Vol. 486: 203–212, 2013
doi: 10.3354/meps10330

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published July 12

Comparison of population structuring in sympatric octopus species with and without a pelagic larval stage

Kaitlyn L. Higgins[1,*], Jayson M. Semmens[2], Zoë A. Doubleday[3], Christopher P. Burridge[1]

[1]School of Zoology, University of Tasmania, Private Bag 5, Hobart, Tasmania 7001, Australia

[2]Fisheries, Aquaculture and Coasts Centre, Institute for Marine and Antarctic Studies, University of Tasmania, Private Bag 49, Hobart, Tasmania 7001, Australia

[3]Southern Seas Ecology Laboratories, School of Earth and Environmental Sciences, University of Adelaide, DX650 418, South Australia 5005, Australia

ABSTRACT: An understanding of the influence of life history on dispersal capability is central to a range of disciplines within ecology and evolution. While studies have investigated this question by contrasting spatial population structuring in taxa that differ in life history, in the vast majority such comparisons differ in space and time, and therefore environmental factors may have contributed. Here, population structure of a holobenthic (i.e. direct developing) octopus, *Octopus pallidus*, was investigated genetically. This was compared to existing genetic data for a co-occurring merobenthic (i.e. planktonic larvae) species, *Macroctopus maorum*. Greater spatial genetic structuring was evident in *O. pallidus* than *M. maorum*. Patterns were consistent with isolation by distance in *O. pallidus*, but appeared related to oceanographic circulation systems in *M. maorum*, suggesting distance-dependent adult dispersal and current-mediated larval dispersal, respectively. Genetic population structuring in *O. pallidus* also largely corroborated inferences based on stylet microchemistry, indicating the utility of these environmental signatures. This study enables stronger predictions to be made regarding the dispersal capabilities and spatial population structuring of other cephalopods based on life history.

KEY WORDS: Octopus · Microsatellite · Population structure · Sympatric · Isolation by distance · Life history

INTRODUCTION

Knowledge of the relationships between life history attributes and dispersal capabilities in marine taxa is central to the study of population dynamics (Palsbøll et al. 2007), individual fitness and behaviour (Wild et al. 2011), and historical biogeography (Burridge et al. 2012). Likewise, knowledge of dispersal capabilities is important for species management, such as effective marine reserve design (Shanks et al. 2003) and sustainable fisheries (Danancher & Garcia-Vazquez 2009). To date marine studies testing relationships between dispersal and life history have concentrated on fishes and sessile invertebrates with or without pelagic larvae (e.g. Hoffman et al. 2005, Johnson & Black 2006, Underwood et al. 2007). Based on such studies it appears that the presence of a pelagic larval phase usually increases dispersal potential and reduces spatial population structuring, as expected (Bay et

*Email: kaitlyn.l.higgins@gmail.com

al. 2006, Teske et al. 2007, Cowen & Sponaugle 2009, Weersing & Toonen 2009). However, in some cases long distance dispersal of 'sedentary' taxa may occur (Fraser et al. 2011), and strong structuring has been observed in species with pelagic larvae (e.g. Jones et al. 2005, Baums et al. 2006, Miller & Ayre 2008, Marko et al. 2010). Additionally, few studies have compared taxa with contrasting life histories in the same spatial setting (but see Wilke & Davis 2000, Dawson et al. 2002, Lambert et al. 2003), and therefore geographic features and environmental differences (Baums et al. 2006, Pelc et al. 2009) may also contribute to any observed differences in dispersal capability.

While attracting much less research attention, cephalopods have a range of ecologies and life histories that mirror the diversity in other marine taxa, and therefore represent a phylogenetically independent and important group with which to address how population structuring varies with respect to the same range of life history characteristics. In particular, some cephalopods have a pelagic paralarval phase (merobenthic), while others undertake direct development (holobenthic) (Roper et al. 1984). Previous genetic studies on cephalopods show regional-scale population structuring in species with pelagic larvae (Shaw et al. 1999, Cabranes et al. 2008, Doubleday et al. 2009) and finer spatial structure in those without (Kassahn et al. 2003, Garoia et al. 2004, Juárez et al. 2010), consistent with the perceived importance of pelagic larvae for dispersal. However, as with other marine taxa, apparent relationships between life history attributes and dispersal capabilities may be confounded by differences in the environments where the species occur. Dispersal in sympatric cephalopods with contrasting life histories has not been studied, and, among octopuses, only 2 population genetic studies have been conducted on direct-developing taxa (Allcock et al. 1997, Juárez et al. 2010), despite representation of this life history in approximately one-quarter of octopus species (Guzik 2004). Knowledge of dispersal in cephalopods is also important for their management, because they are under increasing fisheries pressure (Leporati et al. 2009) and are important in marine ecosystems as both predators and prey (Rodhouse & Nigmatullin 1996, Shaw et al. 1999).

Within southeast Australia, 2 common commercially harvested octopus species exhibit overlapping distributions and contrasting life histories. *Octopus pallidus* is a medium-sized (up to 1.2 kg) holobenthic octopus which has a lifespan of 12 to 18 mo (Leporati et al. 2009). Females produce 200 to 400 large (11 mm) eggs per clutch, which hatch into well-developed hatchlings (Guzik 2004, Leporati et al. 2008a,b). In contrast, *Macroctopus maorum* grows up to 15 kg and has pelagic paralarvae (Doubleday et al. 2009), with clutches of >200 000 small (6 mm) eggs (Grubert & Wadley 2000). The lifespan of *M. maorum* is unknown (Doubleday et al. 2011), but is probably short (1 to 2 yr) like other cephalopod species. The duration of the paralarval stage is also unknown, but in other merobenthic species it has been reported to vary between 3 wk and 6 mo (Villanueva & Norman 2008). *M. maorum* can be found sympatrically with *O. pallidus*, with overlapping habitats, although *M. maorum* has both a wider geographic and depth range (0 to 549 m, as opposed to 7 to 275 m) (Stranks 1988, 1996, Grubert & Wadley 2000).

Micro-chemical analysis of stylets (internal vestigial 'shells') suggested significant spatial population structuring in both species (Doubleday et al. 2008a,b). Structuring based on styles was observed at smaller spatial scales in *Octopus pallidus* (<100 km) relative to *Macroctopus maorum* (~450 km); however, the closer proximity of sampling sites in *O. pallidus* (Doubleday et al. 2008a,b) may be involved. In addition, the underlying basis behind differences in stylet microchemistry between populations is unknown, but is assumed to reflect infrequent movement by individuals between regions with different water chemistries, as with otolith microchemistry in fishes (Elsdon et al. 2008). However, inferred structures may only be representative of the sampled generation (Elsdon et al. 2008), rather than the long-term population separation suggested by genetic studies (Warner et al. 2009). Previous genetic research on *M. maorum* suggested coarser population structuring, with differences only between, not within, the oceanographic systems of southeast Australia (the Zeehan Current, Bass Strait and the East Australian Current; see Fig. 1; Doubleday et al. 2009). Therefore, the presence of population genetic structuring within oceanographic systems for *O. pallidus* would provide strong support for the hypothesis of reduced dispersal in direct-developing species.

The aims of this study were: (1) to genetically assess population structuring in the holobenthic octopus *Octopus pallidus*; (2) to compare this with genetic population structure of the merobenthic octopus *Macroctopus maorum* (Doubleday et al. 2009), in order to investigate the influence of life history on dispersal; and (3) to provide a direct comparison of population structuring inferred from the application of both molecular markers and stylet microchemistry to a common set of individuals.

MATERIALS AND METHODS

Field collection and laboratory methods

Octopus pallidus were collected using unbaited plastic pots attached to longlines deployed in 25 to 45 m deep water for approximately 20 d. Samples were collected from 5 sites around Tasmania between 2006 and 2010, with multiple years sampled at 3 sites (see Fig. 1). This temporal replication is important as inferences of dispersal can be confounded by high variance in reproductive success among individuals, altering the allele frequencies within a population over short periods (Hedgecock et al. 2007). The individuals analysed included those previously examined using stylet microchemistry by Doubleday et al. (2008a).

From every sample, an arm tip was excised and preserved in 95% ethanol or 20% DMSO, saturated NaCl and 0.25 M EDTA pH 8.0. Total genomic DNA was extracted using a Qiagen DNeasy protocol. DNA concentrations were quantified using a Nano-Drop (Thermo Scientific). DNA from 351 individuals was amplified for 8 polymorphic microsatellite loci as described by Higgins & Burridge (2012). Allele scoring was performed using Genemapper 4.0 (Applied Biosystems).

Data analysis

Populations were tested for the presence of null alleles, stutter-miscalls, or large allele dropouts at each locus using MICROCHECKER 2.3.3 (Van Oosterhout et al. 2004). Allele frequencies in each population were tested for concordance with Hardy-Weinberg equilibrium and genotypic disequilibrium using GENEPOP 4.0.10 (Rousset 2008). Hardy-Weinberg tests used an 'Exact H-W test', with complete enumeration of p-values for <5 alleles; otherwise, estimation of p-values was carried out via 1000 Markov chain batches. Genotypic disequilibrium tests used the log-likelihood ratio statistic estimated from 1000 Markov chain batches. Allele frequency comparisons between and within sites were performed using *G*-tests in GENEPOP with 1000 Markov chain batches and sequential Bonferroni correction (Holm 1979, Rice et al. 2008).

F_{ST} was estimated using θ of Weir & Cockerham (1984) calculated by FSTAT 1.2 (Goudet 1995). Global G''_{ST} was calculated using Geondive 2.0b22 (Meirmans & Van Tienderen 2004), to facilitate comparisons of population structuring among studies where markers exhibit different heterozygosities (Meirmans & Hedrick 2011). A Mantel test examined the relationship between geographic isolation and genetic divergence — an isolation by distance model of population structuring — using IBDWS 3.16 (Jensen et al. 2005), based on θ and the shortest marine distance between sites measured using the automated distance function in ESRI ArcINFO 9.1 (www.esri.com/software/arcgis/arcgis-for-desktop) and a whole world Mercator projection map georeferenced to WGS84.

Bayesian estimates of gene flow were provided by migrate-n (Beerli 2006, 2009). A Brownian motion mutation model was employed, and loci, the alleles of which could not be explained by mutations in increments of the repeat unit, were excluded (locus *OpaD104* from *Octopus pallidus*). Start genealogies were determined randomly, and starting θ and gene flow were derived from F_{ST}. A simplified migration model was required to achieve convergence between runs, with population sizes assumed equal, and symmetrical gene flow between populations. Uniform priors were employed with lower limits of zero and upper limits of 20 (θ) and 1000 (migrants per mutation), with slice sampling. The sampling increment was set to 100, and 5000 steps were recorded following a burn-in of 10^6. Four parallel chains were run (1 cold, 3 heated according to the STATIC scheme of 1.0, 1.5, 3.0 and 10^6). Ten replicate analyses were run (replicate = YES:10). Estimates of gene flow were tested for a relationship with geographic isolation, as above.

Assignment tests were carried out in Arlequin 3.5.1.2 (Excoffier & Lischer 2010). Bayesian clustering used Structure 2.3.3 (Pritchard et al. 2000), employing 10 000 Markov chain batches under the population admixture model with correlated allele frequencies and potential number of population clusters (K) of between 1 and 4. The model was run both with and without the inclusion of prior population information in the form of sampling locations (Hubisz et al. 2009). G''_{ST}, isolation by distance and Bayesian clustering were also performed for the southeast Australian data for *Macroctopus maorum* (Doubleday et al. 2009).

RESULTS

Following Bonferroni correction, genotypes across loci of *Octopus pallidus* were independent ($p > 0.01$) and none deviated from Hardy-Weinberg equilib-

Table 1. *Octopus pallidus*. Summary statistics for each locus, comprising number of alleles observed, mean expected (H_E) and observed (H_O) heterozygosity per population, size range of PCR products and Hardy-Weinberg p-values (ranges from individual tests of populations)

Locus	Alleles	H_E	H_O	Size range (bp)	Hardy-Weinberg p-values
Opa149	4	0.65	0.66	149–162	0.01–0.48
Opa211	7	0.38	0.37	202–220	0.31–0.69
Opa212	3	0.35	0.37	208–216	0.45–1.00
Opa244	2	0.02	0.02	244–248	1.0
Opa301	3	0.45	0.47	301–309	0.02–0.70
Opa320	13	0.87	0.84	315–362	0.008–0.40
Opa347	14	0.75	0.67	347–361	0.01–0.77
Opa354	3	0.35	0.29	354–362	0.02–1.00

rium (Table 1). Levels of polymorphism were adequate for tests of population structuring, with the number of alleles per locus ranging from 2 to 14 and expected heterozygosity from 0.02 (*Opa244*) to 0.87 (*Opa320*) (Table 1).

There was no significant temporal variation of allele frequencies at any site ($p > 0.23$), so this should not bias spatial comparisons. Therefore, temporal replicates were combined hereon. There was significant population structuring in allele frequencies among sites (*G*-test, $p < 0.0001$), with Mercury Passage ($p < 0.0001$) and Northwest Bay ($p < 0.0001$) distinct from all other sites. East Flinders Island was distinct from Stanley ($p < 0.001$), but not from West Flinders Island ($p = 0.02$), and West Flinders Island was not distinct from Stanley ($p = 0.03$), following sequential Bonferroni correction (Fig. 1).

F_{ST} for *Octopus pallidus* was $\theta = 0.038$ ($p < 0.001$), and the corresponding G''_{ST} estimate of structuring was 0.158. G''_{ST} for *Macroctopus maorum* in southeast Australia was 0.151. Pairwise θ among sites for *O. pallidus* are shown in Table 2, and Mantel tests revealed a significant relationship with geographic distance among sites (isolation by distance; $p = 0.035$, $Z = 316.67$, $r = 0.54$; Fig. 2). An isolation by distance relationship was lacking for *M. maorum* in southeast Australia ($p = 0.65$, $Z = 104.34$, $r = -0.29$; Fig. 2). Similarly, isolation by distance was rejected for *M. maorum* based on results from migrate-n ($p = 1.00$, $Z = 46\,228.7$, $r = 0.913$). While Mantel tests based on the modes of posterior distributions from migrate-n were not significant for *O. pallidus* ($p = 0.06$, $Z = 78\,030.6$, $r = -0.55$), the posterior distributions of gene flow estimates between Stanley and Mercury Passage, and Northwest Bay and Mercury Passage, were tri- and bi-modal, respectively, and the highest peaks gave the 2 largest gene flow estimates observed for the species. Conducting Mantel tests using peaks that correspond to lower rates of gene flow produced a significant isolation by distance relationship ($p = 0.04$, $Z = 62\,992.4$, $r = -0.55$), as did analysis with Mercury Passage removed from the analysis ($p = 0.04$, $Z = 31\,509.4$, $r = -0.836$).

A high proportion of *Octopus pallidus* individuals were correctly assigned to their collection locality for East Flinders Island, Mercury Passage and Northwest Bay (>85% correctly assigned) (Fig. 3). At Stanley and West Flinders Island, ~40% of the individuals were correctly assigned to their location of capture, with ~25% of individuals assigned to the alternate population and ~15% assigned to East Flinders Island (Fig. 3).

Bayesian clustering of *Octopus pallidus* without prior population collection information suggested a single homogenous population [$Pr(K = 1) = 0.99$]. When prior population information was provided, 2 genetically distinct clusters were best supported

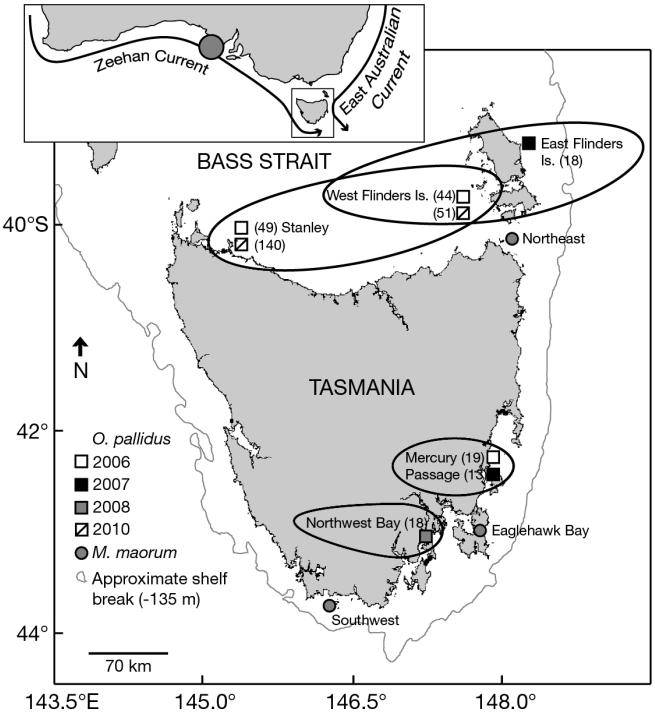

Fig. 1. Sampling locations for *Octopus pallidus* and *Macroctopus maorum* (Doubleday et al. 2008b). Ellipses represent samples of *O. pallidus* that do not differ significantly in allele frequencies. Years denote cohorts sampled. Sample sizes for *O. pallidus* are given in parentheses. Inset map shows *M. maorum* site 'South Australia'

Table 2. *Octopus pallidus*. Pairwise θ (below diagonal) and minimum marine distance in kilometres (above diagonal) for population pairwise comparisons

	Stanley	West Flinders Island	East Flinders Island	Mercury Passage	Northwest Bay
Stanley		201	298	481	600
West Flinders Island	−0.0003		96	292	420
East Flinders Island	0.017[a]	0.0058		313	460
Mercury Passage	0.027[a]	0.027[a]	0.036[a]		158
Northwest Bay	0.156[a]	0.168[a]	0.206[a]	0.129[a]	

[a]Population pair significantly differentiated by a *G*-test following sequential Bonferroni correction

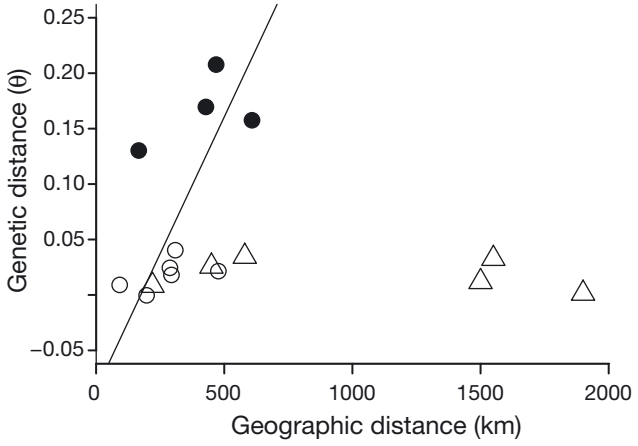

Fig. 2. *Octopus pallidus*, *Macroctopus maorum*. The relationship between genetic distance (θ) and straight-line marine geographic distance (km) between sampled populations of *O. pallidus* (regression line $r^2 = 0.54$, $p = 0.035$). Comparisons involving Northwest Bay are indicated by filled circles, all other *O. pallidus* comparisons are indicated by open circles. *M. maorum* comparisons are indicated by triangles

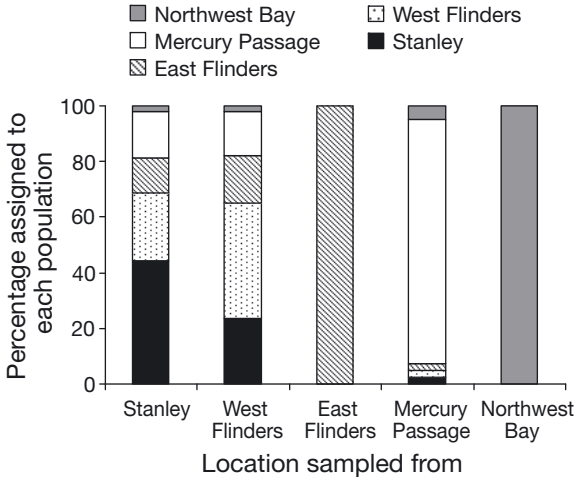

Fig. 3. *Octopus pallidus*. Assignment of individuals to sampling locations based on the genotypes of individuals obtained from each location

[Pr(K = 2) = 0.96], Northwest Bay as one cluster, with the majority of northern Tasmanian individuals (Stanley, West Flinders, East Flinders) best assigned to the other cluster; Mercury Passage individuals had intermediate assignment probabilities to both clusters (Fig. 4). Analyses using higher values of K produced similar patterns of individual clustering, with Northwest Bay individuals again appearing as a distinct cluster and Mercury Passage individuals having some ancestry with this cluster, but also with the clusters to which the northern Tasmanian individuals had ancestry (Fig. 4). Increasing K did not substantially increase differences among individuals with respect to apportioning ancestry to clusters. In *Macroctopus maorum*, panmixia was supported without prior population information [Pr(K = 1) = 1.0]. Two clusters, with the Northeast site separated, were supported when prior information was available [Pr(K = 2) = 0.99] (Fig. 5).

DISCUSSION

Population genetic structuring in a holobenthic octopus

Octopus pallidus exhibited significant spatial genetic structuring, with the magnitude of genetic differentiation correlated with the shortest marine sea-floor distance (agreeing with the isolation by distance model). Structuring existed within and between ocean current regions (e.g. East Flinders vs. Mercury Passage and East Flinders vs. Stanley, respectively; Fig. 1). Temporal variation was not found, indicating that the spatial population structuring is stable and not a product of vagaries in reproductive success among individuals, which can be observed across small numbers of generations (Christie et al. 2010). The lack of differentiation between East Flinders and West Flinders might be explained by Type II error from the small East Flinders sample, but this is unlikely given the evidence for isolation by distance across the study range. The significant isolation by distance relationship for *O. pallidus* is consistent with dispersal mediated by benthic adults and does not suggest a contribution by pelagic ocean currents (see also Keeney et al. 2009). Furthermore, the relationship is consistent with the absence of intervening bathypelagic

Fig. 4. *Octopus pallidus*. Bayesian clustering of individuals. Models (top to bottom): $K = 2$, 3 and 4 clusters with prior population collection information

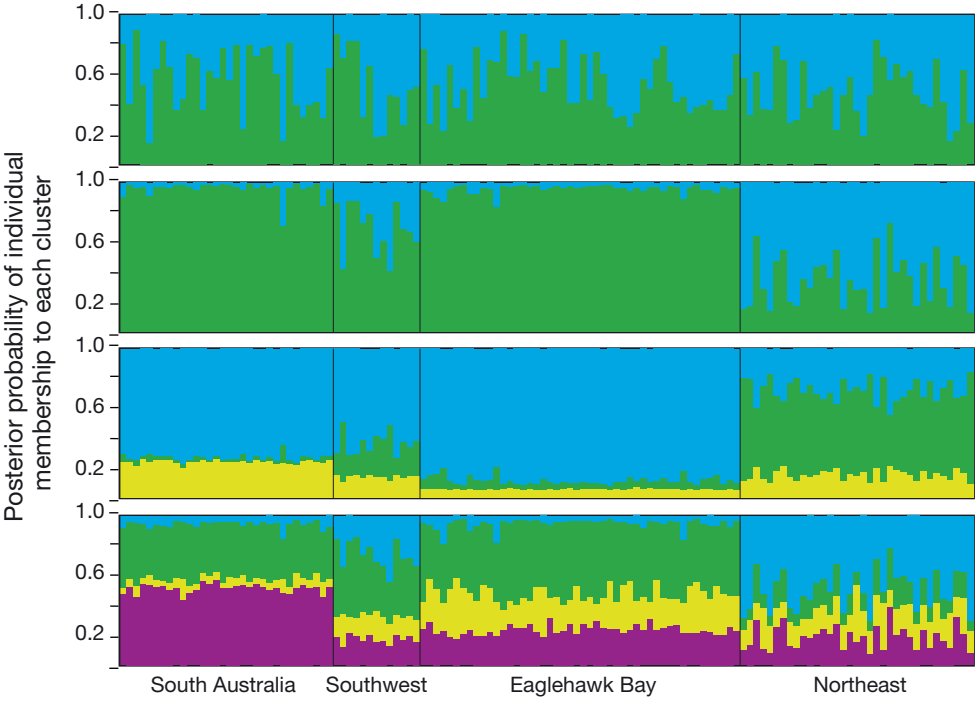

Fig. 5. *Macroctopus maorum*. Bayesian clustering of individuals. Models (top to bottom): $K = 2$ without prior population information, $K = 2$, 3 and 4 with prior population information

(>1000 m depth) habitats between study sites, which appear to reflect a barrier to dispersal in another holobenthic octopus lacking pelagic larvae (Allcock et al. 1997).

Contrasting population structure in a co-distributed merobenthic octopus — the influence of life history

Genetic structuring in *Macroctopus maorum* was inconsistent with isolation by distance: relatively proximate populations (~450 km apart) showed heterogeneity, while more distant population pairs (~1500 km) were homogenous (Doubleday et al. 2009). This pattern is consistent with prevailing ocean currents (Doubleday et al. 2009). In particular, populations of *M. maorum* from South Australia, Southwest Tasmania and Eaglehawk Bay (all 1 genetic cluster) may experience larval connectivity through the seasonal Zeehan Current (Fig. 1), which is active during *M. maorum* spawning (Grubert & Wadley 2000, Doubleday et al. 2009).

Genetic structuring estimated using G''_{ST} for *Octopus pallidus* (0.158) was slightly larger than that for *Macroctopus maorum* (0.151), despite the latter being measured across twice the spatial scale, suggesting *M. maorum* has stronger dispersal potential. *O. pallidus* sites within the same oceanographic system (East Flinders Island and Mercury Passage) were genetically heterogeneous, concordant with structur-

ing predominantly related to raw geographic separation. While our results are consistent with expectations based on the presence or absence of pelagic larvae, a caveat is that these 2 octopus species are likely to be relatively distantly related (Guzik et al. 2005), and therefore they are more likely to differ in other features that influence population structuring than if they were sister taxa (Dawson et al. 2002). Furthermore, collection sites were not identical for each species, reflecting fisheries operations, which may have contributed to the differences observed.

Towards a generalisation for dispersal and life history in octopuses

It appears that ocean currents do not influence dispersal in holobenthic octopuses, and isolation by distance, mediated by the movement of benthic adults, is the likely pattern of population differentiation in continuous habitats. These generalisations can be made based on the results for *Octopus pallidus* from the current study and Doubleday et al. (2008a), as well as genetic studies on other holobenthic octopuses. A preliminary study of *O. maya* using microsatellites revealed subtle population structure over 3 sites (Juárez et al. 2010) in a manner consistent with isolation by distance; homogeneity detected during an earlier allozyme study (Pérez-Losada et al. 2002) likely reflects the limited polymorphism available (3 of 30 loci polymorphic, overall H_O = 0.009). *Pareledone turqueti* allozymes (Allcock et al. 1997) also indicate the inability of individuals to disperse between sites separated by depths >1000 m. Therefore, isolation by distance is expected for holobenthic octopuses within continuous habitat, and the strength of population structuring will reflect the spatial extent of that habitat and adult dispersal capabilities; population structuring should be expected across habitat breaks.

Studies of other direct-developing marine taxa typically show strong population structure over small spatial scales (e.g. Hoffman et al. 2005, Bernardi 2008), although some studies have revealed genetic heterogeneity and homogeneity in different parts of a species' range (Sponer & Roy 2002, Garoia et al. 2004, Holmes et al. 2004). For genetic homogeneity over larger spatial scales, adult dispersal, such as rafting, may be involved (Fraser et al. 2011), but this is unlikely to be readily exploited by holobenthic octopuses, particularly those that make use of the substrate, rather than algae, for refuge (Allcock et al. 1997).

In contrast to holobenthic species, population structure in merobenthic octopuses shows less consistent patterns. *Octopus vulgaris* showed evidence for isolation by distance within ocean basins, and finer spatial structure than observed for *Macroctopus maorum*, despite having a similar life history (Casu et al. 2002, Murphy et al. 2002, Cabranes et al. 2008). This discrepancy may be caused by *M. maorum* having a longer larval duration than the 8 wk pelagic phase of *O. vulgaris* (Villanueva & Norman 2008), although this has yet to be validated (Doubleday et al. 2011). Other factors, such as habitat choice and ocean current regimes, may also be influential. Similarly, Casu et al. (2002) suggested that philopatric behaviour, larval mortality and reduced fitness post-settlement might reduce the significance of long-distance dispersal in *O. vulgaris*.

While widespread genetic homogeneity is typically observed in other marine taxa with pelagic larval stages (Sherman et al. 2008, Matschiner et al. 2009, Shulzitski et al. 2009), a growing number of studies shows the effects of phylogeny (Kinlan & Gaines 2003), physical barriers and behaviour-limiting gene flow (e.g. Jones et al. 2005, Baums et al. 2006, Miller & Ayre 2008). Therefore, while dispersal in merobenthic species appears to be greater than that in holobenthic species, some merobenthic species could have similarly low realised dispersal.

Comparison and combination of genetic and stylet microchemistry inferences of population structure

This study provides a unique opportunity to compare population structures inferred from molecular and microchemistry markers for an octopus species, and contrast this with similar comparisons in fish (e.g. Burridge & Smolenski 2003, Miller et al. 2005, Bradbury et al. 2008). Stylet microchemistry distinguished all *Octopus pallidus* populations (Doubleday et al. 2008a), while genetic analyses failed to distinguish adjacent populations in northern Tasmania. This difference probably does not reflect recent population isolation, as attainment of migration drift equilibrium is suggested by the presence of an isolation by distance relationship (Hutchison & Templeton 1999). Similarly, for *Macroctopus maorum*, stylets were able to distinguish more populations than genetics (Doubleday et al. 2008b, 2009). Lower power of molecular relative to environmental markers in octopodids is consistent with observations from analogous markers in fishes (otolith microchemistry), and it has been explained

in terms of molecular markers quantifying averaged gene flow over generations, whereas microchemistry methods test for movement only in the sampled generation (Campana & Thorrold 2001, Doubleday et al. 2009).

The use of multiple methods to investigate dispersal patterns and spatial population structure can not only provide a basis for validating novel techniques and circumstantial results, but can also provide complementary data over a range of spatial and temporal resolutions. Directly comparing genetic and microchemical data from the same individuals of *Octopus pallidus* largely validated the previous conclusions drawn from the novel method of stylet microchemistry, despite untested assumptions regarding the causes of stylet microchemistry variation. The combination of techniques also provides greater confidence that population structuring is stable across generations, and suggests that dispersal in *O. pallidus* is low even where populations are genetically homogeneous, as significant heterogeneity in environmental markers still exists. This further highlights that interrogations of markers which are inherited and markers which are retained for only the lifetime of individuals are, in concert, particularly useful for studying population structure (e.g. Campana & Thorrold 2001, Jones et al. 2005, Miller et al. 2005, Bradbury et al. 2008).

Management recommendations

Sustainable and efficient fisheries management requires accurate stock delineation; failure to identify distinct stocks leads to local overexploitation risks, while overestimating the number of stocks may result in inefficient exploitation (Palsbøll et al. 2007). While several holobenthic octopus species are the focus of commercial fisheries, these species are often managed without understanding their ecology (Leporati et al. 2009). The amount of dispersal relevant to managers is usually several orders of magnitude larger than that resulting in genetic homogeneity (Palsbøll et al. 2007). Therefore, significant genetic structure between *Octopus pallidus* populations advocates their separate management. Significant differences in stylet microchemistry were present among genetically homogenous populations; therefore, while dispersal exists among these populations, the levels are unlikely to influence population dynamics (Waples 1998, Campana & Thorrold 2001, Palsbøll et al. 2007), and these populations should also be managed separately.

Acknowledgements. Samples were collected with the assistance of the Hardy family, S. Leporati, Spring Bay Seafoods and N. Beeton. We thank J. Worth and A. Smolenski for assisting with laboratory analyses, and P. Unmack, N. Beeton and the Tasmanian Department of Primary Industries, Parks, Water and the Environment for assistance with figures. This study was supported by the W. V. Scott Charitable Trust and the Tasmanian Department of Primary Industries, Parks, Water and the Environment.

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Editorial responsibility: Philippe Borsa, Montpellier, France

Submitted: May 16, 2012; Accepted: March 10, 2013
Proofs received from author(s): June 26, 2013