Synopsis of population connectivity studies of marine organisms within the Hawaiian Archipelago

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Bird et al. 2007

Mitochondrial DNA was used to investigate the population structure from Hawaii island to Kure Atoll (Mokuapapa) of three sympatric endemic Hawaiian broadcast-spawning opihi (*Cellana* spp.) with similar life histories. All three species have planktonic larvae that are competent to settle within 4 days.

Significant population partitioning was detected in all three species of Hawaiian limpets, but regional patterns of differentiation were not consistent among species. One common feature was that there were gene-flow restrictions between northwestern and southeastern populations. For two species (*C. exarate, C. sandwicensis*)*,* a minor restriction was identified between the NWHI and MHI, while for the other (*C. talcosa*) a major restriction was identified between Kauai (northwest end of distribution) and remaining MHI samples. Island land masses are not barriers to gene flow but rather deep open ocean channels and variable currents among islands.

Despite close phylogenetic affinity and similar life histories, the endemic Hawaiian *Cellana* exhibit distinctly different population structures. 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.

Craig et al. 2010

Genetic analysis of three endemic Hawaiian butterflyfishes indicates that all three species have a single, genetically homogeneous population within the Hawaiian Archipelago.

Other studies examining the population structure of Hawaiian reef fishes have similarly found homogeneous populations in soldierfishes (Craig et al., 2007), pygmy angelfishes (Schultz et al., 2007) and introduced snappers (Lutjanidae; Gaither et al., 2010).

 In contrast, the Hawaiian Grouper, *Epinephelus quernus*, demonstrated marginally restricted gene flow on an archipelago scale (Rivera et al., 2004), and population differences have been found in two endemic damselfishes (Ramon et al., 2008) and an endemic surgeonfish (Eble et al., 2009).

These results indicate that patterns of genetic connectivity can vary by an order of magnitude among species sampled across the same geographic area. This lack of a consistent pattern in gene flow indicates that designing conservation strategies for reef fishes based on genetic data will be a complex process.

Dibattista et al. 2011

Mitochondrial DNA (mtDNA) analysis found little evidence for population genetic differentiation of the Blueline Surgeonfish, *Acanthurus nigroris* within the Hawaiian archipelago from Kure Atoll to Hawai'i island (2600 km).

This indicates that populations from each of the separate islands either freely exchanged propagules or have done so in the recent past.

A comparison of 10 genetic studies within the Hawaiian archipelago showed that 6 out of the 14 species surveyed displayed clear genetic breaks between NWHI and the MHI. The other 8 species did not have such genetic breaks.

There was no obvious correlation between genetic structure and pelagic larval duration (PLD), reproductive strategy or habitat preference of the different species.

There was also no agreement among even closely related surgeonfish species with similar life-history characteristics. For example Kole, *Ctenochaetus strigosus* shows genetic structure (mtDNA) within Hawai'i whereas other surgeonfishes studied – *A. nigroris*, Lavender Tang, *A. nigrofuscus* and Yellow Tang, *Zebrasoma flavescens* did not. Connectivity between the NWHI and MHI thus needs to be evaluated on a case-by-case basis.

Estimated migration rates for *A. nigroris* using the program MIGRATE supported an emerging trend for a northwestward flow of larvae from the MHI to the NWHI indicating that Monument may be a recipient, rather than a source of propagules to replenish reef resources.

Eble et al. 2009

Mitochondrial DNA variation was examined in three surgeonfish species with vastly different ranges: *Ctenochaetus strigosus* (Hawaiian endemic), *Zebrasoma flavescens* (North Pacific) and *Acanthurus nigrofuscus* (Indo-Pacific).

Analyses demonstrated that all three species are capable of maintaining population connectivity on a scale of thousands of km. However there were modest but significantly different patterns of gene flow among the three species surveyed, with the degree of genetic structure increasing as range size decreases.

In other studies done to date, three wide ranging reef fishes surveyed exhibited complete or nearly complete genetic homogeneity among Hawaiian locations while four endemics had significant population subdivisions.

Because the identification of even slight genetic spatial patterning indicates a lack of demographically meaningful levels of larval dispersal, contrasting patterns observed between endemic and non-endemic Hawaiian reef fishes indicate that benefits from the Papahānaumokuākea Marine Monument will differ among these groups. Having exhibited nearly complete genetic homogeneity, Indo-Pacific reef fishes show that wide ranging species are more capable of maintaining population connections compared to the dispersal limited Hawaiian endemics.

If this pattern holds for Hawaiian marine endemics in general, then the establishment of one of the world's largest marine protected areas will do little to alleviate management concerns for the depleted reefs of the main Hawaiian Islands.

Eble et al. 2011a

Analysis of mitochondrial DNA diversity in the widely distributed Brown Surgeonfish (*Acanthurus nigrofuscus*), revealed significant genetic structure only at the extremes of the range. Collections from Hawai'i to the Eastern Indian Ocean comprise one large, undifferentiated population.

This pattern of limited genetic subdivision across reefs of the central Indo-Pacific has been observed in a number of large-range reef fishes. Conversely, small-range fishes are often deeply structured over the same area

The broad genetic connectivity consistently observed in the most widely distributed Indo-Pacific fishes highlights an emerging relationship between reef fish range size and genetic connectivity. In particular, Soldierfishes (genus *Myripristis* , Pygmy Angelfishes (genus *Centropyge*), Trumpetfishes (genus *Aulostomus*), Unicornfishes (genus *Naso*), Moray Eels (genus *Gymnothorax*), and at least some Snappers (genus *Lutjanus*) and Surgeonfishes (genus *Acanthurus*) have demonstrated an ability to maintain genetic homogeneity across tens of thousands of kilometers.

Eble et al. 2011b

Genetic analyses (mtDNA & nuclear microsatellites) of Yellow Tang populations indicates several isolated stocks within (1) the northern-most islands of the Hawaiian Archipelago (Kure, Midway, and Pearl and Hermes), (2) the broad region of the central archipelago from French Frigate Shoals to Oahu, (3) adjacent Maui and Molo kai, and (4) possible multiple management units on Hawaii Island.

Population designations are generally concordant with population discontinuities in other Hawaiian fishes, invertebrates, and marine mammals (Bird et al. 2007, Andrews et al. 2010, Polato et al. 2010, Toonen et al. 2011).

Since the Yellow Tang population within French Frigate Shoals to Oahu spans portions of both the PMNM and MHI reefs, evidence of genetic connectivity between these regions indicates the potential for some larval spillover. However, prevailing northwest surface currents may limit opportunities for larval dispersal from the PMNM to the MHI. Rather, the impacted reefs of the MHI may serve as a larval source for the PMNM.

Gaither et al. 2011

Genetic analyses using Mitochondrial DNA and microsatellites collected from Hawai'i to the western Indian Ocean indicate that the deepwater snapper *P. filamentosus* is a highly dispersive species with low but significant population structure due entirely to the isolation of Hawai'i.

P. filamentosus harbors low genetic diversity in Hawai'i, a common pattern in marine fishes, and our data indicate a single archipelago-wide stock.

Kobayashi & Polovina 2006

Larval transport and oceanographic conditions experienced by pelagic larvae in the Northwestern Hawaiian Islands were simulated using an individual-based approach to track daily movements. Larval dispersal was simulated for each month of the year from 1993-2002 for 3, 6, and 12 month larval durations. Four release locations were evaluated: Midway Island, Maro Reef, Necker Island, and Oahu. Five thousand simulated larvae were released for each model treatment for a total of 7.2 million individuals. Each individual was tracked daily for the entire larval duration.

Larval retention was strongly related to year and larval duration and had weak relationships to month and site. Larval settlement at Oahu was strongly dependent on spawning site. Larval settlement at Oahu examined by source also appeared to be a proximity effect, with settlement negatively correlated with distance from Oahu. Larval duration was an important effect when examining Oahu settlement from the adjacent site at Necker; however, even at the longest larval durations, the numbers reaching Oahu from Necker did not surpass the number being retained around Oahu from Oahu.

Ramon et al. 2008

The population structures of two damselfishes, *Stegastes fasciolatus* and *Dascyllus albisella*, were examined throughout the Hawaiian Archipelago using mitochondrial control region sequences. Overall, *Stegastes fasciolatus* was shown to have little population structure in the majority of the Hawaiian Islands except for the northernmost island of Kure. There are no known oceanographic factors that might explain the genetic isolation of *S. fasciolatus* at Kure, but the atoll has only a single, relatively narrow, natural pass, which might constrain the dispersal of propagules produced within its lagoon.

In contrast, *Dascyllus albisella* exhibited very strong population structure throughout the Hawaiian Islands. Ecological (e.g. spawning seasonality) and environmental factors (seasonal differences in oceanic currents and eddies) rather than pelagic larval duration can explain the striking difference in population structure between the two species.

Rivera et al. 2011

Genetic analyses using Mitochondrial DNA and microsatellites revealed relatively high connectivity for the Hawaiian Grouper, *Epinephelus quernus* across the Hawaiian archipelago.

There are however genetically distinct populations in the mid-archipelago at Necker and especially Gardner which may be due to recent connectivity with Johnston Atoll, the only location outside of Hawai'i where this species has been reported.

Comparisons of genetic analyses and simulated larval dispersal patterns based on oceanic currents provide evidence that dispersal is predominately from the MHI to the NWHI and dispersal in the opposite direction is probably low.

Skillings et al. 2011

Mitochondrial DNA examination of the sea cucumber *Holothuria atra* revealed significant genetic population structure across the surveyed portion of the range. There are two patterns to this structure. Excluding Laysan Island, there are no significant differences between any other islands in the NWHI (spanning nearly 2000km), suggesting that the NWHI, excluding Laysan, comprises a single large population.

In contrast, there is significant structuring within the MHI (roughly 600km) and between the NWHI and the MHI. Analysis shows the division between the NWHI and the MHI to be the strongest barrier to gene flow within the Archipelago. Migration across this barrier is heavily one sided, where migration from the MHI into the NWHI dominates.

Holothuria atra must be managed on a local scale; migration between archipelagos, and often between islands, does not occur in ecologically relevant time frames.

Szabó et al. 2014

Mitochondrial DNA analyses of the Manybar Goatfish *Parupeneus multifasciatus* was examined to determine whether larval exchange occurs between the NWHI and the MHI.

No evidence was found of barriers to gene flow indicating that larval dispersal is sufficient to homogenize genetic distributions from one end of the archipelago to the other.

While migration results were contradictory, the predominant direction of larval flow seems to be from the MHI toward the NWHI consistent with the dominant surface currents. and as with previous genetic surveys (Gaither et al. 2011, DiBattista et al. 2011, Toonen et al. 2011). The management implications of this finding are that the heavily-fished MHI cannot be quickly replenished by the protected NWHI.

Tenggardjaja et al. 2014

Genetic analyses of mitochondrial and nuclear markers in the Threespot Chromis (*Chromis verater*) indicated that there was no significant genetic differentiation by depth, indicating high levels of vertical connectivity between shallow and deep water (30-150m) populations of C. verater.

Low but significant population structure was detected across the Hawaiian Archipelago. The population structure within the archipelago was driven by samples from the island of Hawai'i at the southeast end of the chain and Lisianski in the middle of the archipelago. The analysis of the archipelago identified a genetic break between the island of Hawai'i and the rest of the Hawaiian populations.

Within the Hawaiian Archipelago, there was greater gene flow from the NWHI into the MHI than from the MHI into the NWHI.

Toonen et al. 2011

Studied 27 taxonomically and ecologically diverse species. Overall dataset indicates reveal four concordant barriers to dispersal within the Hawaiian Archipelago. Additionally, much of the NWHI is well connected despite greater average distances among the sites whereas the MHI show greater structure on average despite geographic proximity

the NWHI are far more connected on average (and therefore comparatively robust) than the MHI, but that connectivity between the MHI and NWHI is limited.

The results highlight that the Main Hawaiian Islands are isolated in terms of resource management and will not receive substantial subsidy from the Papahānaumokuākea Marine National Monument; the MHI must stand alone in management of marine resources. Furthermore, even the comparatively small MHI are not a single panmictic unit, and future management plans should incorporate knowledge of the substantial isolation among multiple regions within the MHI.

Vaz 2012

Connectivity analysis based on particle movement (simulated fish larvae) within the Hawaiian Archipelago for 3 species of bottomfishes (onaga, ehu & 'ōpakapaka) revealed 4 distinct larval dispersal zones within the Archipelago:
Zone 1; Hawai'i Island – O'ahu
Zone 2; Kaua'i – Necker
Zone 3; French Frigate Shoals – Lisianski
Zone 4; Pearl & Hermes – Kure

Larvae released in each zone is mostly locally retained but there is a high degree of larval transport and connectivity between NWHI sites.

Direct connectivity between NWHI and MHI was limited for all species and scenarios. Larvae originating in the NWHI tend to be locally retained and not exported to MHI., i.e. local retention of larvae.

Larval exchange is mainly from MHI to NWHI which is consistent with the dominant surface currents.

Simulations indicated that the islands/reefs within Zone 2 (Kaua'i – Necker) which include Middle Bank, may act as steeping stones and an ecological corridor, connecting the NWHI and the MHI through larval dispersal which is mainly from MHI to NWHI. This emphasizes the necessity of protecting this Zone although it is noted that the location of Middle Bank is insufficient for management and fishery regulations.

Results are consistent with previous genetic surveys which have found larval movement predominately from MHI to NWHI: Rivera et al. 2011, Toonen et al. 2011.

Wren et al. 2016

The study provides a comprehensive estimate of connectivity of passive pelagic particles released from coral reef habitat throughout the Hawaiian Archipelago using a particle transport model coupled with currents generated by an oceanographic circulation model. The results show an isolation-by-distance pattern with sites far away from each other having little or no potential connectivity and a surprising degree of self-recruitment. There is limited potential connectivity between the northwestern Hawaiian Islands (NWHI) and the Main Hawaiian Islands (MHI) and the direction of dispersal is predominantly from the MHI to NWHI.

There are three breaks in connectivity for both year-round and seasonal particle release and very few particles successfully cross these breaks. These breaks are more pronounced during spawning season releases. The southernmost break between Nihoa and Necker is the most pronounced and no particles cross this break into or out of the MHI, effectively cutting the MHI off from the NWHI. The central break at Gardner Pinnacles and Maro Reef is traversed only by particles to and from Raita Bank. The northern break between Lisianski and Pearl and Hermes Atoll effectively isolates Kure Atoll and Midway Islands, resulting in high self-recruitment for the northernmost islands in the archipelago.

One of the hopes for establishing the Papahānaumokuākea Marine National Monument (PMNM), was a spillover effect where the protected fish populations in PMNM would replenish fish stock in the MHI. Unfortunately, this hope has been little supported among studies to date of both invertebrates and fishes (Bird et al. 2007, Friedlander et al. 2009, Rivera et al. 2011, Skillings et al. 2011). The lack of spillover from PMNM to the MHI has been attributed to the prevailing surface currents moving larvae up the island chain from the MHI towards the NWHI (Kobayashi et al. 2006, Rivera et al. 2011).

The current management strategy for the MHI is based in part on the unfished stock in PMNM that is expected to spill over and replenish fished stocks in the MHI. Our results, coupled with previous genetic work, do not support this expectation, warranting revision of stock boundaries and resource management plans. A growing number of studies support directional dispersal in the Hawaiian Islands for corals [15,36,83], limpets [37], cucumbers [38], and fish [35].

Although the probability of larval transport is greater from the MHI to the NWHI and not the other way around, it is important to note that the total number of larvae transported may in fact be greater from the NWHI down to the MHI when accounting for the larger standing stock biomass in the NWHI.

References

Bird CE, Holland BS, Bowen BW, Toonen RJ. 2007. Contrasting phylogeography in three endemic Hawaiian limpets (*Cellana* spp.) with similar life histories. Mole Ecol. 2007; 16: 3173±3186. doi: 10.1111/j.1365- 294X.2007.03385.x PMID: 17651195

Craig MT, Eble JA, Bowen BW. 2010. Origins, ages, and populations histories: comparative phylogeography of endemic Hawaiian butterflyfishes (genus *Chaetodon*). J Biogeogr. 37:2125–2136. http://dx.doi.org/10.1111/j.1365-2699.2010.02358.x

Dibattista JD, Wilcox C, Craig MT, Rocha LA, Bowen BW. 2011. Phylogeography of the Pacific blueline surgeonfish Acanthurus nigroris reveals a cryptic species in the Hawaiian Archipelago. J Mar Biol. Article ID 839134. http://dx.doi.org/10.1155/2011/839134

Eble JA, Toonen RJ, Bowen BW. 2009. Endemism and dispersal: comparative phylogeography of three surgeonfishes across the Hawaiian Archipelago. Mar Biol. 156:689–698. http://dx.doi.org/10.1007/s00227-008-1119-4

Eble JA, Rocha LA, Craig MT, Bowen BW. 2011a. Not All Larvae Stay Close to Home: Insights into Marine Population Connectivity with a Focus on the Brown Surgeonfish (*Acanthurus nigrofuscus*). J Mar Biol. Article ID 518516. http://dx.doi:10.1155/2011/518516

Eble JA, Toonen RJ, Sorenson L, Basch LV, Papastamatiou YP, Bowen BW. 2011b. Escaping paradise: larval export from Hawaiʾi in an Indo-Pacific reef fish, the yellow tang (*Zebrasoma flavescens*). Mar Ecol Prog Ser. 428:245−258. http://dx.doi.org/10.3354/meps09083

Friedlander, A, Keller K, Wedding L, Clarke A, Monaco M. (eds.). 2009. A Marine Biogeographic Assessment of the Northwestern Hawaiian Islands. NOAA Technical Memorandum NOS NCCOS 84. Prepared by NCCOS's Biogeography Branch in cooperation with the Office of National Marine Sanctuaries Papahanaumokuakea Marine National Monument. Silver Spring, MD. 363 pp.

Gaither MR, Jones SA, Kelley C, Newman SJ, Sorenson L, Bowen BW. 2011. High connectivity in the deepwater snapper *Pristipomoides filamentosus* (Lutjanidae) across the Indo- Pacific with isolation of the Hawaiian Archipelago. PLoS One. 6(12):e28913. http://dx.doi. org/10.1371/journal.pone.0028913

Kobayashi DR, Polovina JJ. 2006. Simulated seasonal and interannual variability in larval transport and oceanography in the Northwestern Hawaiian Islands using satellite remotely sensed data and computer modeling. Atoll Res Bull. 543: 365-390.

Ramon ML, Nelson PA, DeMartini E, Walsh WJ, Bernardi G. 2008. Phylogeography, historical demography, and the role of post-settlement ecology in two Hawaiian damselfish species. Mar Biol. 153:1207−1217. http://dx.doi.org/10.1007/s00227-007-0894-7

Rivera MAJ, Andrews KR, Kobayashi DR, Wren JL, Kelley C, Roderick GK, Toonen RJ. 2011. Genetic analyses and simulations of larval dispersal reveal distinct populations and directional connectivity across the range of the Hawaiian grouper (*Epinephelus quernus*). J Mar Bio. 2011:Article ID 765353, 11 pp.

Skillings DJ, Bird CE, Toonen RJ. 2011. Gateways to Hawai`i: genetic population structure of the tropical sea cucumber *Holothuria atra*. Journal of Marine Biology Volume 2011, Article ID 783030, 16 pages doi:10.1155/2011/783030

Szabó et al. 2014. Phylogeography of the manybar goatfish, *Parupeneus multifasciatus*, reveals isolation of the Hawaiian Archipelago and a cryptic species in the Marquesas Islands. Bull Mar Sci. 90(1):493–512. 2014 http://dx.doi.org/10.5343/bms.2013.1032

Tenggardjaja KA, Bowen BW, Bernardi G. 2014. Vertical and Horizontal Genetic Connectivity in *Chromis verater*, an Endemic Damselfish Found on Shallow and Mesophotic Reefs in the Hawaiian Archipelago and Adjacent Johnston Atoll. PLoS ONE 9(12): e115493. doi:10. 1371/journal.pone.0115493

Toonen RJ, Andrews KR, Baums IB, Bird CE, Concepcion CT , Daly-Engel TS , Eble JA, Faucci A, Gaither MR, Iacchei M, et al. 2011. Defining boundaries for applying ecosystem-based management: a multispecies case study of marine connectivity across the Hawaiian Archipelago. J Mar Biol. Article ID 460173. http://dx.doi.org/10.1155/2011/460173

Vaz AC 2012 Here today, gone tomorrow: Flow variability, larval dispersal and fisheries management in Hawai'i. Ph.D. Dissertation, University of Hawai'i at Mānoa. 122p.

Wren JLK, Kobayashi DR, Jia Y, Toonen RJ. 2016. Modeled Population Connectivity across the Hawaiian Archipelago. PLoS ONE 11(12): e0167626. doi:10.1371/journal.pone.0167626