Escaping paradise: larval export from Hawaii in an Indo-Pacific reef fish, the yellow tang *Zebrasoma flavescens*

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ABSTRACT: The depauperate marine ecosystems of the Hawaiian Archipelago share a high proportion of species with the southern and western Pacific, indicating historical and/or ongoing connections across the large oceanic expanse separating Hawaii from its nearest neighbors. The rate and direction of these interactions are, however, unknown. While previous biogeographic studies have consistently described Hawaii as a diversity sink, prevailing currents likely offer opportunities for larval export. To assess interactions between the remote reefs of the Hawaiian Archipelago and the species-rich communities of the Central and West Pacific, we surveyed 14 nuclear microsatellite loci (nDNA, n = 857) and a 614 bp segment of mitochondrial cytochrome *b* (mtDNA, n = 654) in the yellow tang *Zebrasoma flavescens*. Concordant frequency shifts in both nDNA and mtDNA reveal significant population differentiation among 3 West Pacific sites and Hawaii (nDNA F'_{CT} = 0.116; mtDNA ϕ_{CT} = 0.098, p < 0.001). SAMOVA analyses of microsatellite data additionally indicate fine scale differentiation within the 2600 km Hawaiian Archipelago (F'_{SC} = 0.026, p < 0.001), which has implications for management of this heavily-exploited aquarium fish. Mismatch analyses indicate the oldest contemporary populations are in the Hawaiian Archipelago (ca. 318 000 yr) with younger populations in the West Pacific (91 000 to 175 000 yr). Estimates of yellow tang historical demography contradict expectations of Hawaii as a population sink and instead indicate asymmetrical gene flow, with Hawaii exporting rather than importing yellow tang larvae.

KEY WORDS: Acanthuridae · Larval dispersal · Larval retention · Marine connectivity · Phylogeography · Stock assessment

INTRODUCTION

The marine fauna of Hawaii is considerably less diverse than that of the tropical West and South Pacific but includes many of the same species (Randall 1998, Mundy 2005). Community similarities indicate the possibility of ongoing connections between the geographically remote Hawaiian Archipelago and the broader Indo-Pacific, but the rate of connectivity is difficult to assess. The broad distribution of many species similarly limits the identification of dispersal corridors and the directionality of colonization (Hourigan & Reese 1987, Jokiel 1987, Craig et al. 2010). Nevertheless, Hawaii's marine fauna is widely regarded as a biogeographic 'dead end', with diversity flowing into but not out of the islands (Hourigan & Reese 1987, Jokiel 1987, Kay & Palumbi 1987, Randall 1998, Briggs 1999).

Dispersal corridors

Affinities between reef fish communities in Hawaii and southern Japan have prompted the suggestion of larval exchange via the Kuroshio Current (KRC) and the North Pacific Current (NPC; Randall 1998), which encounters Kure and Midway Atoll in the recently established Papahânaumokuâkea Marine National Monument (PMNM; Fig. 1). Sister taxa for 2 of Hawaii's 3 endemic butterflyfishes (family Chaetodontidae) occur only in the West Pacific (including southern Japan), indicating likely colonization via the NPC (Craig et al. 2010). Drogues released off Japan have made their way to the PMNM (McNally et al. 1983), though the drogues required more than a year to make the journey, which is far longer than most species' pelagic larval duration (PLD). Formation of a land bridge between Taiwan and the southern Ryukyu Islands of Japan during recent glacial maxima de-

flected the Kuroshio Current eastward (Ujiie et al. 2003), potentially reducing travel time to Hawaii. Alternatively, dispersal may be aided by juvenile rafting with flotsam (Jokiel 1987, Randall 2007).

Dispersal to Hawaii may also occur along the eastward flowing Hawaiian Lee Countercurrent (HLCC), which attains speeds of up to 8 cm s^{-1} (Kobashi & Kawamura 2002) as it flows past Wake Atoll and northern portions of the Marshall Islands before terminating near Johnston Atoll 800 km southwest of the Hawaiian archipelago (Fig. 1). Johnston Atoll has been proposed as a link between Hawaii and other Central Pacific communities (Kobayashi 2006), though faunal affinities and recent genetic studies indicate that Johnston is more likely an outpost of Hawaii rather than a link to the broader Pacific (Hourigan & Reese 1987, Skillings et al. 2011, Timmers et al. 2011). Johnston Atoll's apparent inability to facilitate dispersal to Hawaii may be because dispersal to the atoll via the HLCC is prohibi-
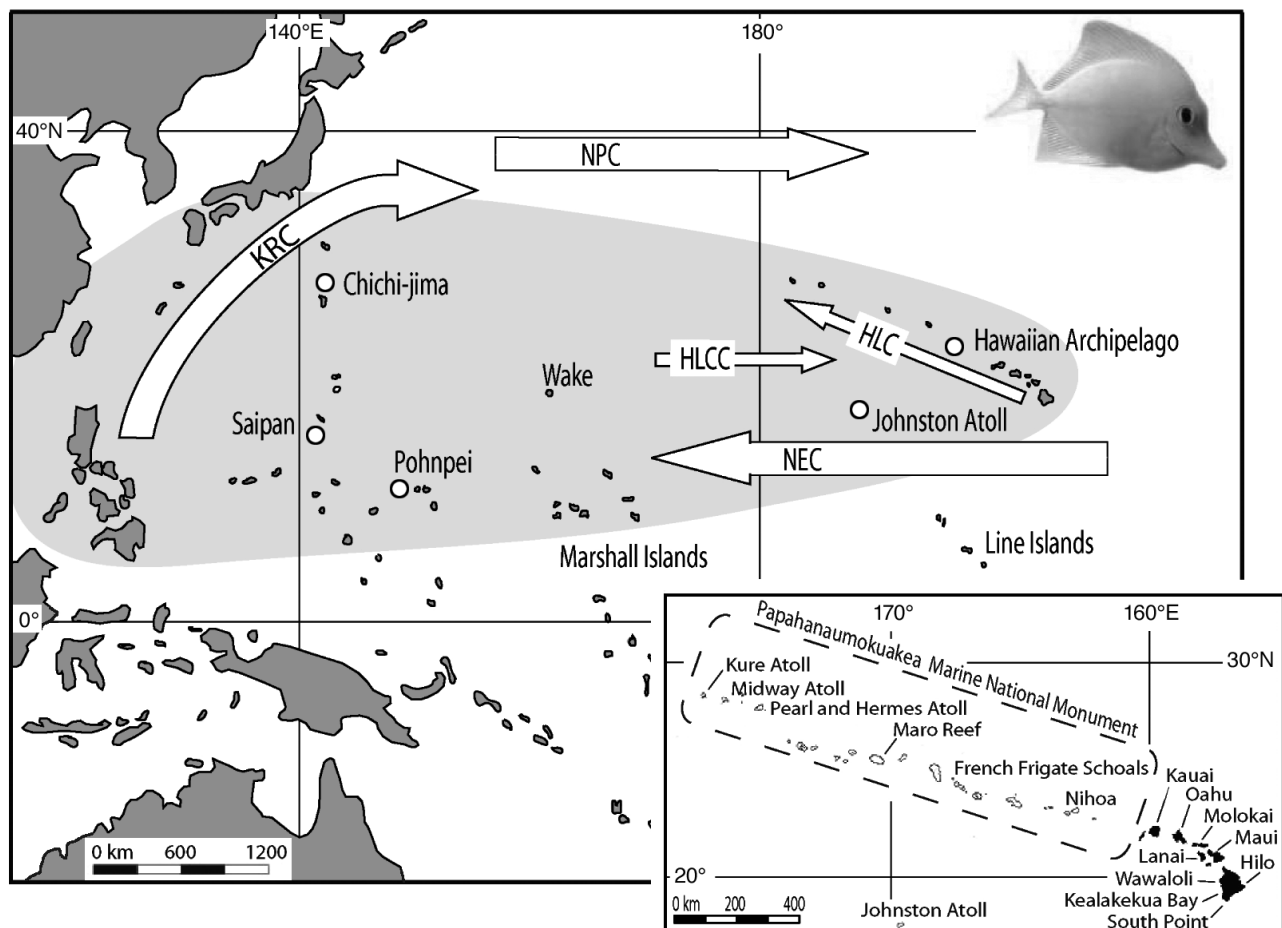

Fig. 1. *Zebrasoma flavescens.* Yellow tang collection sites (○). Hawaiian sampling sites are detailed in the inset. Collections were made from June 2004 to July 2005. Major currents (arrows): KRC = Kuroshio Current; NPC = North Pacific Current; HLC = Hawaiian Lee Current; HLCC = Hawaiian Lee Counter Current; NEC = North Equatorial Current

tively long and, like contemporary dispersal via the NPC, would require a minimum journey of nearly a year (Kobashi & Kawamura 2002).

The Line Islands, 1800 km south of Hawaii (Fig. 1), have also been proposed as a source for larvae dispersing to the archipelago (Myers 1989) and occasional strays and migrants have been observed (Randall 2007). Nonetheless, opportunities for exchange between the Line Islands and Hawaii are likely rare because of the need to cross the broad, fast and westward flowing North Equatorial Current (NEC), which regularly attains speeds greater than 25 cm s^{-1} and sometimes exceeds 60 cm s^{-1} (Kashino et al. 2009). These velocities are well beyond maximum sustainable swimming speeds for reef fishes (Fisher et al. 2005). Moreover, unlike the Southern Equatorial Current (SEC) that can experience dramatic inter-annual changes in current velocity and direction in response to El Niño/La Niña conditions (Johnston & Merrifield 2000), the NEC is considerably more stable, slowing only slightly during La Niña (Qiu & Joyce 1992, Kashino et al. 2009).

While the consistency and velocity of the NEC would appear to limit opportunities for larval exchange with the Line Islands, these same features may facilitate downstream export of Hawaiian born larvae (Jokiel & Martinelli 1992, Connolly et al. 2003). Anti-cyclonic eddies forming off the leeward shore of Hawaii Island have been recorded travelling as far west as the Marshall Islands under the influence of the NEC (Calil et al. 2008), and larvae from a diverse set of nearshore taxa have been found entrained within the eddies (Lobel & Robinson 1988). The minimum estimated travel time along the NEC is 70 d, which is considerably shorter than dispersal estimates for other proposed corridors, and is within estimated larval durations for many fishes, particularly when considering the potential for many taxa to extend their pelagic period in the absence of suitable substrate (e.g. Toonen & Pawlik 2001) and that larval behavior may further reduce travel time (Fisher 2005, Cowen & Sponaugle 2009).

Genetic insights into larval dispersal

Recent phylogeographic assessments of Pacific reef fishes have revealed that larvae at least occasionally bridge Hawaii's isolation (Craig et al. 2007, Reece et al. 2010, Eble et al. 2011). Connectivity rates and directionality have not explicitly been assessed, with the exception of a recently published survey of range-wide patterns of gene flow in the widely distributed ruby-lipped parrotfish *Scarus rubrioviolaceus*, which revealed intriguing evidence of larval dispersal from Hawaii to reefs in the Central Pacific (Fitzpatrick et al. 2011). Additional support for larval export from Hawaii

can be found in the bullethead parrotfish *Chlorurus sordidus*, which revealed Hawaiian-derived mitochondrial lineages in West Pacific populations (Bay et al. 2004). Here we employ a multi-locus, range-wide genetic survey of the Indo-Pacific reef fish, the yellow tang *Zebrasoma flavescens*, to assess connectivity patterns across the northern tropical and subtropical Pacific. A previous survey of yellow tang mitochondrial DNA (mtDNA) variation within the Hawaiian Archipelago revealed no population subdivisions (ϕ_{CT} = 0.001, p = 0.38; Eble et al. 2009), indicating the potential for high rates of population connectivity across long distances. We build on the previous mtDNA survey with range-wide coverage, larger sample sizes, and the inclusion of 14 microsatellite loci developed for yellow tang (Christie & Eble 2009).

Yellow tang are abundant reef herbivores in Hawaii (Walsh 1987, Tissot et al. 2004) but also occur in lower numbers throughout the tropical and subtropical North Pacific (Randall 1998). Juveniles and adults are relatively sessile (Claisse et al. 2009, Williams et al. 2009), restricting inter-population connectivity to the estimated 55-d planktonic larval phase (determined by otolith microdissection; Basch et al. 2003). In Hawaii, yellow tang comprise ~85% of the ornamental fish harvest with an estimated 300 000 juveniles collected annually (Tissot & Hallacher 2003). Accordingly, one of the rationales for the recent establishment of the 360 000 km^2 PMNM is that the region's uninhabited islands and atolls may be an important source of larvae for the depleted reefs of the main Hawaiian Islands (MHI; McClanahan & Mangi 2000).

MATERIALS AND METHODS

Sample collection. To identify patterns of genetic structure and connectivity at multiple spatial scales, we sampled juvenile and adult yellow tang throughout its range, resulting in 857 individuals from 19 locations (Fig. 1, Table 1). Previous collections from Hawaii and Johnston Atoll (Eble et al. 2009; n = 560) were supplemented with 297 additional specimens from the same locations as well as collections at 3 locations in the West Pacific (Chichi-jima, Saipan, and Pohnpei). Hawaiian collections spanned the full 2600 km of the archipelago and included 6 sites within the newly established PMNM and 9 sites within the MHI, including 4 sites on the largest island in the archipelago, Hawaii Island. Collections were made with pole-spears while using SCUBA or snorkeling. Tissue specimens (fin clips) were stored in a saturated salt-dimethylsulfoxide (DMSO) buffer (Seutin et al. 1991), and total genomic DNA was extracted using a standard salting out protocol (Sunnucks & Hales 1996).

Table 1. *Zebrasoma flavescens*. Yellow tang collection sites with sample size (N) for mtDNA sequencing (mtDNA) and microsatellite genotyping (nDNA). Haplotype diversity (h), nucleotide diversity (π), allelic richness (A) standardized for sample size, and observed (H_O) and expected heterozygosity (H_E) with SD in parentheses. Chichi: Chichi-jima, Japan; Sai.: Saipan, Northern Marianas Islands; Poh.: Pohnpei, Federated States of Micronesia; Joh.: Johnston Atoll; Kure: Kure Atoll; Mid.: Midway Atoll; PH: Pearl and Hermes Atoll; Maro: Maro Reef; FFS: French Frigate Atoll; Mol.: Molokai; Waw.: Wawaloli; Kea.: Kealakekua; SP: South Point

Site	N mtDNA	N nDNA	h	π	A	H_O	H_E
Chichi	32	36	0.85 (0.06)	0.003 (0.002)	9.95	0.79 (0.02)	0.84 (0.02)
Sai.	33	35	0.85 (0.05)	0.003 (0.002)	10.40	0.75 (0.02)	0.86 (0.02)
Poh.	29	29	0.70 (0.10)	0.002 (0.002)	11.01	0.85 (0.02)	0.87 (0.02)
Joh.	32	47	0.79 (0.03)	0.003 (0.002)	9.02	0.79 (0.01)	0.80 (0.04)
Kure	35	55	0.80 (0.04)	0.004 (0.002)	8.73	0.76 (0.01)	0.80 (0.04)
Mid.	33	53	0.74 (0.04)	0.004 (0.002)	8.99	0.79 (0.01)	0.81 (0.04)
PH	29	55	0.77 (0.04)	0.004 (0.002)	8.70	0.78 (0.01)	0.80 (0.04)
Maro	26	29	0.70 (0.04)	0.003 (0.002)	8.37	0.74 (0.02)	0.79 (0.04)
FFS	40	50	0.73 (0.03)	0.003 (0.002)	8.72	0.76 (0.01)	0.80 (0.05)
Nihoa	20	32	0.81 (0.05)	0.004 (0.002)	8.64	0.77 (0.01)	0.80 (0.04)
Kauai	42	55	0.71 (0.04)	0.003 (0.002)	8.62	0.76 (0.01)	0.79 (0.04)
Oahu	35	50	0.70 (0.04)	0.003 (0.002)	8.56	0.78 (0.01)	0.79 (0.04)
Mol.	48	48	0.70 (0.04)	0.004 (0.002)	8.53	0.77 (0.01)	0.79 (0.04)
Maui	39	52	0.76 (0.03)	0.003 (0.002)	8.55	0.78 (0.01)	0.80 (0.04)
Lanai	35	33	0.69 (0.06)	0.003 (0.002)	8.53	0.73 (0.02)	0.79 (0.04)
Waw.	31	53	0.74 (0.05)	0.003 (0.002)	8.24	0.75 (0.02)	0.78 (0.04)
Kea.	36	45	0.78 (0.05)	0.004 (0.003)	8.79	0.77 (0.01)	0.81 (0.04)
SP	37	50	0.70 (0.04)	0.003 (0.002)	8.78	0.76 (0.01)	0.79 (0.04)
Hilo	42	50	0.69 (0.04)	0.003 (0.002)	8.78	0.78 (0.01)	0.81 (0.04)
Total / Mean	654	857	0.75 (0.05)	0.003 (0.002)	8.94	0.77 (0.01)	0.81 (0.04)

Mitochondrial DNA (mtDNA). Fish isolates were sequenced to produce a 614 bp fragment of the mitochondrial cytochrome *b* gene with heavy strand primer (5'-GTG ACT TGA AAA ACC ACC GTT G-3') and light strand primer (5'-AAT AGG AAG TAT CAT TCG GGT TTG ATG-3') designed by Song et al. (1998) and Taberlet et al. (1992), respectively. Polymerase chain reaction (PCR) and sequencing protocols are described in Eble et al. (2009). All specimens were sequenced in the forward direction, and rare or questionable haplotypes were sequenced in the reverse direction to confirm identity with an ABI 3130xl automated sequencer (Applied Biosystems).

Sequences were aligned in MAFFT 6.62 (Katoh et al. 2002) and edited with SEQUENCHER 4.6 (Gene Codes). Haplotype (h) and nucleotide (π) diversities were calculated in ARLEQUIN 3.11 (Excoffier et al. 2005), which implements diversity index algorithms described in Nei (1987), and a statistical parsimony network was constructed using the software TCS 1.21 (Clement et al. 2000) with default settings.

Range-wide patterns of population structure were assessed with a spatial analysis of molecular variance (SAMOVA 1.0; Dupanloup et al. 2002). SAMOVA removes bias in group designation by implementing a simulated annealing procedure to identify maximally differentiated groupings without *a priori* assumptions about

group identity. To ensure validity of the final *K* groupings, the simulated annealing process was repeated 100 times with a different random partition of samples into *K* groups. The configuration with the largest among-group differentiation (ϕ_{CT}) is retained as the best sample grouping. SAMOVA was run with values of $K = 2$ to 14 to identify the most likely number of sample groups. Deviations from random expectations were tested with 20 000 permutations. In ARLEQUIN, patterns of genetic differentiation among individual sampling sites were estimated with pairwise ϕ_{ST} values. A Mantel test implemented in ARLEQUIN with 10 000 simulations was used to test for an isolation-by-distance (IBD) signature (a positive correlation between genetic and geographic distance measured as shortest route over water; Slatkin 1993). To provide insight into how the spatial scale of gene flow may differ across closely associated islands and large stretches of open ocean, IBD tests were conducted on the full data set and separately on Hawaii and Johnston Atoll samples because limited sampling within the West Pacific precluded testing for IBD.

Estimates of migration between populations were calculated with MIGRATE 2.1.3 (Beerli & Felsenstein 2001) on the University of Hawaii's 96 node dual Xeon 3.2 GHz 'Dell Cluster'. MIGRATE offers a robust framework for testing migration between more than 2 popu-

lations, whereas similar analyses are constrained by the assumption that a single population has split into 2 daughter populations (Hey & Nielsen 2007). Roy-Choudhury & Stephens (2007) found MIGRATE-based estimates of gene flow were significantly different from expected for a simulated data set, but their analysis employed an earlier version of MIGRATE (1.7.3) with default settings. Subsequent tests of the same data set in MIGRATE 2.1 found bias and error was low and similar to that observed in other widely accepted programs (e.g. AMOVA; Beerli 2007). We employed the recommended Bayesian Markov chain Monte Carlo (MCMC) search strategy of a single, replicated, one million step chain (Beerli 2009). Chain convergence was assessed by ensuring (1) prior and posterior parameter estimates differed and (2) concordance in posterior parameter estimates over 10 replicate runs with different random number seeds (Beerli 2004). Starting population parameters for diversity (Θ) and migration (*M*) were estimated from Wright's fixation index (F_{ST}). Initial runs were conducted with default exponential priors and an unrestricted migration model. Resulting posterior distributions for Θ and *M* were used to inform priors for the final set of replicated runs. Estimates of the number of immigrants per generation (Nm) were calculated by multiplying final estimates (mode, 2.5%, and 97.5% quantile) of Θ and *M*.

To test for deviations from selective neutrality we generated *F** and *D** (Fu & Li 1993) in DnaSP 4.10.9 (Rozas et al. 2003). Female effective population sizes (N_{ef}) were estimated from the equation $\theta = N_{ef}2\mu t$ with θ estimated in ARLEQUIN from the mean number of segregating sites (θ_S), μ is the estimated annual fragment mutation rate and *t* is the estimated generation time. Population ages in years were estimated from the population age parameter (τ), $\tau = 2\mu T$, where *T* is the time since the most recent bottleneck. We provisionally applied a generation time of 5 years for yellow tang (Claisse et al. 2009). Divergence estimates for cytochrome *b* have been obtained for a number of reef fishes though never specifically for an Acanthurid. We therefore employed within-lineage mutation rates that encompass the range of cytochrome *b* evolutionary rates reported for reef fishes: 1% per million years (Bowen et al. 2001) and 2.5% per million years (Lessios 2008).

We tested for a signature of population expansion with *Fs* (Fu 1997) and by comparing observed and expected mismatch distributions (Rogers & Harpending 1992) in ARLEQUIN with 90 000 simulated samples. Fu (1997) noted that *Fs* is particularly sensitive to deviations from a constant population size with population expansion resulting in a significant negative *Fs*.

Nuclear DNA (nDNA). Fish were genotyped at 14 microsatellite loci (Table 2) using the procedures

Table 2. *Zebrasoma flavescens*. Loci details with sample size (N), fragment size (bp), number of mtDNA haplotypes (h), number of nDNA alleles (A), observed haplotype diversity (*h*; ±SD), and observed allelic heterozygosity (H_O; ±SD)

Locus	N	bp	h or A	*h* or H_O
mtDNA	654	614	45	0.74 (0.07)
*Zefl*01	810	129–243	33	0.83 (0.06)
*Zefl*02	808	175–253	21	0.83 (0.05)
*Zefl*08	814	133–195	12	0.75 (0.07)
*Zefl*09	815	146–250	32	0.89 (0.05)
*Zefl*10	818	198–246	14	0.67 (0.08)
*Zefl*12	820	259–297	13	0.31 (0.10)
*Zefl*14	811	170–300	50	0.89 (0.05)
*Zefl*15	810	307–356	16	0.84 (0.05)
*Zefl*17	814	275–396	21	0.80 (0.07)
*Zefl*19	811	234–284	26	0.84 (0.05)
*Zefl*20	814	131–189	20	0.77 (0.05)
*Zefl*21	818	182–235	14	0.84 (0.04)
*Zefl*22	814	182–250	29	0.87 (0.06)
*Zefl*23	813	162–186	13	0.69 (0.05)

described in Christie & Eble (2009). Unlabeled reverse primers were obtained from Integrated DNA Technologies. Forward primers were labeled with 6-FAM, VIC, NED, and PET proprietary dyes (Applied Biosystems). PCR products were scored relative to a known size standard on an ABI 3100 automated sequencer and visualized using ABI PRISM GENEMAPPER 3.0 (Applied Biosystems).

Quality control followed Selkoe & Toonen (2006) and included tests for null alleles, loci scorability, linkage disequilibrium, and Mendelian inheritance. Departures from Hardy-Weinberg proportions (Guo & Thompson 1992) and linkage disequilibrium were tested using GENEPOP 3.2 (Raymond & Rousset 1995) with a Bonferroni correction for multiple pairwise comparisons (Bonferroni 1936). Tests of significance were combined over all loci using Fisher's combined probability test (Sokal & Rohlf 1981). We employed MICRO-CHECKER 2.2.3 (van Oosterhout et al. 2004) to infer scoring errors resulting from null alleles, large allele drop-out, and stutter peaks. In addition, a random subset of 10% of the samples were re-amplified, re-scored and compared to initial scores, which indicated a scoring error of <2% overall. Per locus estimates of allelic richness were standardized for sample size by rarefaction in FSTAT 2.9.3 (Goudet 2001).

Estimates of genotypic population structure were conducted according to the methods described for sequence data. Estimates of population subdivision based on F_{ST} are impacted by the amount of genetic variation within populations with high levels of within population genetic variation leading to lower estimates of population differentiation without a corresponding effect on estimates of significance (Neigel 2002,

Hedrick 2005). Therefore, microsatellite-based esti-
mates of population differentiation were standardized
relative to the maximum attainable value given ob-
served within-population genetic variance using the
standardization method of Hedrick (2005) as imple-
mented in RecodeData 0.1 (Meirmans 2006; F'_{ST}:
among paired sites; F'_{CT}: among groups; F'_{SC}: within
groups). A Mantel test implemented in ARLEQUIN was
used to test for a relationship between pairwise F'_{ST}
and ϕ_{ST} (mtDNA).

Population groupings were re-estimated in STRUC-
TURE 2.3.2 (Hubisz et al. 2009), which assigns individu-
als to one or more populations by minimizing devia-
tions from Hardy-Weinberg and linkage equilibria.
Because of an expectation of weak genetic structure
(Eble et al. 2009), sample locations were used as infor-
mative priors (Hubisz et al. 2009). For each run we con-
ducted a 100 000 step burn-in followed by 100 000
MCMC iterations with the admixture model and corre-
lated allele frequencies, as this configuration was
determined to be the best one in cases of subtle popu-
lation structure (Falush et al. 2003). We performed 10
runs for each estimated number of groups (K), from $K =$
1 to $K = 10$, and calculated the mean probability for
each K over all replicate runs (Pritchard et al. 2007).
Evanno et al. (2005) proposed calculating the change
in mean probability for each K (ΔK) to identify the most
likely number of groups. Because ΔK cannot be calcu-
lated for $K = 1$, we instead calculated the posterior
probabilities of each K to identify the most appropriate
number of groups (Pritchard et al. 2007). Where subdi-
vision was indicated, we tested for further structure by
running each of the subdivided groups independently
as recommended by Pritchard et al. (2007).

Recent population contractions or founder events will
confound estimates of population differentiation and
migration. We therefore tested for bottlenecked popu-
lations by assessing a number of characteristic traits in-
cluding reduced allelic richness, excess heterozygosity
(Maruyama & Fuerst 1985, Cornuet & Luikart 1996),
and a reduced value for the mean ratio of the number of
alleles to the range of allele size (Garza & Williamson
2001). Allelic richness (A) was compared among groups
in FSTAT 2.9.3. Heterozygosity excess relative to expec-
tations under mutation-drift equilibrium was tested
with the Wilcoxon's signed-rank test of BOTTLENECK
1.2.02 (Cornuet & Luikart 1996) using the recom-
mended 2-phase mutational model (95% frequency of
step-wise mutations; Piry et al. 1999). The mean ratio of
the number of alleles to the range in allele size was cal-
culated according to Garza & Williamson (2001). Signif-
icance was assessed by a comparison of the mean allele
size/range ratio across all loci for each sample grouping
with values less than 0.68 indicating a recent bottle-
neck (Garza & Williamson 2001).

Estimates of migration rates were calculated in
MIGRATE 2.1.3 with allele frequency data (in units of
number of repeats). Runs were conducted with
MIGRATE's Brownian motion approximation of step-
wise microsatellite evolution. Initial runs consisted of
the recommended Bayesian MCMC search strategy of
a single, replicated, 1 million step chain with 5 repli-
cates (Beerli 2009). For allelic data, initial test runs
indicated a lack of convergence after 1 million steps,
but convergence was observed after 2 million steps
with a 20 000 step burn-in and this setting was used on
all subsequent runs. As with mtDNA sequence based
runs, priors included an unrestricted migration model,
and initial estimates of Θ and M were used to inform
priors for the final set of replicated runs.

RESULTS

Cytochrome *b* diversity

Sequences from 654 yellow tang revealed 39 haplo-
types (Table 2; GenBank accession numbers FJ376767–
FJ376787 and GU320254–GU320271) with the number
of haplotypes per site ranging from 20 to 28. Haplotype
and nucleotide diversity ranged from $h = 0.69–0.85$ and
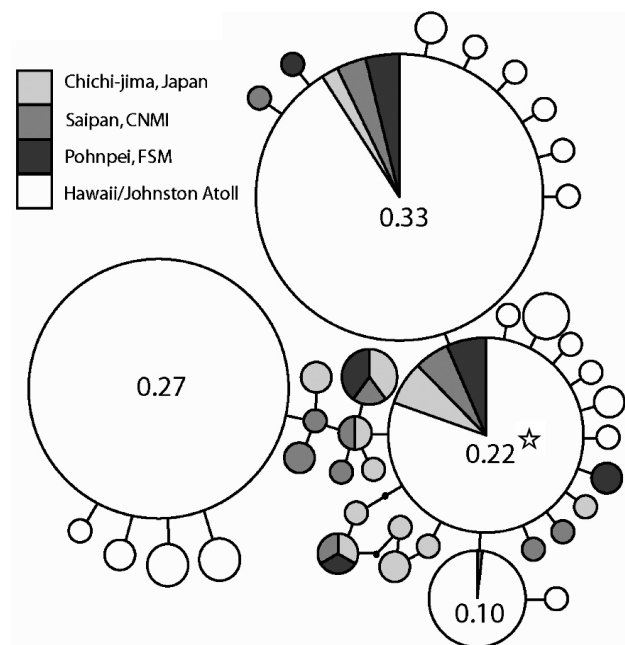$\pi = 0.002–0.004$, respectively (Table 1). The statistical

Fig. 2. *Zebrasoma flavescens*. Statistical parsimony network
for yellow tang. Area of circle is proportional to the frequency
of the respective haplotype, with the smallest circles for
haplotypes found in only 1 fish and exact frequencies pro-
vided for the 4 most common haplotypes. Shades represent
haplotype location. TCS analysis was used to identify the
putative ancestral haplotype (☆)

parsimony network indicated a cluster of closely related haplotypes (Fig. 2), a common outcome for marine fishes (Grant & Bowen 1998). Two of the 3 most common haplotypes were observed at every site and included the putative ancestral haplotype (Fig. 2).

Microsatellite diversity

A sample of 857 yellow tang genotyped at 14 loci revealed 14–50 alleles per locus, and allelic richness per site ranging from A = 8.24–11.01 (Table 1). Mean expected heterozygosity ranged from H_E = 0.79–0.87, and mean observed heterozygosity ranged from H_O = 0.73–0.85. There were no significant deviations from Hardy-Weinberg proportions after applying a Bonferroni correction for multiple tests. Significant linkage disequilibrium was detected in only 27 of 2548 comparisons among the 14 loci after Bonferroni correction within populations. There was no consistent tendency towards linkage disequilibrium between any loci or within any population with the exception of Midway Atoll, where 7 out of 91 loci comparisons exhibited Bonferroni adjusted significance. While evidence of linkage disequilibrium within the Midway Atoll sample may be indicative of population natural history or selection, the pattern is more likely the result of scoring errors. Although null alleles were detected in only 4 of 266 within-sample comparisons with no consistent pattern observed within loci or samples, locus Zefl 14 was found to contain null alleles in the Midway Atoll sample and, notably, was also present in 4 of the 7 significant tests for linkage. Because the presence of null alleles can confound estimates of population differentiation and historical demography, we compared pairwise F_{ST} estimates for Midway with and without locus Zefl 14. A paired t-test revealed no significant change in F_{ST} due to the presence of null alleles (t = 2.11, p = 0.38, df = 340), we therefore retained Zefl 14 in all subsequent analyses.

Population structure

Population genetic comparisons reveal shared microsatellite (nDNA) alleles and mtDNA haplotypes across the species range, though we observed significant pairwise differences in mtDNA haplotype distributions (ϕ_{ST}) in 49 of 171 comparisons (Table 3) and in nDNA allele frequencies (F'_{ST}) in 70 of 171 comparisons (Table 3). Significant estimates of pairwise population structure were ϕ_{ST} = 0.037–0.291 and F_{ST} = 0.013–0.169. Pairwise differentiation was consistently greatest between Hawaii and West Pacific collection sites, though neither nDNA nor mtDNA exhibited a significant IBD correlation at this scale. A Mantel test comparing pairwise F'_{ST} and ϕ_{ST} val-

Table 3. Zebrasoma flavescens. Results of pairwise tests for yellow tang population structure with mtDNA (ϕ_{CT}) above diagonal, and standardized microsatellites (F'_{ST}) below diagonal. Site abbreviations as in Table 1. *p < 0.05, **p < 0.01, ***p < 0.001

	Joh.	Kure	Mid.	PH	Maro	FFS	Nihoa	Kauai	Oahu	Mol.	Maui	Lanai	Waw.	Kea.	SP	Hilo	Chichi	Sai.	Poh.
Joh.		-0.012	-0.015	-0.023	-0.005	-0.017	-0.035	-0.005	-0.002	0.010	-0.019	0.040	0.037	0.018	0.008	0.001	0.070*	0.048*	0.147**
Kure	0.002		-0.019	-0.016	-0.006	-0.017	-0.014	-0.002	-0.019	-0.019	-0.017	-0.006	0.007*	-0.014	-0.005	-0.005	0.121**	0.092**	0.119**
Mid.	-0.010	-0.019		-0.002	0.021	-0.007	-0.006	0.023	0.005	0.001	-0.003	0.003	0.140*	0.011	0.027	0.023	0.109**	0.096**	0.230**
PH	0.001	-0.007	-0.005		-0.017	-0.017	-0.039	-0.029	-0.018	-0.008	-0.024	0.030	0.027	-0.006	-0.012	-0.020	0.098**	0.061*	0.132*
Maro	-0.004	0.008	-0.006	0.002		-0.022	-0.022	-0.025	-0.025	-0.001	-0.024	0.050	0.010	0.001	-0.030	-0.025	0.086*	0.034	0.100*
FFS	0.000	0.008	-0.005	-0.003	0.002		-0.021	-0.010	-0.014	-0.003	-0.022	0.027	0.041	0.002	-0.012	-0.009	0.083*	0.045*	0.144*
Nihoa	0.018	0.018	0.008	0.008	0.017	-0.010		-0.027	-0.017	0.001	-0.029	0.047	0.002	0.006	-0.020	-0.020	0.067*	0.034	0.106*
Kauai	0.006	0.024**	0.006	0.013*	0.014	-0.010	0.002		-0.017	0.001	-0.018	0.051	0.013	0.002	-0.024	-0.022	0.103**	0.053*	0.101*
Oahu	0.006	0.014	0.008	-0.001	0.012	-0.009	-0.003	0.002		-0.018	-0.020	0.012	0.051	-0.017	-0.006	-0.021	0.118**	0.072**	0.153**
Mol.	0.002	0.022*	0.000	0.003	0.003	-0.001	-0.001	-0.008	0.006		-0.006	-0.006	0.087*	-0.019	-0.016	-0.005	0.147	0.108**	0.189**
Maui	0.000	0.007	-0.010	0.000	0.003	-0.005	-0.003	-0.002	-0.003	-0.005		0.030	0.029	0.000	0.040	-0.017	0.090**	0.052*	0.129**
Lanai	0.002	0.008	-0.005	-0.005	-0.002	-0.007	0.012	0.015*	0.010	-0.010	0.000		0.170	-0.005	0.030	0.040	0.191**	0.166**	0.291**
Waw.	0.015*	0.026**	0.012	0.001	0.010	0.001	0.004	-0.001	-0.002	0.000	0.017	0.012		0.087*	-0.005	0.025	0.076**	0.021	0.008
Kea.	0.019*	0.016	0.000	0.007	0.034***	0.006	0.018	0.019*	0.019*	0.004	-0.001	-0.001	0.024**		0.087**	-0.005	0.151**	0.109**	0.182**
SP	0.035***	0.042***	0.032***	0.023***	0.024*	0.014	0.021*	0.017*	0.008	0.007	0.012	0.015*	0.017*	0.037***		-0.023	0.117*	0.063*	0.118*
Hilo	0.009	0.012	-0.006	0.001	0.008	0.003	0.007	0.011	-0.003	0.002	-0.007	0.006	0.007	0.001	0.029**		0.114*	0.063*	0.112*
Chichi	0.108***	0.088***	0.072***	0.101***	0.108***	0.090***	0.081***	0.100***	0.102***	0.099***	0.088***	0.103***	0.090***	0.092***	0.117***	0.080***		-0.010	0.121**
Sai.	0.123***	0.101***	0.108***	0.127***	0.138***	0.133***	0.118***	0.134***	0.140***	0.151***	0.137***	0.142***	0.146***	0.125***	0.169***	0.139***	-0.018		0.054*
Poh.	0.147***	0.128***	0.135***	0.143***	0.145***	0.116***	0.093***	0.155***	0.129***	0.145***	0.154***	0.128***	0.132***	0.136***	0.160***	0.139***	0.037	0.020	

ues indicated strong agreement in estimates of range-wide nDNA and mtDNA population structure ($r^2 = 0.749$, $p < 0.001$).

Tests for IBD in Hawaii were non-significant for both marker sets. However, exclusion of the Hawaii Island collections yielded a significant IBD signature in pairwise F'_{ST} estimates across the remainder of the Hawaiian archipelago ($r^2 = 0.12$, $m = 4 \times 10^{-6}$, $p = 0.008$). This result is likely because collections around Hawaii Island, which were separated by as little as 50 km, exhibited genetic subdivision equivalent to comparisons between Hawaii Island and Midway Atoll, a distance of more than 2000 km (Table 3). Notably, exclusion of all the main Hawaiian Island samples increased the strength of the nDNA IBD correlation ($r^2 = 0.43$, slope = 1×10^{-5}, $p = 0.009$). Although the rate of change in genetic distance with increasing geographic distance was small, genetic differentiation increased consistently and did not plateau, likely indicating drift-migration equilibrium and stable populations throughout the majority of the archipelago. Hierarchical SAMOVA for both nDNA and mtDNA indicated $K = 4$ maximally differentiated groupings: Chichi-jima, Saipan, Pohnpei, and Hawaii, which included Johnston Atoll, Table 4. Among these groupings, estimates of differentiation were highly significant ($p < 0.001$) and remarkably similar between data sets ($\phi_{CT} = 0.098$, $F'_{CT} = 0.116$). Within-group differentiation (ϕ_{SC}), however, differed markedly between nDNA and mtDNA. Where the mtDNA data set returned a non-significant estimate of within-group differentiation at $K = 4$ ($\phi_{SC} = 0.002$, $p = 0.38$), nDNA data indicated further population subdivision in Hawaii ($F'_{SC} = 0.026$, $p < 0.001$). Tests for mtDNA cytochrome b selective neutrality (F^* and D^*) within the 4 SAMOVA populations were uniformly non-significant, indicating observed patterns of population structure are not the result of differential selection among collection sites (Table 5).

While SAMOVA clearly identified 4 maximally differentiated groupings for both data sets, within Hawaii non-random allele frequency shifts provided further evidence of fine-scale genetic subdivision, with $K = 13$ being the smallest number of sample groups returning a non-significant estimate of within-group differentiation ($F'_{SC} = -0.01$, $p = 0.13$; Table 4). These groupings demonstrate subtle genetic divisions between all collection sites with the exception of 3 undifferentiated sample groupings: (1) Kure, Midway, and Pearl and Hermes Atoll, (2) French Frigate Shoals, Nihoa, Kauai, and Oahu, and (3) Maui and Molokai. In contrast, STRUCTURE indicated only 2 populations (West Pacific and Hawaii) with posterior and mean probabilities highest for the full data set at $K = 2$, and for each region at $K = 1$. The discrepancy between STRUCTURE and SAMOVA is likely due to the inherent difficulty of resolving fine-scale population structure with individual clustering algorithms (Pritchard et al. 2007). Evanno et al. (2005) found the Bayesian clustering method of STRUCTURE was generally able to detect only the uppermost hierarchical levels of population structure

Table 4. *Zebrasoma flavescens*. Structural analysis of molecular variance (SAMOVA) with maximally differentiated groupings (K) for (a) mtDNA ($K = 1$ to 4) and (b) microsatellites ($K = 1$ to 4, 13). Site abbreviations as described in Table 1. df: degrees of freedom; VC: variance components; fixation indices for mtDNA among-groups (ϕ_{CT}) and within groups (ϕ_{SC}), standardized nDNA among-groups (F'_{CT}) and within groups (F'_{SC}), and non-standardized nDNA among-groups (F_{CT}) and within groups (F_{SC}). *p < 0.05, **p < 0.01, ***p < 0.001

(a)

K	Grouping	df	VC	% variation	ϕ_{CT}	df	VC	% variation	ϕ_{SC}
1	All					18	0.03	2.43	0.024**
2	Poh. / Sai., Chichi, Hawaii	1	0.13	10.99	0.110	17	0.02	1.67	0.019*
3	Poh. / Sai. / Chichi, Hawaii	2	0.09	7.83	0.078*	16	0.01	1.26	0.014
4	Poh. / Sai. / Chichi / Hawaii	3	0.11	9.80	0.098***	15	0	0.18	0.002

(b)

K	Grouping	df	VC	% variation	F'_{CT} (F_{CT})	df	VC	% variation	F'_{SC} (F_{SC})
1	All					18	0.03	0.45	0.026*** (0.005)
2	Poh., Sai. / Chichi, Hawaii	1	0.11	1.99	0.095** (0.019)	17	0.01	0.24	0.010*** (0.002)
3	Poh. / Sai. / Chichi, Hawaii	2	0.11	2.01	0.103** (0.020)	16	0.01	0.24	0.011*** (0.002)
4	Poh. / Sai. / Chichi / Hawaii	3	0.11	1.93	0.116*** (0.022)	15	0.01	0.13	0.005*** (0.001)
13	Poh. / Sai. / Chichi / Joh. / Kure, Mid., PH / Maro / FFS, Nihoa, Kauai, Oahu / Lanai / Maui, Mol. / Waw. / Kea. / SP / Hilo	12	0.03	0.61	0.032*** (0.006)	6	0	–0.12	–0.011 (–0.002)

Table 5. *Zebrasoma flavescens*. Estimates (±95% CI) of yellow tang historical demography for the 4 SAMOVA populations. θ$_S$: theta estimates; N$_{ef}$: female effective population size for within lineage mutation rates of 1% and 2.5% per million years; SSD: test for deviations from the sudden expansion model of mismatch analysis with associated significance; τ: population age parameter; age: population age (yr) for within lineage mutation rates of 1% and 2.5% per million years; Fs: tests for population expansion; F^* and D^*: selective neutrality for mtDNA haplotypes. *p < 0.05, **p < 0.01, ***p < 0.001

Population	θ$_S$	N$_{ef}$ (1%)	N$_{ef}$ (2.5%)	Mismatch analyses SSD	τ	age (1%)	age (2.5%)	Fs	Selective neutrality F^*	D^*
Chichi-jima	2.85 (1.64–4.06)	46 416 (26 710–66 123)	18 567 (10 684–26 450)	0.002 (p = 0.73)	2.15 (0.68–3.72)	175 081 (55 375–302 932)	70 033 (22 150–121 173)	−6.17***	0.47	0.01
Saipan	3.14 (1.83–4.45)	51 140 (29 804–72 475)	20 456 (11 922–28 990)	0.004 (p = 0.57)	1.94 (0.48–3.13)	157 980 (39 088–254 886)	63 192 (15 635–101 954)	−6.67***	−1.67	−1.85
Pohnpei	1.26 (0.51–2.01)	20 521 (8 306–31 596)	8 208 (3 322–13 094)	0.015 (p = 0.62)	1.12 (0.54–2.12)	91 205 (43 974–172 638)	36 482 (17 590–69 055)	−2.01**	−1.36	−1.59
Hawaii	2.74 (1.94–3.54)	44 625 (31 596–57 654)	17 850 (12 638–23 061)	0.044 (p = 0.16)	3.90 (2.09–7.75)	317 590 (170 196–631 107)	127 036 (68 078–252 443)	0.51	0.19	0.44

and did not detect more subtle (but significant) genetic subdivision. In contrast, SAMOVA permutes samples among groups within the AMOVA framework, essentially testing every reasonable combination of sample sites (Dupanloup et al. 2002). The permutation-based strategy offers an enhanced ability to resolve fine-scale structure because when predetermined sample sites correspond closely with actual populations, tests for allele frequency shifts are more powerful than individual clustering based on linkage disequilibrium and deviations from Hardy-Weinberg equilibrium (Pritchard et al. 2007).

Historical demography

Microsatellite tests for recent population bottlenecks were uniformly non-significant (data not shown), but all sites demonstrated a high frequency of closely related mtDNA haplotypes (Fig. 2) consistent with the sudden expansion model of mismatch analysis (Table 5). Mismatch analyses indicated time since expansion to be on the order of 90 000 to 175 000 yr in the West Pacific and 320 000 yr in the Hawaiian group (assuming a within-lineage mutation rate of 1% per million years; Table 5), which may explain our observation of non-significant Fs values in the Hawaii collections and significant negative values for Fs in the 3 West Pacific ones (Table 5). Simulations have shown Fs to be more sensitive to recent population expansion than other tests of demographic history (Fu 1997), so we place greater emphasis on Fs when interpreting each population's most recent demographic trajectory. Coalescence estimates for individual sites in Hawaii (300 000 to 375 000 yr) were similar to the average for the archipelago (320 000 yr), indicating that differences in the estimated age of extant West Pacific and Hawaiian populations were not artifacts of Hawaii biased sampling. Female effective population sizes derived from θ$_S$ values were similar for all sites with 95% confidence intervals (CI) ranging between approximately 20 000 and 70 000 ind. region^{-1} (for μ = 1%; Table 5). θ$_S$ values for individual collection sites from Hawaii Island (1.19–2.17) were not significantly different from those from other sites in the archipelago (1.16–2.00; t = 2.78, p = 0.65), indicating that the recent decline of yellow tang due to aquarium collecting (Tissot & Hallacher 2003) has not led to a corresponding loss of genetic diversity. Coalescence based migration estimates for both mtDNA and nDNA reveal strongly asymmetrical gene flow with larval export from Hawaii at least 16 times greater than the reciprocal (Table 6). Migration rates, which are not scaled for population size, were likewise asymmetrical in favor of dispersal from Hawaii for both nDNA and mtDNA data sets. Assuming a within-lineage mutation rate of 10^{-8}

Table 6. *Zebrasoma flavescens.* Estimates (±95% CI) of yellow tang larval dispersal (migrants per generation) derived from MIGRATE for 14 microsatellites (nDNA) and mtDNA cytochrome *b* sequence data

West Pacific populations	nDNA		mtDNA	
	From Hawaii	To Hawaii	From Hawaii	To Hawaii
Chichi-jima	6.05 (3.16–8.42)	0.26 (0.00–0.61)	1.97 (0.00–29.25)	0.00 (0.00–0.03)
Saipan	4.60 (1.63–6.50)	0.15 (0.00–0.51)	2.49 (0.00–64.84)	0.01 (0.00–0.08)
Pohnpei	4.18 (0.98–6.39)	0.25 (0.00–0.62)	6.43 (0.53–22.31)	0.00 (0.00–0.04)

for mtDNA (1% per million years, Bowen et al. 2001) and an average per repeat mutation rate of 10^{-5} (Jarne & Lagoda 1996) for microsatellite loci, the migration rate from Hawaii was 4.2×10^{-4} to 5.8×10^{-4} (nDNA) and 2.1×10^{-5} to 1.4×10^{-5} (mtDNA), while the migration rate to Hawaii was 7.5×10^{-5} to 1.2×10^{-4} (nDNA) and 2.5×10^{-6} to 4.9×10^{-6} (mtDNA). Posterior distributions of parameter estimates consistently departed from priors, and results were consistent over multiple runs, indicating chain convergence (Beerli 2009). The exceptions to this pattern of convergence were migration estimates among West Pacific sites. Replicate migration estimates among these 3 sites varied from run to run but were consistently high, indicating that gene flow within this region is greater than can be resolved accurately (Beerli 2004).

To test whether more extensive sampling of the Hawaiian Archipelago confounded migration estimates, MIGRATE was re-run 10 times with 50 randomly drawn individuals from Hawaii. Migration estimates derived from the randomly drawn Hawaiian samples concurred with estimates from the full data set, demonstrating that the observed pattern of westward dispersal was not an artifact of intensive sampling in Hawaii.

DISCUSSION

Counter to expectations of Hawaii as exclusively a recipient of external biodiversity (Briggs 1999, Hourigan & Reese 1987, Randall 2007), nDNA and mtDNA migration estimates reveal a strong pattern of asymmetric gene flow between Hawaii and the West Pacific, with Hawaii exporting yellow tang alleles and haplotypes, presumably as larvae (Table 6). However, the frequency of larval export is insufficient to homogenize populations across the range. SAMOVA tests for population structure revealed significant genetic differentiation between Hawaii and the West Pacific (ϕ_{ST} = 0.008–0.230, F'_{ST} = 0.072–0.169) as well as significant subdivision within the West Pacific (ϕ_{ST} = 0.010–0.121, F'_{ST} = 0.018–0.037), and

fine-scale partitions within the Hawaiian Archipelago were detected with microsatellites but not mtDNA (ϕ_{SC} = 0.002, p = 0.38; F'_{SC} = 0.026, p < 0.001; Table 4). While nDNA and mtDNA markers differ in their resolution of population subdivisions within Hawaii, a Mantel test comparing pairwise F'_{ST} and ϕ_{ST} values indicated strong agreement in estimates of range-wide population structure (r^2 = 0.749, p < 0.001). Yellow tang are known to occasionally hybridize with congeners (J.E. Randall pers. comm.), and the presence of hybrids within the sample might confound interpretation of the data. However, the limited genetic distance between mtDNA haplotypes (Fig. 2) and the ubiquity of admixed individuals (nDNA STRUCTURE plot, data not shown) indicates that hybrids were not likely sampled.

Population structure within Hawaii

We observed microsatellite allele frequency shifts that provide clear evidence of an IBD signature across the majority of the Hawaiian Archipelago, indicating a general pattern of reduced larval exchange with increased distance. No IBD pattern, however, was observed in the mtDNA sequence data, likely because Hawaiian collections were dominated by the 3 most common haplotypes. The significance of the microsatellite-based IBD relationship was confounded by inclusion of Hawaii Island samples that were significantly differentiated across ≤50 km, indicating that factors other than IBD may be driving patterns of larval exchange at smaller spatial scales (e.g. near-shore currents; Selkoe et al. 2010, White et al. 2010).

The population structure of yellow tang in Hawaii has ramifications on at least 2 conservation fronts. First, the genetic resolution of populations indicates isolated stocks with structure primarily corresponding to (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 Molokai, and (4) multiple management units on Hawaii Island [though this latter designation deserves further research given recent indications of yellow tang larval exchange among Hawaii Island reefs (Christie et al. 2010)]. Population designations are consistent with the linear geography of the archipelago (Fig. 1) and 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).

Second, since one of the yellow tang populations defined above (French Frigate Shoals to Oahu) spans portions of both the PMNM and the impacted reefs of the MHI, evidence of genetic connectivity between these regions indicates the potential for some larval spillover. Prevailing northwest surface currents (HLC; Fig. 1) may, however, limit opportunities for larval dispersal from the PMNM to the MHI (Calil et al. 2008, Rivera et al. 2011, DiBattista et al. 2011). Rather, the impacted reefs of the MHI may serve as a larval source for the PMNM (Bird et al. 2007). A recent assessment of parentage within Hawaii Island yellow tang identified 4 parent-offspring pairs, with larval dispersal from natal reefs consistently to the north (Christie et al. 2010). While the extrapolation of patterns from within a single island to the broader archipelago is questionable, observed northward dispersal matched predictions from the authors' oceanographic model and indicates the potential for dispersal downstream from the MHI to the PMNM.

Larval export from Hawaii

The geographic distribution of yellow tang nDNA and mtDNA diversity reveal a pattern of westward biased gene flow, with dispersal from Hawaii roughly 16 times greater than the reciprocal (Table 6). Because of the high likelihood of larval exchange with unsampled yellow tang populations in the Central and West Pacific, migration rates cannot be interpreted as direct estimates of larval exchange between Hawaii and West Pacific collection sites (Beerli 2004). Rather, migration estimates offer a qualitative assessment of the direction and tempo of gene flow across the large expanse of open ocean separating Hawaii from its nearest neighbors. Furthermore, coalescent based migration estimates represent a historic average over the time scale of genetic drift (e.g. $4N_e$ for diploid markers; Beerli 2004) and therefore may not reflect current conditions. Migration estimates derived from 10 randomized subsamples of Hawaiian collections matched results from the full data set, demonstrating that evidence of westward dispersal was not an artifact of our extensive sampling in Hawaii.

Yellow tang are particularly abundant among the southernmost islands of Maui Nui (Maui, Molokai, and Lanai) and Hawaii Island where they are the dominant herbivore (Walsh 1987). Yellow tang are less common outside of Hawaii (J.E. Randall pers. comm.), raising the possibility that the observed pattern of asymmetrical larval export may in part result from differences in population size and corresponding reproductive output (Cowen & Sponaugle 2009). This, however, does not appear to be the case since migration rates (which are not scaled for population size) were likewise asymmetrical in favor of dispersal from Hawaii for both nDNA and mtDNA data sets.

Larval export from Hawaii does not appear to be restricted to yellow tang. Ember parrotfish *Scarus rubroviolaceus* are common throughout the Indo-Pacific and East Pacific (Randall 2007), and estimates of the number of migrants per generation (m) derived from 15 microsatellite markers revealed a similar pattern of asymmetric larval export, with migration from Hawaii to the Central West Pacific (1.70, 0.98–2.21; mean, 95% CI), approximately an order of magnitude greater than the reciprocal (0.14, 0.03–0.49; Fitzpatrick et al. 2011). A similar, though substantially more balanced, pattern of larval export was revealed in an assessment of mtDNA (CO1) diversity in the Indo-Pacific sea cucumber *Holothuria atra* (Skillings et al. 2011). Overall, *H. atra* larval export from Hawaii (0.02–1.02) was marginally greater than larval import (0.01–0.84) and indicates a pattern of bidirectional larval exchange. Evidence of larval export from Hawaii can also be found in a phylogenetic reconstruction of mtDNA control region sequences from the bullethead parrotfish *Chlorurus sordidus* (Bay et al. 2004). Three highly differentiated, monophyletic lineages were resolved, with lineages corresponding to the Indian Ocean, the West Pacific, and Hawaii. However, several fish collected in the West Pacific contained haplotypes derived from the Hawaiian lineage, with the depth of the partitions between lineages indicating a period of extended isolation followed by more recent larval export (Bay et al. 2004).

Trans-Pacific biodiversity feedback

While much of Hawaii's marine biodiversity clearly derives from the West Pacific (Hourigan & Reese 1987, Jokiel 1987, Kay & Palumbi 1987, Randall 1998, Briggs 1999, Craig et al. 2010), evidence of larval export in yellow tang and other reef species reveal Hawaii to be more than a simple diversity sink. Broader taxonomic sampling is required before we can determine the true balance between larval export and import; nonetheless, the consistency of larval export in initial migration assessments begs the question of whether Hawaii may be exporting more than just genes.

Our phylogeographic assessment of the yellow tang reveals 3 lines of evidence that indicate yellow tang may have been a Hawaiian endemic that subsequently 'escaped' to the west. (1) Mismatch analyses indicate more recent population coalescence in the West Pacific (91 000 to 175 000 yr compared to 317 000 yr in Hawaii; Table 5), an unexpected finding under a scenario of West Pacific origin especially considering the likeli-

hood of a population bottleneck upon colonization of Hawaii and the higher rates of population turnover in peripheral populations (Frankham 1996, Pardo et al. 2005). (2) *Fs* values (Fu 1997; Table 5) indicate recent population expansion in the 3 West Pacific collection sites and stable populations in Hawaii. (3) The asymmetrical gene flow described above runs counter to expectations of a West Pacific origin. While we cannot rule out colonization of Hawaii from the West Pacific followed by the establishment of a prevailing pattern of westward dispersal, estimates of historical demography and migration indicate a possible Hawaiian origin for yellow tang.

However, regardless of yellow tang's origins, evidence of larval export from Hawaii provides insights into evolutionary interactions between the remote reefs of the Hawaiian Archipelago and the species-rich communities of the West Pacific. Rather than being a biogeographic 'dead end', biological and genetic diversity arising in Hawaii may be able to escape its remote origins, ultimately contributing to community diversity across the Indo-Pacific in a process of biodiversity feedback (sensu Rocha et al. 2008). Taken together with evidence of recent dispersal from Hawaii in other reef organisms, these findings indicate that the remote archipelagos of the central Pacific may function as both a source and recipient of Indo-Pacific marine diversity.

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