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Asymmetrical gene flow in five co-distributed syngnathids explained by ocean currents and rafting propensity

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Ocean circulation driving macro-algal rafting is believed to serve as an important mode of dispersal for many marine organisms, leading to predictions on population-level genetic connectivity and the directionality of effective dispersal. Here, we use genome-wide single nucleotide polymorphism data to investigate whether gene flow directionality in two seahorses (*Hippocampus*) and three pipefishes (*Syngnathus*) follows the predominant ocean circulation patterns in the Gulf of Mexico and northwestern Atlantic. In addition, we explore whether gene flow magnitudes are predicted by traits related to active dispersal ability and habitat preference. We inferred demographic histories of these co-distributed syngnathid species, and coalescent model-based estimates indicate that gene flow directionality is in agreement with ocean circulation data that predicts eastward and northward macro-algal transport. However, the magnitude to which ocean currents influence this pattern appears strongly dependent on the species-specific traits related to rafting propensity and habitat preferences. Higher levels of gene flow and stronger directionality are observed in *Hippocampus erectus*, *Syngnathus floridae* and *Syngnathus louisianae*, which closely associated with the pelagic macro-algae *Sargassum* spp., compared to *Hippocampus zosterae* and the *Syngnathus scovelli*/*Syngnathus fuscus* sister-species pair, which prefer near shore habitats and are weakly associated with pelagic *Sargassum*. This study highlights how the combination of population genomic inference together with ocean circulation data can help explain patterns of population structure and diversity in marine ecosystems.

1. Background

Across a diverse range of marine taxa, rafting on macro-algae has been proposed as a fundamental mode of 'hitchhiking dispersal' between coastal regions [1–3]. Macro-algae such as pelagic *Sargassum* spp. provide the structure needed to support a drifting ecosystem, in which a diverse community of inhabitants find prey, seek shelter, develop and may ultimately disperse to distant locations [4–8]. Owing to the positive buoyancy and holopelagic reproductive cycle, the movement of pelagic *Sargassum* is largely controlled by ocean circulation [9,10]. For

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several marine species, rafting with marine macrophytes (such as *Sargassum* spp.) has been invoked as a means of transport leading to the habitation and connectivity of oceanic archipelagos [11–13], as well as trans-oceanic dispersal [14–17].

Syngnathids (commonly known as seahorses, sea-dragons and pipefishes) are generally considered poor swimmers and are all direct developers that commonly settle in benthic habitat shortly after birth, limiting planktonic larval dispersal [18]. Rafting dispersal has been hypothesized as the primary means of transport in these species [6,14,19], as they are among the most abundant fish groups present in algal rafts carried by the Gulf Stream current [4,20–22]. Movement by fishes (and other taxa) to and from *Sargassum* rafts provides a mechanism by which they can achieve long-distance transport by these major ocean currents [20]. If rafting dispersal is the primary mode of transportation, then ocean circulation directionality should be consistent with gene flow directionality, and this correspondence should be stronger in species with higher rafting propensity. In the western North Atlantic, mats of pelagic *Sargassum* algae occur annually (March–July) within the Gulf of Mexico [5,22]. These mats follow the dominant ocean circulation pattern of the Gulf Stream System (the Loop Current in the Gulf of Mexico, the Florida Current in the Straits of Florida and Gulf Stream that traces the eastern coast of the United States before bending eastwards into the North Atlantic near Cape Hatteras, North Carolina) [5,9,22]. The Gulf Stream system has existed in its present form since the closing of the Isthmus of Panama approximately 4 Ma [23], suggesting consistent eastward gene flow directionality of rafting individuals within the Gulf and northward gene flow along the Atlantic coast over many generations.

To inform the general predictions of the hypothesis that rafting propensity and habitat preference can influence gene flow directionality and magnitude, we first investigate patterns of ocean circulation by using data from drifter trajectories available at Adrift.org.au. Then, we test this hypothesis using genome-wide single nucleotide polymorphism (SNP) data from five partially co-distributed taxa of syngnathids that include two seahorses (*Hippocampus erectus* and *Hippocampus zosterae*) and three pipefishes (*Syngnathus floridae*, *Syngnathus louisianae* and the *Syngnathus scovelli*/*Syngnathus fuscus* sister-species pair), which represent different ecologies, to infer population structure and connectivity. The hypothesis that rafting drives dispersal directionality in the species included in this study carries two general predictions with respect to model-based parameter estimates of gene flow magnitude and directionality: (i) for taxa with greater observed rafting propensity (*H. erectus*, *S. floridae* and *S. louisianae*), estimates of gene flow asymmetries should follow the currents of the Gulf Stream system; (ii) for taxa with less propensity for rafting because of ecological constraints and habitat preference (*H. zosterae*, *S. scovelli*/*S. fuscus*), the magnitude of gene flow should be lower. Hypothesis testing then involved comparing these predictions with the parameter estimates under the inferred demographic histories of divergence with asymmetric gene flow given the genome-wide SNP data from the five focal species.

2. Material and Methods

(a) Oceanic transport estimates

To provide oceanographic context for hypothesized population structure and gene flow, we used Adrift.org.au, a freely available tool for tracking the movement of objects drifting at the ocean surface [24]. This method combines empirical data from approximately 17 000 drifter trajectories deployed throughout the global ocean from 1979 to 2013 [25] to determine the probability of an object moving from a given 1° latitude × 1° longitude location to any other 1° × 1° location across the rest of the ocean at two-month intervals [24]. This approach produces a wide-range of transport possibilities that are not specifically tied to seasonality or particular years, making it particularly useful for examining questions of historical biogeography [17]. Approximately half of the trajectories are of drifters drogued at 15 m depth, to minimize the impact of winds blowing across the top of the float; the other half are missing these drogues [24]. Thus, the predicted pathways generated by this approach are appropriate for tracking the movement of algal rafts under the combined effects of ocean currents and winds [10].

In our analyses, we examined transport from six sites where genetic sampling occurred: (i) the western Gulf of Mexico (WGM), 28°N, 97°W; (ii) the northern Gulf of Mexico (NGM), 30°N, 88°W; (iii) the eastern Gulf of Mexico (EGM), 27°N, 83°W; (iv) the Florida Keys (FK), 25°N, 80°W; (v) the southeast Atlantic coast of Florida (SAC) 27°N, 80°W; and (vi) the northeast Atlantic coast of Virginia (NAC), 37°N, 75°W. We determined the cumulative probability of drifters from each site reaching the surrounding coastal region every two months up to 24 months, a drift time that is consistent with other studies modelling rafting [17,26]. For each site, we divided the cumulative probability of drifter transport to each region by the sum of values across the six regions to generate a relative index within the study system of which regions were most likely to receive inputs from each site.

(b) Sampling

In this study, individuals from five species of Syngnathids, *H. erectus*, *H. zosterae*, *S. floridae*, *S. louisianae* and the sister-species pair *S. scovelli*/*S. fuscus*, were collected from 15 sites throughout the Gulf of Mexico and along the Atlantic coast (figure 1; electronic supplementary material, table S1, species ranges shown in the electronic supplementary material, figure S1). Details on sampling, restriction site associated DNA sequencing (RADseq) library preparation, sequencing and bioinformatics processing can be found in the electronic supplementary material, Information S1. Genomic data and accompanying metadata have been deposited to NCBI with Bioproject ID PRJNA575862 (accession numbers SAMN12912667-SAMN12912781) and linked to GEOME (https://geome-db.org/workbench/project-overview?projectId=212).

(c) Population structure and phylogenetic summaries

To characterize population structure and assign individual genotypes to putative populations for downstream model-based demographic inference, we took several exploratory approaches. To visually summarize the genetic differentiation of individual genotypes and explore potential population structure, principal component analyses (PCA) were executed per species (and in the case for *S. scovelli* and *S. fuscus* for both species combined) using the PCA function in the R package *adegenet* [27,28]. We used the sparse non-negative matrix factorization algorithm (sNMF) integrated in the LEA package [29] to further explore population structure and the assignment of individuals to putative populations by inferring ancestry coefficients, representing the proportions of each individual's genome that originated from a given gene pool. sNMF estimates individual ancestry without inferring independent ancestral gene pools (K) based on the assumption of Hardy–Weinberg or linkage equilibrium. We explored K values ranging from 1 to 10, each with 20 repetitions, and testing four values for the alpha regularization parameter (1, 10, 100 and 1000). The number of ancestral populations was determined by using a cross-entropy criterion. To visually explore the phylogenetic relationships between populations, we used the program SPLITSTREE [30].

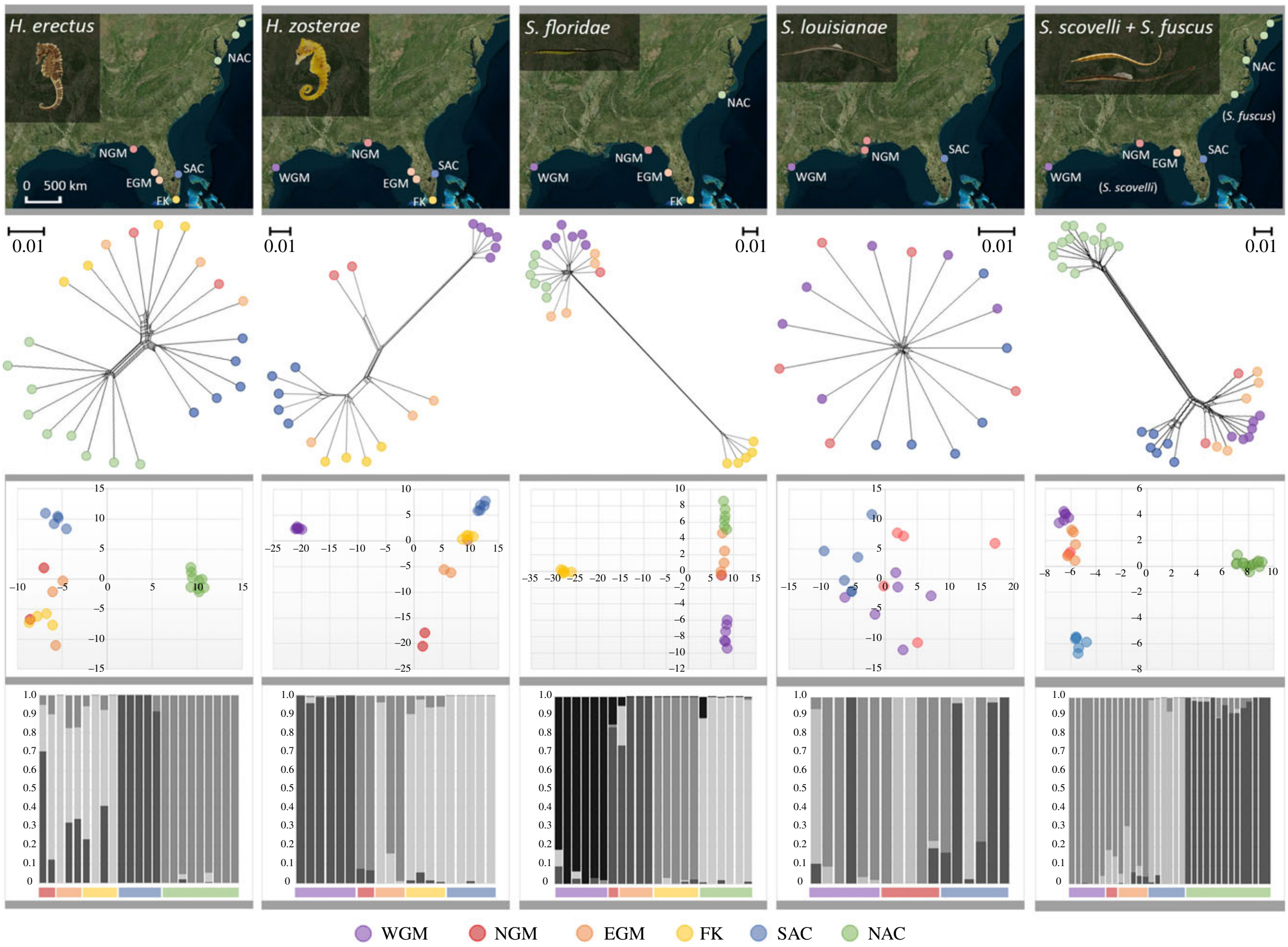


Figure 1. Population genetic analyses for *H. erectus*, *H. zosterae*, *S. floridae*, *S. louisianae* and the *S. scovelli*/*S. fuscus* sister-species pair. Upper row: sampling locations for each of the species. Second row: evolutionary network computed by SPLITSTREE analyses. Third row: PCA plot. Bottom row: barplot from sNMF analyses, in which each bar represents one individual and grey shading represents assignment to ancestral clusters. Sampling regions are indicated by abbreviations and colour code. WGM, Western Gulf of Mexico; NGM, Northern Gulf of Mexico; EGM, Eastern Gulf of Mexico; FK, Florida Keys; SAC, South Atlantic Coast; NAC, North Atlantic Coast. (Online version in colour.)

(d) Inference of gene flow and demographic histories

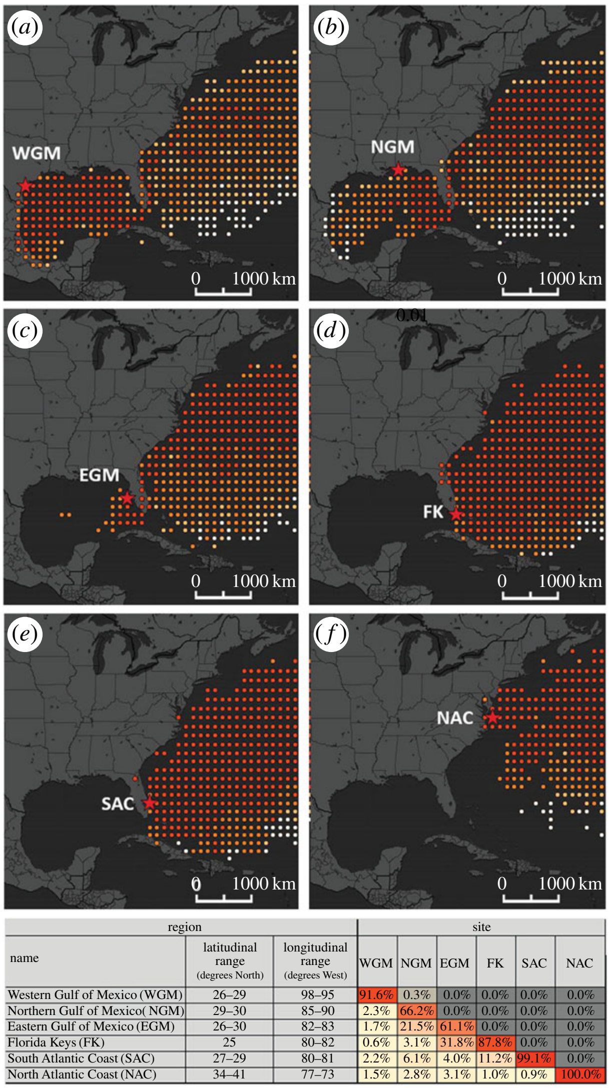
We explored the extent of corridors and barriers to effective migration between sampling localities for each species using estimated effective migration surfaces (EEMS) [31]. EEMS uses deviations from the expected decay of genetic similarity under an isolation by distance model to highlight geographical regions of inflated connectivity as well as regions of inflated isolation. In order to explore potential restrictions to migration without making any assumptions about individual demes or population structure, we used the sampling localities to calculate pairwise genetic dissimilarities using the function dist.genpop in the R package *adegenet* [27,28]. The EEMS method incorporates isolation-by-distance as a null-model for the decay of genetic similarity with increasing geographical distance, and therefore habitat discontinuity that hinders gene flow is expected to result in spatial zones of inflated isolation. Three independent runs were performed, using 10 million Markov chain Monte Carlo steps and discarding the first 5 million MCMC steps as burn-in. Proposal variances were tuned as suggested in the documentation, using 1 and 2 for mSeedsProposalS2 and mEffctProposalS2, respectively, and 2 and 0.02 for qSeedsProposalS2 and qEffctProposalS2, respectively.

To obtain estimates of potentially asymmetric gene flow based on a historic demographic model, we used generalized phylogenetic coalescent sampler (G-PhoCS), which applies a full Bayesian coalescent-based method to estimate effective population sizes, divergence times and continuous bi-directional rates of migration [32]. To choose an appropriate number of populations and assign individual genotypes to putative populations, we used the exploratory analyses of sNMF and PCA (figure 1), whereas population topologies were informed by the phylogenetic inferences obtained by maximum likelihood using SPLITSTREE (figure 1). We include gene flow parameters between any two of the neighbouring populations in each model, with the exception of gene flow to and from the Florida population in *S. floridae* (because of the long branch length of this population, see Results and Discussion) and gene flow between the sister species *S. fuscus* and *S. scovelli*. We performed four independent runs, each of 500 000 MCMC steps, sampling every 100 generations with $\alpha = 1.0$ and $\beta = 1000.0$ for the gamma distribution used for all priors of τ and θ parameters, and $\alpha = 1.0$ and $\beta = 0.00001$ for the gamma distribution used for migration rates. Runs for a single species were assessed and combined in TRACER v.1.6 [33]. We used a mutation rate of 1×10^{-9} site yr^{-1} to transform estimates of θ and τ to Ne and divergence time, respectively.

3. Results

(a) Oceanic transport estimates

Estimates of oceanic transport from sample sites indicate the prevalence of west to east movement across the Gulf of Mexico and northeastward transport into the Atlantic Ocean (figure 2). While large-scale movements are apparently likely, successful dispersal from one region to another may be less common. Over the 2 years of tracking, local retention tended



region			site					
name	latitudinal range (degrees North)	longitudinal range (degrees West)	WGM	NGM	EGM	FK	SAC	NAC
Western Gulf of Mexico (WGM)	26–29	98–95	91.6%	0.3%	0.0%	0.0%	0.0%	0.0%
Northern Gulf of Mexico(NGM)	29–30	85–90	2.3%	66.2%	0.0%	0.0%	0.0%	0.0%
Eastern Gulf of Mexico (EGM)	26–30	82–83	1.7%	21.5%	61.1%	0.0%	0.0%	0.0%
Florida Keys (FK)	25	80–82	0.6%	3.1%	31.8%	87.8%	0.0%	0.0%
South Atlantic Coast (SAC)	27–29	80–81	2.2%	6.1%	4.0%	11.2%	99.1%	0.0%
North Atlantic Coast (NAC)	34–41	77–73	1.5%	2.8%	3.1%	1.0%	0.9%	100.0%

Figure 2. Results of ocean transport estimates, in which the distribution of surface drifters was determined from six different sites (panels *a–f*: red stars) after six months (red-orange), 12 months (dark orange), 18 months (light orange) and 24 months (light yellow). The table indicates pairwise drifter percentages after 12 months for the localities which were used for sampling in this study. (Online version in colour.)

to predominate, with probabilities of remaining within the region of origin ranging from 61% (EGM) to 100% (NAC). When cross-region transport was observed, west to east connectivity was predominant; the only site from which westward transport to coastal regions was likely was from NGM to WGM (0.3%) (figure 2, electronic supplementary material, table S2). All other sites contributed to each of the coastal regions ‘downstream’, although the magnitude of potential connectivity did not necessarily scale linearly with geographical distance. For instance, WGM, NGM and EGM were each predicted to contribute more to NAC than either FK or SAC (electronic supplementary material, table S2).

(b) Sequencing

Across all sampled individuals, we obtained a total of 427 253 311 single-end reads generated on the Illumina HiSeq platform. A total number of sequence reads per sample ranged from 1 098 313 (*H. erectus*) to 5 486 466 (*H. zosterae*), and the total number of reads per species ranged from 73 835 708 (*H. erectus*) to 128 387 912 (*S. scovelli*/*S. fuscus*). Total numbers, as well as minimum and maximum number of reads per individual per species are summarized in the electronic supplementary material, table S3. The number of loci per species varied from 1349 to 8035 and the number of SNPs varied from 8047 to 29 489 (electronic supplementary material, table S3).

(c) Population structure and phylogenetic summaries

Based on the PCA and Splitstree analyses, we identified putative topologies for three population models (*H. erectus*, *H. zosterae*, *S. louisianae* and the *S. scovelli*/*S. fuscus* sister-species pair) and a four population model (*S. floridae*) (figure 1). The sNMF results further corroborated our chosen population assignments (figure 1). Based on this information, we constructed historical models of population splitting and migration for each species to be used for downstream coalescent model-based inferences of demographic and evolutionary histories (models used for demographic analyses shown in figure 4).

Unlike the two seahorse species, which show the genetic similarity between individuals sampled from the tropical FK and the EGM, the FK population of the pipefish *S. floridae* shows a pronounced divergence from all other warm-temperate/temperate populations of *S. floridae*, ranging from the WGM to NAC. Apart from this strong differentiation of the FK population, the strongest differentiation in *S. floridae* is found between populations from WGM and populations further to the east. A similar pattern, with a strong differentiation of the WGM population, is observed in *H. zosterae*. However, for *H. erectus* (for which no WGM population was sampled) and the *S. scovelli*/*S. fuscus* sister-species pair, the strongest differentiation is found between populations from NAC and populations further to the south. Differentiation in *S. louisianae* is less profound, although the populations on the east side of the Florida peninsula are somewhat differentiated from the seemingly more admixed populations west of the Florida peninsula.

(d) Gene flow and demographic analyses

The effective migration surfaces obtained from EEMS corroborate population structure identified with sNMF and PCA. For *S. floridae* the FK population was excluded, as was the case for the demographic analyses, based on the strong divergence from all other sampling localities. Main barriers were found between the most strongly diverged populations for each species (figure 3, left side panels). In addition, the results suggest relatively higher levels of gene flow between NAC (*H. erectus*, *S. fuscus*), EGM (*H. erectus*, *S. scovelli*) and the WGM-NGM (*S. louisianae*, *S. scovelli*) sampling localities. The population genetic diversity obtained from EEMS showed the highest levels of diversity associated with areas in the central part of its sampled range (figure 3, right side panels). By contrast, lower levels of diversity were found in peripheral areas.

Estimated numbers of migrants per generation from the G-PhoCS analyses indicate that migration in *H. zosterae* and *S. scovelli* is generally low (less than 0.5 migrant generation^{-1}) (figure 4, electronic supplementary material, table S4). However, in the other three taxa, we detect higher levels of asymmetric gene flow. Gene flow from SAC to NAC (*H. erectus*) and NGM-EGM to NAC (*S. floridae*) is estimated to be 70–80 times stronger than gene flow in the opposite

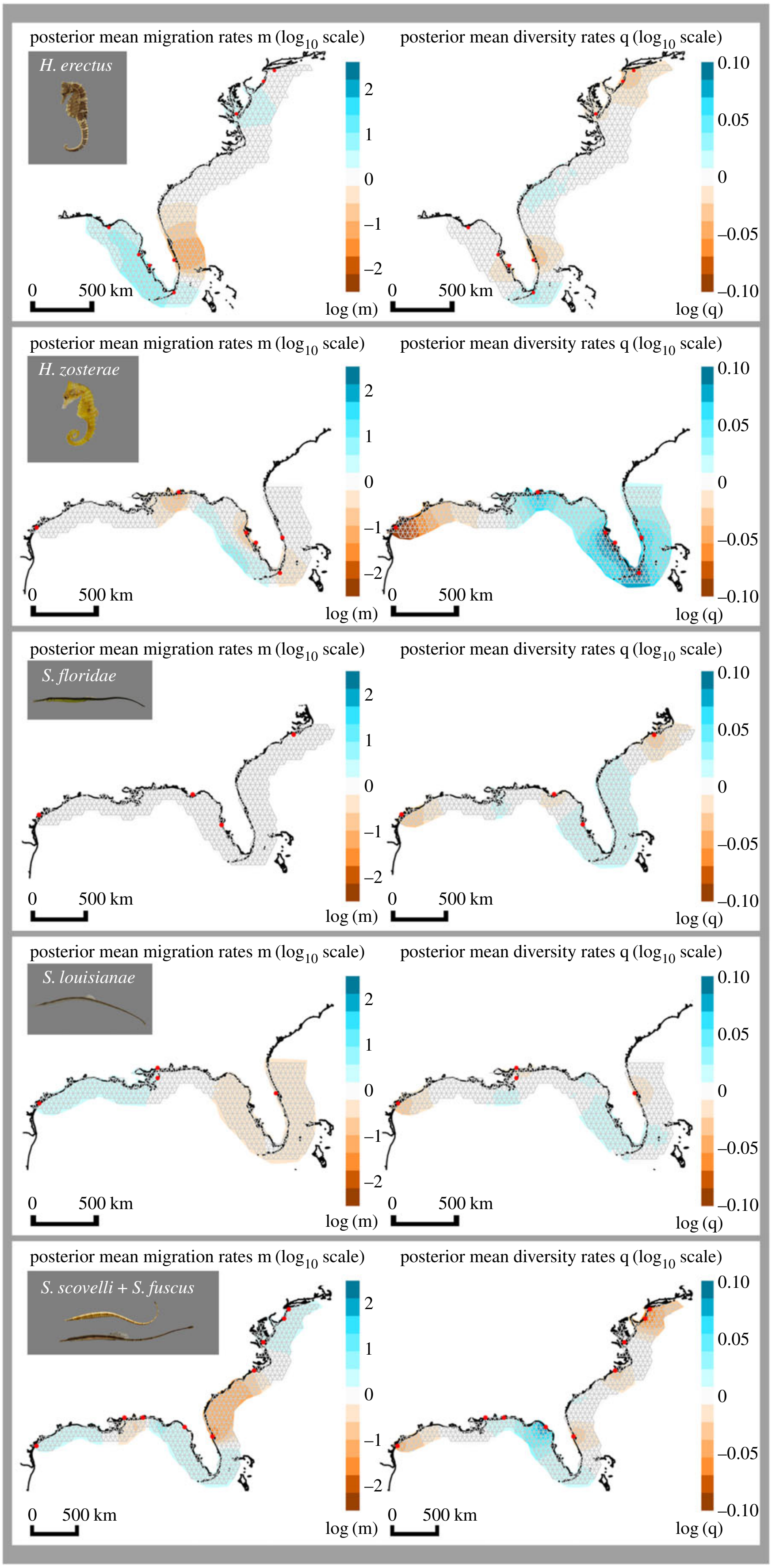


Figure 3. Posterior mean migration rates m (left column) and posterior mean diversity rates q (right column) as estimated by EEMS for *H. erectus*, *H. zosterae*, *S. floridae*, *S. louisianae* and the *S. scovelli*/*S. fuscus* sister-species pair. (Online version in colour.)

direction. In the less structured species *S. louisianae*, estimates suggest overall eastward gene flow (WGM to NGM and NGM to SAC) to be 1.5× as strong as westward gene flow. The patterns of asymmetric gene flow are robust to the influence of effective population size (Nm versus pairwise m) and in general, gene flow estimates tended to be eastwards within the Gulf and northwards on the Atlantic coast. However, 95% confidence intervals for most of the

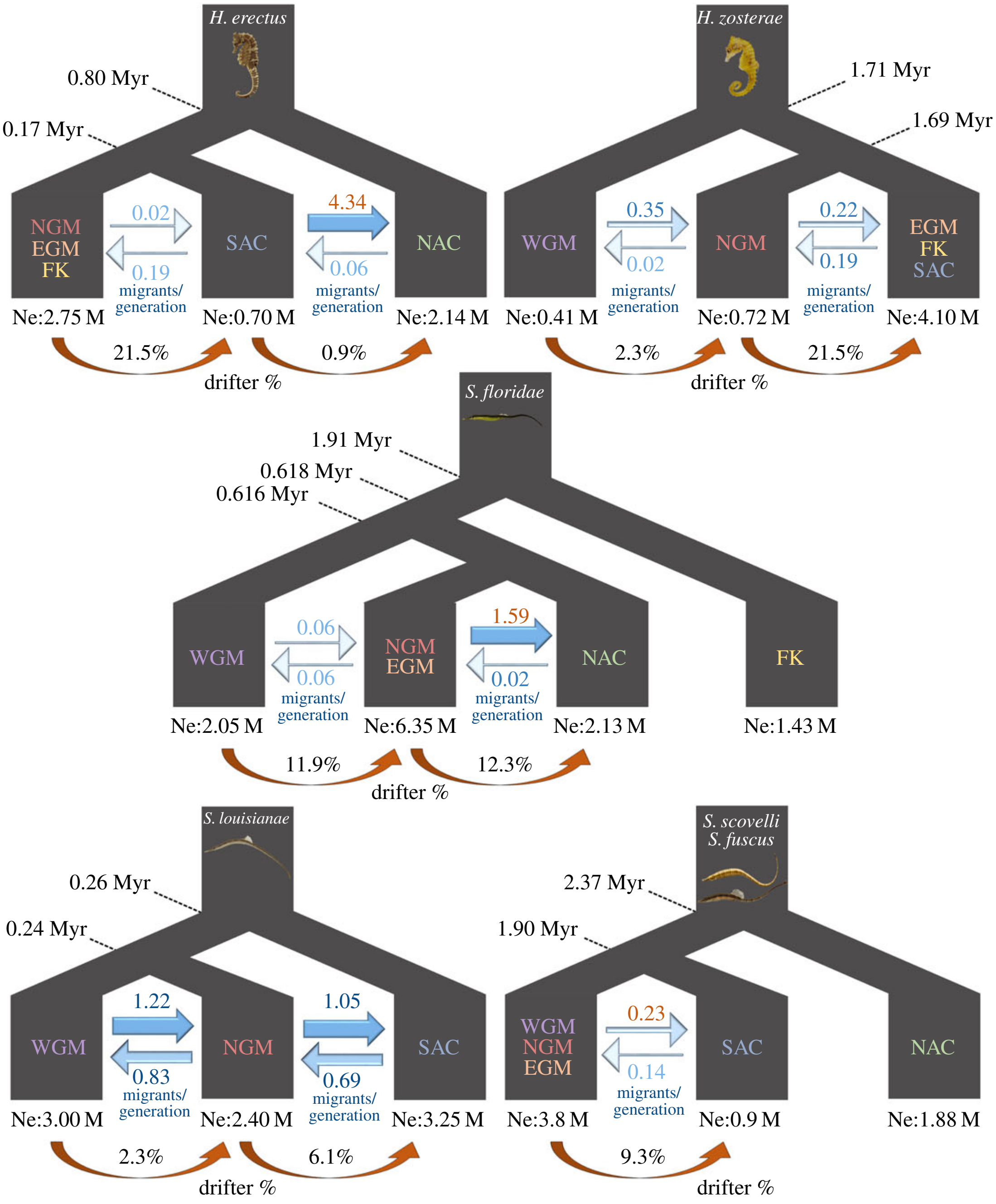


Figure 4. Demographic models and estimated parameters from G-PhoCS analysis for *H. erectus*, *H. zosterae*, *S. floridae*, *S. louisianae* and the *S. scovelli*/*S. fuscus* sister-species pair. Divergence times depicted in millions of years (Myr), effective population size (Ne) depicted in millions (M), migration depicted in number of migrants per generation (Bayesian ratios of model probabilities of directional gene flow of 1 : 5 and higher are indicated in orange). Drifter % indicates the percentage of drifters released at the source site and subsequently retrieved at the target site. In the case of the combination of multiple sites as a single population, the percentages between adjacent sites were averaged. Drifter % are only shown for west-to-east and south-to-north, because percentages for the opposite directions were negligible (see figure 2). Abbreviations and colour code for each sampling region correspond to figure 1. (Online version in colour.)

pairwise estimates show overlap, with the exception of *H. erectus* SAC-NAC and *H. zosterae* WGM-NGM gene flow estimates. To better characterize the posterior estimates of asymmetric gene flow, we also present the posterior densities of a compound parameter that is calculated as the difference between east/north bound and west/south bound gene flow. Posterior densities of directional migration (west/south bound gene flow subtracted from east/north bound gene flow) are shown in the electronic supplementary material, figure S2, corroborating the previously described results for *H. erectus* and *S. floridae*, as well as bi-directional gene flow in *S. louisianae*. In both *H. zosterae* and *S. scovelli*, the species which show less propensity for rafting owing to their ecology and habitat preference, the posterior estimates of asymmetric gene flow are centred more closely around zero, suggesting low gene flow magnitudes.

This compound parameter further allows us to treat asymmetric gene flow as a model comparison problem by partitioning the space of this parameter into eastward (less than 0.0) and westerward (greater than 0.0) models whereby the posterior ratio approximates the Bayes factor given that both directions have an equal prior probability. The table in the electronic supplementary material, figure S2 presents these posterior ratios and provides additional support for migration following oceanic currents in *H. erectus* SAC-NAC, and *S. floridae* NGMEGM-SAC, as well as *S. scovelli* WGMNGEGM-SAC, although the magnitude of gene flow in the latter species is low.

4. Discussion

In this study, we used oceanographic drifter data to help generate hypotheses of gene flow directionality and used genomic data to test the hypothesis that gene flow is asymmetric and follows ocean currents between populations for those syngnathids that have been observed to be associated with *Sargassum* rafting. We inferred the population structure and asymmetric gene flow in five co-distributed syngnathid species (in one case a sister-species pair) based on genome-wide SNP datasets. We viewed these gene flow estimates in the context of ecological traits, such as habitat preference and rafting propensity. Our results generally support asymmetric gene flow concordant with oceanic transport via rafts (such as *Sargassum*) that depend on ecological constraints.

Detailed ocean circulation data have become a useful means to generate hypotheses about the potential directionality of ocean current-driven dispersal and colonization [3,34–37] which can be further evaluated with genetic data [38–43]. Additional population-genetic-based approaches of marine species dispersal have proved informative in demonstrating how oceanographic processes can influence the frequency of larval exchange [38,44–48], and genetic structure and diversity [45,49–54]. Meta-analyses of fish species have been conducted to correlate various life-history traits with distribution data as drivers of dispersal capacity [15,55,56], with some studies suggesting that seascape features are more important than dispersal traits [57]. Our comparative study is, to our knowledge, the first one to use empirical ocean transport estimates jointly with genome-wide population genetic data across partially co-distributed species. We find that both ocean currents and dispersal traits can jointly explain the directionality and magnitude of marine dispersal.

(a) Phylogeographic breaks in marine species around the Florida peninsula

Studies on population structure in marine species spanning the Florida peninsula have described a strong phylogeographic break coinciding with the Florida peninsula in some species, yet absent in others [58–60]. Based on these observations, Avise [58] proposed that the Florida peninsula acted as a strong barrier during prolonged Pleistocene cooling periods and associated lower sea levels for a large swath of this regional marine biota. By contrast, others discovered widely distributed marine species with little divergence across the Florida peninsula, implying that the generality of this regional cryptic divergence breaks down when considering taxa with strong dispersal capabilities and/or those that experienced local extinction followed by recent trans-regional recolonization events [61,62]. With regards to the species studied here, only in *H. erectus* and *S. fuscus*/*S. scovelli* does the deepest phylogenetic split coincide with the Florida peninsula. In both of these cases, the gulf populations are more strongly delineated from Atlantic coast populations by an area near Cape Canaveral on the outer coast, an observation in line with a number of other marine datasets presenting this ‘Atlantic/Gulf’ phylogeographic break [58,63–66]. This break is also consistent with the previous genome-wide population genetic study of *S. scovelli* that used a much larger sample of individuals [67], although a divergence with a gene flow model was not considered.

(b) Population structure and divergence

Results from PCA, sNMF and SPLITSTREE were used to distinguish a number of populations and their phylogenetic relationships for downstream model-based inferences of demographic history. Considering the genetic distance of the FK population in *S. floridae*, we hypothesize that samples from this site are from a cryptic species that should not be considered a population of *S. floridae* (although demonstrating this would require further detailed investigation). Interestingly, this pattern of strong divergence is not retrieved from the mitochondrial DNA data, because this pattern was not detected when confirming species identification using cytochrome oxidase subunit 1 or cytochrome *b* (electronic supplementary material, Information S1). The data suggest that *H. zosterae* and *S. floridae* are qualitatively congruent with respect to divergence histories. In both, the oldest intra-specific divergences are between the WGM populations and populations further to the east. The Gulf lacks hard allopatric barriers, yet divergence between WGM and populations further to the east (notably in *H. zosterae* and *S. floridae*) may be suggestive of a persistent area of unsuitable habitat between the northern Texas coast and east of the Mississippi river delta [68]. This was confirmed by a comprehensive study of Atlantic syngnathids that reported a near absence of individuals from northern Texas west of the Mississippi river delta [21]. By contrast, *H. erectus* and the *S. scovelli*/*S. fuscus* sister-species pair are congruent with respect to a different divergence history, whereby the oldest split occurs between north Atlantic populations and a nested pair of southern populations on either side of the Florida peninsula that were split at a younger date. While the relative topological splitting pattern is identical between these two taxa, the divergence times are generally much younger in *H. erectus* than *S. scovelli*/*S. fuscus*. Finally, *S. lousianae* does not exhibit a clear population structure, with only moderate divergence of the populations east of the Florida peninsula (SAC) from the ones further to the west, and a very recent estimated divergence time.

(c) Directional gene flow and magnitude predicted by rafting propensity and habitat association

All of our focal taxa have a near shore benthic affinity to sheltered habitat such that dispersal between habitat patches is mainly mediated by rafting [20]. While the partially overlapping distributions of the five taxa could imply similar demographic histories and patterns of population connectivity, there are also ecological differences in shoreline habitat preference, macroclimatic tolerances, and rafting propensity that may contribute to trait-based differences in phylogeographic inference [4,19–22,69]. Based on this, we predict higher and more asymmetric gene flow, and younger divergence times in *H. erectus*, *S. floridae* and *S. louisianae* which have higher empirical rafting observations [4,20–22,69]. This is especially notable in *S. louisianae*, which has been observed to rely on *Sargassum* [22]. Based on recent catch records of 25 fish species inhabiting *Sargassum* off of the coast of Texas, *S. louisianae* made up 1096 of the 10 518 individuals collected [22]. Results from the genomic analyses presented in this study indeed show low regional population divergence and an asymmetric eastward gene flow in *S. louisianae*. Stronger population structure, but also a stronger eastward gene flow is observed in *H. erectus*, and in *S. floridae* gene flow towards the northern populations (NAC) is more pronounced.

In line with lower rafting propensity and different habitat preferences, we expect the dwarf seahorse *H. zosterae* and the euryhaline pipefish *S. scovelli* to exhibit older divergence times, lower gene flow magnitudes and gene flow directions that are less consistent with ocean currents. Indeed, for both taxa we estimate low levels of gene flow, no distinct patterns of asymmetric gene flow, and divergence times substantially older than those found in the three taxa with higher rafting propensities. Specifically, *H. zosterae* has a strong association with seagrass beds [70], while *S. scovelli*/*S. fuscus* has a preference for shallow near shore habitats [21,71]. The *S. scovelli*/*S. fuscus* sister-species pair, unlike other pipefishes included in this study, possesses specific microhabitat adaptations, including the ability to breed in freshwater and inhabit shallow near shore habitats with low salinity [21,71]. Another distinction from its congeners is that *S. scovelli* has not been recorded from depths greater than 6.1 m [21]. It, therefore, remains outside of the range of the oceanographic drifter data used in this study, which do not depict the hydrodynamic processes impacting this species' near shore migration. Moreover, a recent population genetic study concluded that individuals which migrate from coastal populations into estuaries and bays may be less prone to migrate seaward [71], which may further reduce rafting-driven connectivity between populations for this species.

Gaining insight into specific habitat requirements and the role of rafting for dispersal of these species is of additional importance considering the rapid loss of seagrass habitats on a global scale, and local peaks of seagrass die-offs specifically, e.g. around Florida [72]. At the same time, extreme blooms of *Sargassum* have also been reported, with 2018 the first instance of year-round *Sargassum* blooms in the Caribbean Sea, and most recently 'the biggest seaweed bloom in the world' [73]. Because of the potentially detrimental ecological (and economic) consequences [74,75], there is an increasing effort to monitor and predict these *Sargassum* blooms with satellite-based remote sensing [76–78], tracking and modelling their movement [9,79,80]. In order to evaluate the effects of these blooms, it is crucial to understand the drivers, as well as the ecological connections with species associated with *Sargassum* [79]. Seahorses and pipefishes have been suggested as keystone species to assess seagrass communities and aid in the design of marine protected areas [81], thereby representing important indicator species for the status of their habitat.

5. Conclusion

In marine systems, the use of genomics can contribute to insights into the complex nature of divergence and connectivity among populations. Our results suggest that active dispersal ability and habitat preference, coupled with oceanic transport, may play an important role in the asymmetric connectivity of rafting western Atlantic syngnathid species. Inference of post-divergence gene flow supports the hypothesis that *Sargassum* transport by ocean currents may drive the directional connectivity for taxa with higher observed rafting propensity (*H. erectus*, *S. floridae* and *S. louisianae*), while the effect of ocean currents is less pronounced in taxa with lower rafting propensity and habitat preferences consistent with lower dispersal (*H. zosterae* and *S. scovelli*/*S. fuscus*). This study demonstrates that demographic parameter estimates derived from genomic data, coupled with ocean circulation data, can be a powerful tool for understanding the drivers of regional variation in genetic diversity and population connectivity of marine organisms [26,80].

Data accessibility. Genomic data and accompanying metadata have been deposited to NCBI with Bioproject ID PRJNA575862 (accession numbers SAMN12912667-SAMN12912781) and linked to GEOME (https://geome-db.org/workbench/project-overview?projectId=212).

Authors' contributions. L.D.B. and J.T.B. wrote the manuscript with contributions from N.F.P. and M.J.H. L.D.B., J.T.B. and I.O. did the bioinformatic and downstream inferential analyses. J.T.B. carried out the fieldwork and the molecular laboratory work with the help of M.J.H. N.F.P. performed the ocean circulation analysis. A.T.X., J.D.R., S.H. and C.C.B. provided useful contributions to the analyses. M.J.H. coordinated the study and supervised the analyses. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

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