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Larval spatial distributions and other early life-history characteristics predict genetic differentiation in eastern Pacific blennioid fishes

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In marine organisms, a pelagic larval stage increases the opportunities for long-distance dispersal and is often associated with little genetic differentiation over large geographical distances. Here we test the hypothesis that early life-history characteristics, including larval spatial distributions, affect the rates of dispersal and, therefore, the levels of genetic partitioning among three Gulf of California reef fishes: *Axoclinus nigricaudus*, *Malacoctenus hubbsi* and *Ophioblennius steindachneri*. These three blennioid fishes have markedly different early life histories: *A. nigricaudus* has a short larval duration (18 days) and develops inshore, *M. hubbsi* has an intermediate larval duration (24 days) and most individuals develop inshore and *O. steindachneri* has a long larval life (50 days) and disperses offshore. Estimates of genetic partitioning from mtDNA control region sequences differed greatly between these species and were in the same rank order as predicted by their early life-history characteristics (*A. nigricaudus* $N_{ST} = 0.536$, *M. hubbsi* $N_{ST} = 0.261$ and *O. steindachneri* $N_{ST} = 0.000$). These results indicate that larval strategies may be good predictors of population genetic structure in some marine fishes.

Keywords: gene flow; Gulf of California; larval behaviour; mitochondrial DNA; pelagic larval duration; reef fish

1. INTRODUCTION

Dispersal ability varies greatly among marine organisms. The majority of marine species spawn planktonic eggs from which feeding larvae hatch, whereas some invertebrates and a few fish species bypass a planktonic larval stage altogether by brooding their young, hatching non-dispersing juveniles directly from benthic-attached eggs or even bearing live young. Intermediate strategies are also common. There is no unifying explanation for the diversity of egg types and larval forms found among marine organisms (reviewed by Leis 1991; Pechenik 1999; Bonhomme & Planes 2000).

It seems intuitive that limited dispersal ability should result in greater genetic differentiation. In fact, comparisons between species that differ greatly in their dispersal ability, namely direct development versus planktonic larvae, almost always show a greater population genetic structure in the direct-developing species (e.g. Hunt 1993; Hellberg 1996; Arndt & Smith 1998). In contrast, attempts to correlate life-history characteristics that might have a more subtle effect on dispersal, such as benthic versus planktonic egg stages, feeding versus non-feeding planktonic larvae or varying larval duration with population genetic structure, are generally unsuccessful (reviewed by Hedgecock 1986; Shulman 1998). For example, Doherty *et al.* (1995) estimated the dispersal potentials of seven Great Barrier Reef fishes based on their pelagic larval durations (PLDs), while Waples (1987) combined fecundity, PLD and larval capture data in order to predict the dispersal ability of 10 Californian fishes. The observed negative correlation between dispersal ability and population structure in both studies is primarily driven by direct-developing species (noted by Bohonak 1999; but see Bonhomme & Planes 2000) and, when comparisons are restricted to species with pelagic larvae, the correlations largely disappear (Bohonak 1999). Similarly, Shulman & Bermingham (1995) found that neither PLD nor egg type (benthic versus planktonic) was a good predictor of geographical differentiation among eight Caribbean reef fishes. In sum, neither egg type nor PLD has been shown to be a strong determinant of population structure.

An unexplored possibility is that larval movement patterns affect rates of dispersal. Several recent studies have examined the swimming abilities of larvae and shown that many invertebrate and fish larvae do not passively drift in the water column, but swim actively and directionally and, consequently, segregate vertically, horizontally and temporally (Cronin & Forward 1986; Leis & Carson-Ewart 1997; Stobutzki 1998; reviews in Burton & Feldman 1982; Leis 1991). These differences in larval behaviours may reflect very different dispersal strategies.

Here, we test the hypothesis that larval dispersal ability, as estimated from a comprehensive set of early life-history characteristics including larval movement patterns, can be used to predict the adult population's genetic structure. Three fish species, *Axoclinus nigricaudus*, *Malacoctenus hubbsi* and *Ophioblennius steindachneri*, were selected because they represent a range of larval dispersal strategies within a single group of reef fishes, the suborder Blennioidei. In addition, we sampled the same geographical locations within the Gulf of California in order to avoid errors that are caused by comparing differing spatial scales. Genetic differentiation was inferred from mitochondrial (mt) DNA sequences.

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2. METHODS

(a) *Early life-history characteristics*

All blennioids have demersal, brooded eggs that hatch after a few days and release larvae into the plankton. Brogan (1992) described the larvae and hatching of several Gulf of California blennioids. PLD was estimated from otolith microstructure (Victor 1991). Otolith size at hatching was obtained from Brogan (1992). Newly recruited individuals (as identified by the presence of larval melanophore patterns and partial transparency) were collected near La Paz, Mexico for all three species and daily otolith increments between hatching and settlement marks were counted as the estimate of their PLDs. Newly settled larval size was used as the estimate of their size at settlement. For comparison to the Gulf of California samples, otoliths of an *O. steindachneri* larva collected directly over the reef in the Galapagos Islands were examined. Larval distribution data were taken from Brogan (1992, 1994).

(b) *Populations sampled*

A total of 175 fish were collected from nine geographical locations in the Gulf of California, including sites in both the northern and central Gulf regions (figure 1). *A. nigricaudus* were collected at all sites (Gonzaga ($n=10$), Los Angeles ($n=10$), Chivato ($n=9$), La Paz ($n=6$), Muertos ($n=10$), Lobos ($n=10$), Libertad ($n=10$), Kino ($n=10$) and Venecia ($n=30$)), while *M. hubbsi* were collected from Los Angeles ($n=9$), Chivato ($n=8$), Lobos ($n=9$) and Venecia ($n=10$) and *O. steindachneri* were collected from Chivato ($n=10$), La Paz ($n=10$), Muertos ($n=6$) and Venecia ($n=8$). Muscle tissue was removed for DNA extraction and each individual was preserved in ethanol and deposited as a voucher specimen in the University of Arizona Fish Collection.

(c) *Mitochondrial DNA amplification and sequencing*

Genomic DNA was prepared from the muscle tissue following standard methods. Universal fish primers A and E (Lee *et al.* 1995) were used for amplifying the first hypervariable region of the mitochondrial control region by the polymerase chain reaction (PCR). The PCR products were sequenced with primers A and E using a chain termination protocol with a United States Biochemical (Cleveland, OH, USA) ThermoSequenase radiolabelled terminator cycle sequencing kit. Approximately 90% of each reported fragment was sequenced in both the forward and reverse directions (total sequence lengths, *A. nigricaudus* = 408 bp, *M. hubbsi* = 399 bp and *O. steindachneri* = 321 bp). The sequencing products were electrophoresed on an 8% acrylamide gel and exposed to film overnight.

(d) *Nucleotide diversity*

Sequences within each species were aligned manually and unique haplotypes, nucleotide polymorphisms and indels were counted. The average number of pairwise differences $\hat{\pi}$ (Nei & Li 1979) and diversity based on the number of segregating sites $\hat{\theta}$ (Watterson 1975) were estimated. In order to check for deviations from neutral expectations for the frequency spectrum of polymorphisms, significance values were calculated for Tajima's (1989) *D*.

(e) *Patterns of geographical subdivision*

One-factor analyses of molecular variance (AMOVAs) (Excoffier *et al.* 1992) were performed for each of the three species in Arlequin (Schneider *et al.* 2000) in order to estimate variation between and within populations. As the *A. nigricaudus* and *M. hubbsi* populations were sampled from two biogeographical regions, two-factor AMOVAs were also used for assessing the contribution of biogeographical regions to population structure. All AMOVA analyses were based on unweighted pairwise differences between haplotypes and the haplotypes were permuted 1000 times.

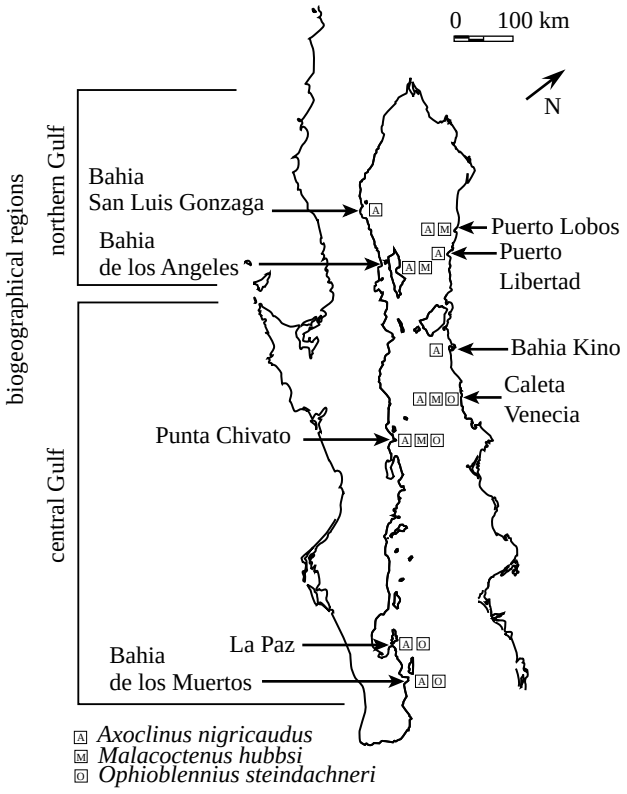

Figure 1. The Gulf of California. The arrows point to individual collecting locations. Boxed As, Ms and Os refer to the locations where *A. nigricaudus*, *M. hubbsi* and *O. steindachneri* were sampled, respectively. The ranges of the biogeographical regions are shown on the left.

Standard *F*-statistics were also calculated. Two criticisms of this approach are that the island model of genetic exchange is biologically unrealistic and that *F*-statistics are affected by within-population variation differences. However, the widespread use of *F*-statistics provides a convenient metric for comparison across species and studies (as in Bohonak 1999). Here, the statistic N_{ST} (Lynch & Crease 1990), which is an estimate of population subdivision based on nucleotide divergence, was used for describing genetic differentiation within species.

In addition, an absolute measure of genetic distance, D_m (Nei 1973), which should be less affected by reductions in within-population variation (Charlesworth 1998), was used. The D_ms of all within-species population pairs were calculated using average pairwise differences as a measure of gene diversity. In addition, average estimates of D_m, corrected for unequal population sizes, were used for qualitatively comparing the genetic distances between the three species.

M. hubbsi and *O. steindachneri* were not collected at all study sites (figure 1), so the sets of populations for these two species are subsets of those available for *A. nigricaudus*. In order to exclude the possibility that the species estimates of genetic divergence were greater in *A. nigricaudus* due to greater geographical

Table 1. Measures of species-wide population structure.

(The predicted dispersal ability is based on early life characteristics (see the text for more details). Φ_{ST} was estimated from a one-factor AMOVA where Φ_{ST} estimates the variance between populations and the probability of the observed value was obtained by permuting the haplotypes 1000 times and recalculating the statistic. The nuclear equivalent F_{ST} is the equivalent F-statistic of a nuclear locus to mitochondrial N_{ST} values, assuming a sex ratio of unity and equal migration of males and females.)

species	predicted dispersal ability	D_m (%)	N_{ST}	Φ_{ST}	p	nuclear equivalent F_{ST}
A. nigricaudus	low	1.555	0.536	0.448	< 0.001	0.224
M. hubbsi	medium	0.198	0.261	0.246	< 0.001	0.081
O. steindachneri	high	-0.001	0.000	0.000	n.s.	0.000

sampling, we compared the genetic distances of *M. hubbsi* and *O. steindachneri* population pairs against reduced sets of *A. nigricaudus* genetic distances. Because genetic distances between population pairs are not independent of each other, we used a non-parametric test that makes no assumptions about the underlying distribution of the values. The Wilcoxon signed-ranks test compares paired values in order to determine whether one group is larger (analogous to a paired *t*-test); in this case *M. hubbsi* and *O. steindachneri* population pairs were compared against *A. nigricaudus* population pairs. *M. hubbsi* and *O. steindachneri* could not be compared in this manner because their sampled distribution only overlapped at two collecting sites (Chivato and Venecia) (figure 1).

Finally, genealogies were estimated under maximum parsimony using PAUP 4.0b2a (Swofford 2000). Parsimony analyses were conducted with transitions and transversions weighted equally and with transversions given a weight that was scaled by the reciprocal of their observed ratio to transitions (transversion:transition ratios = 11:69, 1:14 and 19:76 for *A. nigricaudus*, *M. hubbsi* and *O.steindachneri*, respectively). Heuristic searches were performed using stepwise addition for initial trees and the tree bisection–reconnection method of branch swapping. The maximum limit of trees was set at 1000 for each search and a strict consensus tree was generated. These conditions were repeated 10 times under both transition:transversion weighting schemes.

3. RESULTS

(a) *Early life-history characteristics*

Axoclinus nigricaudus hatches at the largest size of the three blennioids examined, at 3.0 mm total length (TL). Hatching larvae are well developed with no remaining yolk sac, functional mouths and completely developed eyes (Brogan 1992). This species also settles at the smallest size, 11.9 mm standard length (SL) and after a very short PLD of *ca.* 18 days. According to Brogan (1992, 1994), this species is capable of completing its larval life in inshore waters over the reef. This conclusion was based on the presence of all larval sizes in waters over the reef and a rapid drop in larval density with distance from shore (< 100 m). Although this does not mean that no *A. nigricaudus* larvae are ever transported offshore, it indicates that this species generally completes larval development in inshore waters.

In contrast, the larvae of *O. steindachneri* hatch the smallest, at 2.5 mm TL (Brogan 1992). Its congener in the Caribbean, *O. atlanticus*, has been documented as hatching as small as 1.4 mm TL and with a yolk sac and a relatively less developed mouth and eyes (Labelle & Nursall 1985). *O. steindachneri* larvae settle at a very large size, *ca.* 50 mm SL and after *ca.* 50 days in the pelagic environment (in the Gulf of California, as well as the Galapagos Islands). Furthermore, Brogan (1992) found clear evidence that the larvae are rapidly transported offshore, as only newly hatched and ready-to-settle larvae of this species are captured in waters over the reef.

Malacoctenus hubbsi are apparently intermediate in all characters; *M. hubbsi* have a 24 day larval duration and settle at *ca.* 17.2 mm SL. The closest sample we have for hatching size is another local *Malacoctenus* species (*M. gigas*), which hatches at 2.7 mm TL. The larvae of this group of labrisomids are found with a primarily inshore distribution, but are not as concentrated in near-reef waters as *Axoclinus* (Brogan 1992).

(b) *Nucleotide diversity*

The diversity of the mtDNA ranged widely within the three species sampled. All measures of diversity were lowest in *M. hubbsi*: there were proportionately fewer unique haplotypes (17 out of 36), fewer segregating sites (15), no indels, $\theta = 0.85\%$ and $\pi = 0.60\%$. At the other extreme, diversity in *O. steindachneri* was high, with all haplotypes unique, 85 segregating sites, seven indels, $\theta = 6.94\%$ and $\pi = 6.17\%$. The diversity of the *A. nigricaudus* sequences was intermediate to those of *M. hubbsi* and *O. steindachneri* (82% unique haplotypes, 72 segregating sites, two indels, $\theta = 3.39\%$ and $\pi = 2.79\%$). Tajima's (1989) D was negative for all three species, although not significantly different from zero, indicating that there have been no strong deviations from neutral expectations of mtDNA among these three fishes.

(c) *Patterns of geographical subdivision*

The diversity of the haplotypes was significantly partitioned among the populations of *A. nigricaudus* and *M. hubbsi*, but not *O. steindachneri* (table 1). The species-level N_{ST}, Φ_{ST} and genetic distances were all in the same rank order, with the greatest partitioning of genetic variation in *A. nigricaudus*, less genetic partitioning in *M. hubbsi* and no evidence of genetic partitioning in *O. steindachneri* (table 1). The estimates of genetic differentiation in *A. nigricaudus* were not greatly affected by restricting the population sets to the same subsets available for *M. hubbsi* and *O. steindachneri* ($D_m = 1.769\%$ and $N_{ST} = 0.536$ and $D_m = 1.231\%$ and $N_{ST} = 0.478$, respectively). The two-factor AMOVAs of *A. nigricaudus* and *M. hubbsi* revealed significant genetic partitioning between biogeographical

Table 2. Genetic distances between population pairs of *A. nigricaudus* (low dispersal ability) and *M. hubbsi* (medium dispersal ability).

populations	*A. nigricaudus* D_m (%)	*M. hubbsi* D_m(%)
Los Angeles–Chivato	1.093	0.076
Los Angeles–Lobos	0.317	0.139
Los Angeles–Venecia	2.067	0.575
Chivato–Lobos	1.457	−0.034
Chivato–Venecia	1.778	0.282
Lobos–Venecia	2.453	0.099
Wilcoxon signed-ranks test	$z = -2.20$	$p = 0.028$

Table 3. Genetic distances between population pairs of *A. nigricaudus* (low dispersal ability) and *O. steindachneri* (high dispersal ability).

populations	*A. nigricaudus* D_m (%)	*O. steindachneri* D_m (%)
Chivato–La Paz	0.007	0.011
Chivato–Muertos	0.160	0.125
Chivato–Venecia	1.778	0.059
La Paz–Muertos	0.062	−0.291
La Paz–Venecia	1.312	−0.406
Muertos–Venecia	1.576	−0.426
Wilcoxon signed-ranks test	$z = -2.09$	$p = 0.037$

regions in the *A. nigricaudus* populations ($\Phi_{CT} = 0.273$ and $p < 0.001$) but not among the *M. hubbsi* populations ($\Phi_{CT} = -0.002$ and n.s.). Pairwise comparisons of the populations substantiated greater partitioning among the *A. nigricaudus* populations than among either the *M. hubbsi* or *O. steindachneri* populations (tables 2 and 3).

The phylogenetic analyses failed to reveal any strong concordance between geography and phylogeny among the *O. steindachneri* and *M. hubbsi* haplotypes. In contrast, the parsimony analyses revealed a strong concordance between geography and phylogeny in *A. nigricaudus* with three distinct clades present in all analyses: a mostly northern Gulf clade, a mostly western central Gulf clade and an eastern central Gulf clade. Haplotype networks (figure 2) were constructed for each of the three species by randomly selecting one parsimony tree under equal weighting.

4. DISCUSSION

The larval distribution patterns and PLDs of the three species indicate the greatest dispersal ability for *O. steindachneri* followed by *M. hubbsi* and a highly reduced dispersal ability for *A. nigricaudus*. The estimates of genetic differentiation in *A. nigricaudus*, *M. hubbsi* and *O. steindachneri* are entirely consistent with these predicted dispersal abilities. The population structure is greatest for *A. nigricaudus* (table 1), the larvae of which develop over reefs, hatch well developed and settle in 18 days (see also Riginos & Nachman 2001). There is no genetic partitioning in *O. steindachneri*, the long-lived larvae of which appear to complete development in open waters (see also Muss *et al.* 2001). *M. hubbsi* is intermediate in both early life-history features (some inshore development and a 24 day PLD) and genetic partitioning. This qualitative pattern is consistent regardless of the manner in which genetic differentiation is estimated. Restricting comparisons to fishes collected from the same sampling sites also shows that the population structure is highest in *A. nigricaudus* (tables 2 and 3).

Previous studies have failed to find a simple association between genetic structure and PLD. Among the three species examined here, the larval movement patterns and PLDs are correlated (as are hatching and the settlement sizes). Thus, we cannot identify a single factor as responsible for the observed range of genetic partitioning. However, our findings suggest that a more comprehensive evaluation of larval strategies is required in order to determine the features affecting dispersal and population structure. In fact, the behaviours and spatial distributions of larvae may contribute just as much or more than simple measures of larval duration to the true dispersal rates for reef fishes. It is likely that the differences in population structure among the three species examined here are due to *A. nigricaudus* larvae and, to a lesser degree, *M. hubbsi* larvae maintaining a position close to their natal reef and settling locally after a relatively short period. Although the rates of expatriation and dispersal are driven by those individual larvae that lose connection with their natal reef due to accidents or currents, larval behaviour should decrease offshore transport and, thus, sharply reduce the number of migrants and, therefore, the likelihood of long-distance dispersal. Indeed, the extreme genetic partitioning in *A. nigricaudus* ($N_{ST} = 0.536$) indicates that extremely few migrants are exchanged between populations (fewer than one female migrant per generation ($N_m = 0.4$), assuming an island model of migration). It is species with a substantial population genetic structure, such as *A. nigricaudus*, that would be most likely to show a high degree of larval retention and self-recruitment (see Jones *et al.* 1999; Swearer *et al.* 1999; Robertson 2001).

One interesting difference among the species considered here is the genetic partitioning in relation to biogeographical regions. The considerable genetic variation within *A. nigricaudus* is restricted to the two biogeographical regions sampled, as reflected in the AMOVA ($\Phi_{CT} = 0.273$ and $p < 0.001$) and in the phylogenetic analyses where the haplotypes are, for the most part, partitioned between the northern and central Gulf clades (see figure 2 and § 3). In contrast, biogeographical regions do not contribute to the partitioning of the variation among *M. hubbsi* populations ($\Phi_{CT} = -0.002$ and n.s.) and there is no clear concordance between biogeography and phylogeny among the *M. hubbsi* haplotypes (figure 2). Although some biogeographical boundaries are characterized by phylogeographical breaks (Avise 1992), others are not (Burton 1998). Biogeographical regions that are characterized by changes in oceanographic circulation patterns and environmental conditions may differentially impact on species with differing modes of dispersal and may be associated with reduced migration in a single direction, a pattern that is easily overlooked by frequency-based analyses (Wares *et al.* 2001). The factors

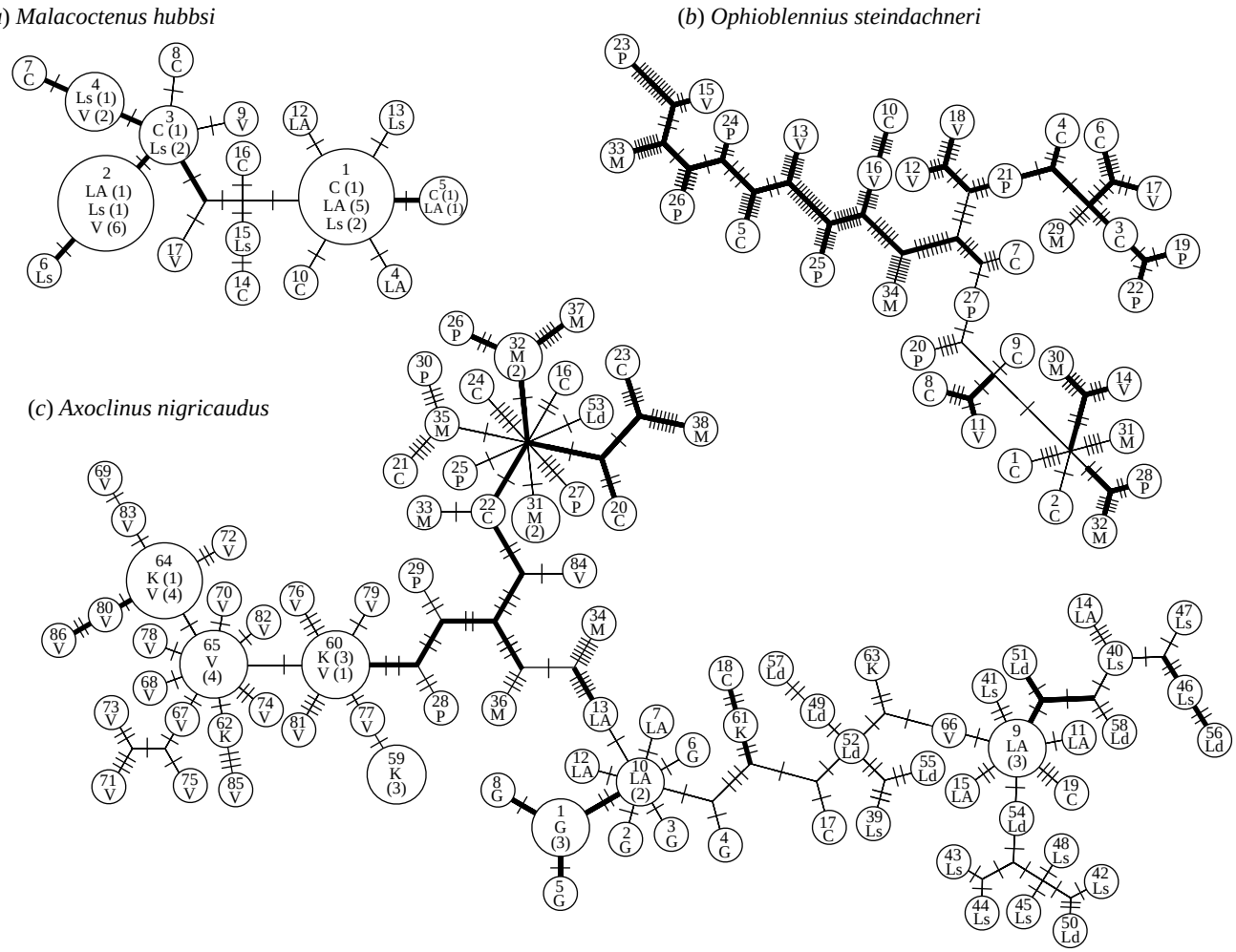

Figure 2. Haplotype networks of the three species studied. (*a*) Haplotype network created from one of 32 unweighted equally parsimonious trees of *M. hubbsi* (tree length = 19 and consistency index = 0.79). (*b*) Haplotype network created from one of 72 unweighted equally parsimonious trees of *O. steindachneri* (tree length = 195 and consistency index = 0.50). (*c*) Haplotype network created from one of 1000 unweighted equally parsimonious trees of *A. nigricaudus* (tree length = 189 and consistency index = 0.42). The haplotypes in each network are indicated by circles that are proportional in area to the number of individuals observed to have that haplotype and the numbers of individuals with each non-unique haplotype are given in parentheses. Hash marks indicate the number of mutational steps separating each haplotype. The number in each circle refers to the haplotype (Genback accession numbers AY026774–A026790 for *M. hubbsi*, AY026791–AY026824 for *O. steindachneri* and AF333610–AF333695 for *A. nigricaudus*) and the letter(s) refer to the geographical location from which each haplotype was sampled (G, Gonzaga; LA, Los Angeles; C, Chivato; P, La Paz; M, Muertos; Ls, Lobos; Ld, Libertad; K, Kino; V, Venecia). Branches present in the strict consensuses of all equally parsimonious trees are indicated in bold.

contributing to biogeographical regions in the Gulf of California are unknown. Regardless, the observed phylogeographical concordance for a low dispersal species (*A. nigricaudus*) but not for a species with greater dispersal ability (*M. hubbsi*) points to dispersal ability as the primary determinant of population structure.

In this study, dispersal ability was assessed based on several early life characteristics including larval duration, size at hatching and settlement and, in addition, the spatial distributions of larvae relative to the reef. Although this study only examined three species, the large range of differences in mtDNA partitioning points to the potential importance that these early life-history characteristics may have in determining the dispersal ability of individual fish and, therefore, the amounts of genetic interchange among geographically distant populations.

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