. annulatus* (Heatwole 1999; Lukoschek et al. 2007a) suggest that *Emydocephalus* also underwent a west to east range expansion event in the late Pleistocene. As such, New Caledonian populations may not yet have reached mutation-drift equilibrium, and the two populations examined in this study are likely to still be in the process of diverging. This hypothesis is supported by the fact that R_{ST}, which takes mutational steps (and thus, time to accumulate divergences) into account, was not significant, whereas F_{ST} (which is based solely on differences in allele frequencies) showed significant differentiation (as also found for *A. laevis*, Lukoschek et al. 2008).

Why, then, does *Emydocephalus* show such extreme philopatry at this very small spatial scale? This species is

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ecologically specialized, feeding exclusively on the eggs of demersal-spawning fishes (Shine et al. 2004; Voris 1966). Although the snakes range widely across all shallow-water reef habitat types (Shine et al. 2003b), the foraging ecology of this species may confer strong advantages to intimate knowledge of a specific small area. High densities of demersal-spawning fishes (blennies, gobies, damselfish) in coral-reef habitats result in the frequent production of egg clutches, capable of sustaining high densities of oophagous predators. Nests of these fishes are cryptic, typically found among coral rubble, or the interstices of live or dead branching corals. If the nest locations remain the same through time (perhaps many years, depending on substrate stability), a snake may be able to harvest eggs at regular intervals by returning to the same sites. Terrestrial snakes have well-developed spatial memories (Brown and Shine 2007) and marine snakes likely possess similar abilities. Social networks also may enforce (or be facilitated by) philopatry; individual *E. annulatus* frequently are captured at the same time as specific other individuals, hinting at cryptic social organization within the population (Shine et al. 2005). However, restricted dispersal is unlikely to be due to resistance from conspecifics; in prolonged observations of these populations, we have never seen any overt behavioral interactions among snakes (other than courtship attempts, Shine 2005).

Our study is the first long-term mark-recapture study of any true sea snake, so the generality of our findings is unclear. Nonetheless, some predictions can be made based on the known habitat preferences and distributions of sea snake species, and existing genetic information. The true sea snakes are typically either strongly reef-associated (most of the 10 species in the *Aipysurus* group) or inter-reefal (most of the 60 remaining species). The olive sea snake, a primarily reef-associated species from the *Aipysurus* group (Lukoschek and Keogh 2006), has small home ranges over short time intervals (Burns and Heatwole 1998), but adult males move between reefs to mate (Lynch 2000). Population genetic data on olive sea snakes support these findings; strong population structure was found for maternally inherited mitochondrial DNA (Lukoschek et al. 2007b) but weaker genetic structure for biparentally inherited nuclear microsatellites, particularly over small spatial scales (Lukoschek et al. 2008). By contrast, philopatry of both males and females is year-round in our study system and is reflected in our microsatellite data. Although *E. annulatus* males move about more actively during the midwinter breeding season than in summer (Shine 2005), our recapture records show site fidelity between as well as within seasons. Several other species in the genus *Aipysurus* are strongly reef-associated and have restricted distributions; three species occur only on a handful of reefs in the Timor Sea and two species are restricted to small stretches of the WA coastline (Cogger 2000). Although species' range sizes are not necessarily indicative of dispersal ability, the restricted range sizes of many *Aipysurus* group species, combined with the disjunct distributions of species with larger range sizes (Lukoschek et al. 2007a), suggest that reef-associated species in the *Aipysurus* group typically have low dispersal and may display similar levels of philopatry to *E. annulatus*.

Our results have implications not only for ecology (e.g., spread of pathogens) and evolution (e.g., opportunities for mate choice, effective population sizes) but also for conservation and management. The combination of extreme philopatry and low rates of reproduction (and thus, of potential population increase) may combine to make sea snakes poor colonists and account for their highly heterogeneous distributions across several spatial scales, particularly in coral reef habitats (Cogger 2000; Lukoschek et al. 2007a). Our findings suggest that local populations of reef-associated sea snake species operate as separate ecological units and, as such, local disturbances will have mostly local impacts. However, replenishment via dispersal following local population declines or extinctions is likely to be slow. These attributes may render sea snakes vulnerable to habitat perturbations brought about by anthropogenic activities or environmental factors, and explain the recent precipitous population declines and patchy local extinctions of turtleheaded sea snakes, as well as other reef-associated species from the genus *Aipysurus* (Guinea 2007; Lukoschek et al. 2007a) that are closely related to turtleheaded sea snakes (Lukoschek and Keogh 2006). These local extinctions include a previously large population of turtleheaded sea snakes at Ashmore Reef in the Timor Sea (Lukoschek, unpublished data) and our results raise concern about the potential for this population to recover, as well as for the recovery of Critically Endangered and Endangered small-range endemics from the genus *Aipysurus*, which have undergone similar local extinctions at Ashmore Reef (IUCN 2011).

Acknowledgments

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Supporting Information

Additional Supporting Information may be found online on Wiley Online Library.

Table S1. Summary statistics for 11 microsatellite loci screened for *Emydocephalus annulatus* in two New Caledonian locations: Baie des Citrons and Anse Vata.

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