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The Role of Wind on the Simulated Dispersal and Recruitment of a Commercially Important Hawai'i Bottomfish

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ABSTRACT

Variability in larval transport has long been hypothesized to drive recruitment fluctuations in fishes, yet evidence for these hypotheses is often lacking. Further, the origins of many of these hypotheses come from temperate to subpolar regions, leaving such questions largely underexplored for other regions, especially the tropics. To assess drivers of larval transport in a tropical archipelago, we simulated the dispersal of a culturally and commercially important bottomfish, uku (*Aprion virescens*), from Penguin Bank, its most prominent spawning location in the main Hawaiian islands. We used Lagrangian particle tracking models forced by a regional ocean model to assess the degree of interisland potential connectivity from this spawning location and the drivers of interannual variability in this potential connectivity across 13 years from 2008 to 2020. Simulated uku larvae released from Penguin Bank primarily reached Maui Nui and O'ahu, the nearest potential settlement areas, with lower potential connectivity to more distant regions. Interannual variability in overall number of connections was pronounced and linked both to local wind speed and direction, with increased particle loss occurring during higher overall wind speeds and more northerly winds. Recruitment deviations from the stock assessment of uku showed a similar pattern, with recruitment estimates significantly decreasing during years of strong northerly winds. Our results provide evidence, derived from a simulation model integrating ecological and physical components, of larval dispersal patterns contributing to the recruitment of a socioeconomically important species and sensitivity of these patterns to local wind forcing. Understanding how these wind patterns will change in a warming climate may be essential to understanding patterns in uku recruitment in coming years.

1 | Introduction

Transport and dispersal during the larval phase are the primary mechanisms for long-distance population connectivity for many reefs and bottomfishes given their high site fidelity and limited movements as adults (Green et al. 2015). As such, the drivers of larval transport and dispersal are critical for understanding how populations are demographically connected and if this varies through time (Pineda, Hare, and Sponaugle 2007). These fluctuations in transport and dispersal through time may affect recruitment of marine species and ultimately influence population dynamics. Indeed, the degree

of retention and connectivity to juvenile habitat has been hypothesized as a key driver of recruitment, for nearly a century (Hjort 1914). Studies have since supported this hypothesis for taxa such as Atlantic herring (*Clupea harengus*; Sinclair and Power 2015), haddock (*Melanogrammus aeglefinus*; Boucher et al. 2013; Lough et al. 2006), barnacles (Cirripedia; Gaines and Bertness 1992), and triplefins (Tripterygiidae; Swearer and Shima 2010).

Isolated archipelagos such as Hawai'i can represent extreme cases of spatial separation of adult habitat, emphasizing the importance of larval dispersal in population connectivity. With little continental shelf, larvae of benthic fishes are exposed to open ocean conditions shortly after being spawned and may be highly sensitive to the processes influencing the hydrodynamics of the pelagic waters surrounding these archipelagos (Stier et al. 2014; Wood et al. 2016). The main Hawaiian islands (MHI) represent one such situation (Figure 1). The prevailing tradewinds are a key characteristic of the MHI, contributing to the variable surface flow and generation of leeward eddies (Patzert 1969; Calil et al. 2008). These leeward eddies and other wind-induced mesoscale activity lead the tradewinds to have a substantial effect on the advection of the region (Lumpkin 1998). With tradewinds having highly variable persistence, direction, and speeds over recent decades (Garza et al. 2012, Nan et al. 2020), understanding how tradewind dynamics affect dispersal, population connectivity, and even recruitment remains an open question in the MHI.

Studies on reef fish dispersal and genetics within the MHI show variability in estimated population connectivity. Population genetic studies, such as one on manini (convict tang, *Acanthurus triostegus*), indicate a high degree of population structure throughout the MHI, suggesting a large degree of self-recruitment in the region (Coleman et al. 2023). However, dispersal simulations, which include relatively high diffusion, indicate a large degree of particle exchange throughout the MHI, with the only significant breaks in connectivity throughout the archipelago occurring north of Ni'ihau

within Papahānaumokuākea (Wren et al. 2016). Modeling from Wren et al. (2016) did indicate a relatively strong degree of self-recruitment within the MHI, especially for the islands of Hawai'i and O'ahu, though interisland dispersal was substantial in the summer months when the persistence of winds is highest. Although the mechanism for greater dispersal distances in summer was not discussed, the potential for enhanced surface flow from tradewinds is a plausible cause (Figure 2; Demmer et al. 2022; Nan et al. 2020). However, the degree to which atmospheric dynamics affect dispersal in the MHI remains unexplored.

Uku (green jobfish; *Aprion virescens*) are a socioeconomically and culturally important bottomfish species throughout the MHI, with the majority of catches occurring during spawning on Penguin Bank (Figure 1; Ayers 2022; Nadon, Sculley, and Carvalho 2020). Uku are rare among the eteline snappers in their proclivity to occupy both deep (> 100 m) and shallow (< 30 m) reef habitats throughout their lifetime (Asher, Williams, and Harvey 2017; Pyle et al. 2016). This range results in the utilization of this species both by shore-based fishers (especially spear fishers) and boat-based commercial fisheries (Ayers 2022; Nadon, Sculley, and Carvalho 2020). Presently, uku are treated as a single stock across the MHI, with the degree of dispersal at both larval and adult stages remaining uncertain (Nadon, Sculley, and Carvalho 2020).

Here, we use Lagrangian particle simulations to estimate larval uku dispersal from Penguin Bank, the largest documented region of uku spawning within the MHI (Nadon, Sculley, and Carvalho 2020). Specifically, we aim to estimate interannual patterns in retention, potential connectivity to other islands, and overall frequency of connections throughout the MHI for simulated uku larvae released from Penguin Bank. We hypothesize that interannual variability in these processes will be linked to larger atmospheric forcing. We further explore how these interannual dynamics relate to the estimated recruitment of uku, an important step toward ecosystem-based management of this species.
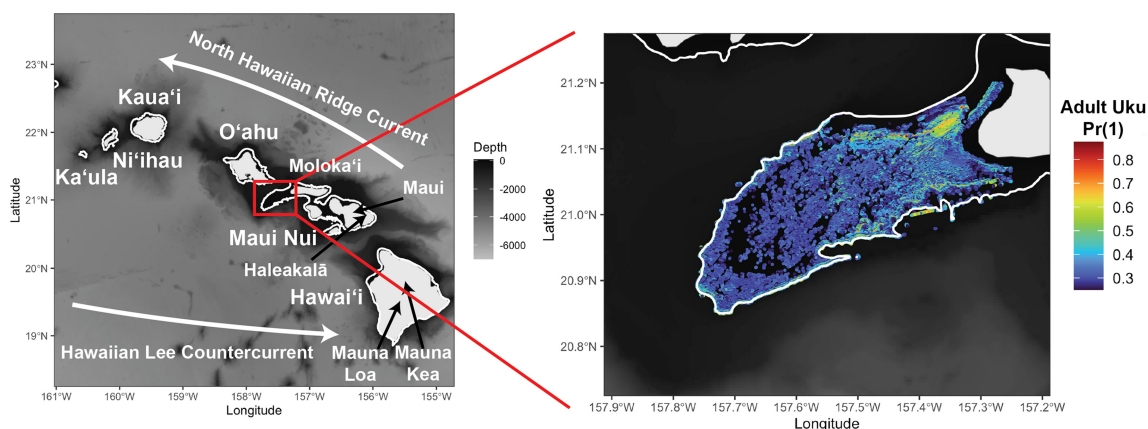

FIGURE 1 | Map of the main Hawaiian islands along with the 150 m isobath (white line) with the six settlement areas labeled. Settlement areas are labeled with larger text. Maui Nui represents the geological area containing Maui, Moloka'i, Kaho'olawe, Lāna'i, and Penguin Bank. Inset: Penguin Bank with the 150 m isobath in white. Release locations for larval uku dispersal simulations presented with color indicating the probability of occurrence of adult uku from a habitat suitability model (Franklin 2021).
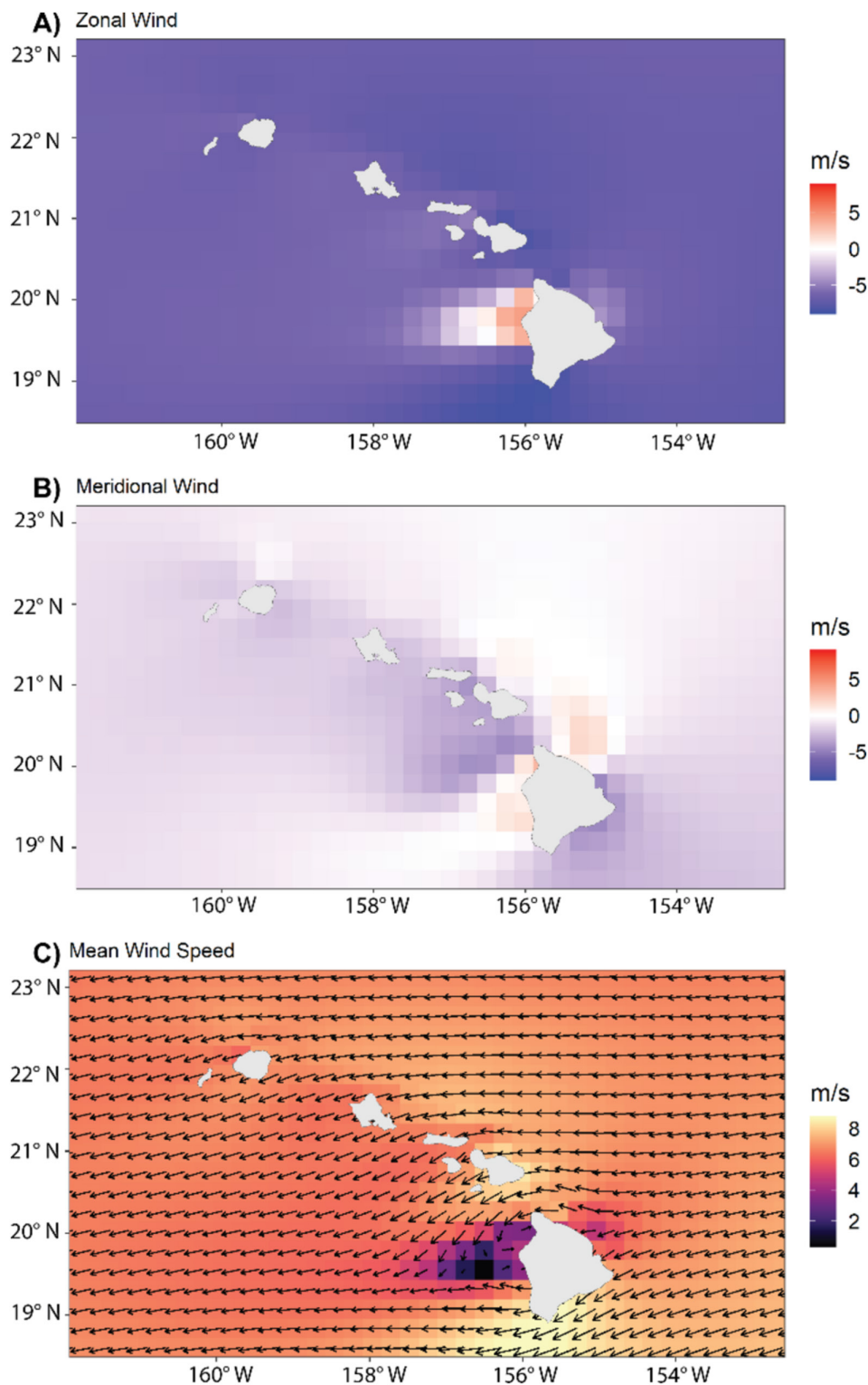
FIGURE 2 | Mean zonal wind (easterly negative/westerly positive; A), meridional wind (northerly negative/southerly positive; B), and mean wind speed (C) from April through November from 1988 to 2020 throughout the MHI. Data from National Centers for Environmental Information.

2 | Methods

2.1 | Study Region

Penguin Bank (Figure 1) represents a large shoal southwest of Moloka'i and the largest area of mixed edge and reef habitat shallower than 150 m throughout the MHI (Pyle et al. 2016).

The region represents both the area of the largest commercial landings of uku and an area where spawning aggregations are noted (Nadon, Sculley, and Carvalho 2020), with these two factors being inextricably linked. The region is unique within the MHI, characterized by a typically narrow shelf, in its shallow bathymetry while simultaneously being far from exposed and populated land masses. Despite Penguin Bank representing

an essential bottomfish fishing and spawning ground (Parke 2007; Sackett et al. 2014), this area was not included in past dispersal modeling exercises because of past work focusing on fringing reef systems and shallower-dwelling reef fishes (Wren et al. 2016; Storlazzi et al. 2017; Lindo-Atchati et al. 2020), resulting in uncertainty about how dispersal patterns from this region compare to those from the fringing reef surrounding the MHI. We focus on Penguin Bank as it is the only noted spawning area for uku at this time and is often assumed to represent a large portion of uku reproductive output in the MHI (Nadon, Sculley, and Carvalho 2020).

The current structure around Hawaiʻi, including Penguin Bank, is heavily shaped by the islands themselves. The prevailing Hawaiian ridge current generates a westward flow north of the chain, whereas in the lee of the chain, the interaction between the prevailing trade winds and the islands generates a complex network of mesoscale eddies and other features (Lumpkin 1998). Tradewinds are funneled through the highest peaks of Hawaiʻi island (Mauna Kea and Mauna Loa) and Maui (Haleakalā), generating highly variable surface wind stress between the channels and the lees of these peaks (Calil et al. 2008). The resulting eddy field leads to a hydrodynamic system that is heavily influenced by winds and rarely exhibits persistent current patterns (Patzert 1969; Calil et al. 2008).

2.2 | Hydrodynamic Model

We used the MHI Regional Ocean Modeling System reanalysis (MHI ROMS; URL:https://pae-paha.pacioos.hawaii.edu/erddap/griddap/roms_hiig_reanalysis.html, Date Accessed 2023-08-09) as the hydrodynamic forcing for estimating uku dispersal throughout the MHI (Matthews, Powell, and Janeković 2012). MHI ROMS has 32 vertical terrain following layers and a 4-km horizontal spatial resolution bounded at 164–153 W and 17–23 N. Boundary conditions for MHI ROMS are set using the 1/12° (~9-km) global HYbrid Coordinate Ocean Model (HYCOM) and applied daily. The MHI ROMS current field is updated at a three-hourly resolution throughout the domain with atmospheric and tidal forcing coming from the high-resolution Weather Regional Forecast (WRF-ARW 2017) and Oregon State University Tidal prediction software (Egbert, Bennett, and Foreman 1994), respectively. The downscaling of this model improved the flow estimates around the abrupt bathymetry of the region, which was poorly resolved at the 1/12° scale of HYCOM (Partridge, Friedrich, and Powell 2019).

2.3 | Particle Tracking and Biological Characterization

We used PARCELS (Probably A Really Computationally Efficient Lagrangian Simulator) for our Lagrangian particle tracking of simulated uku larvae (Lange and van Sebille 2017; Delandmeter and Van Sebille 2019). PARCELS is an open-source particle tracking model that interpolates velocities to the individual particles using a fourth-order Runge–Kutta time stepping scheme to resolve advection and has been used in a number of larval dispersal works in recent years (Krumhansl

et al. 2023; Grimaldi et al. 2022.; Schilling, Froyland, and Junge 2020).

Particles were released throughout the full temporal window of the uku spawning season, running from April 15 to September 30 (Everson, Williams, and Ito 1989) from 2008 through 2020, encompassing the availability of the MHI ROMS reanalysis product. Spawning locations were set according to habitat suitability model estimates for uku within the deeper portion (> 40 m) of their range over Penguin Bank (Figure 1; Franklin 2021). We restricted potential spawning locations to the deeper portion as this represents the habitat for the majority of uku throughout the MHI (Nadon, Sculley, and Carvalho 2020), and our lack of ability to calibrate occurrence probabilities between the separate methods used to estimate uku density within shallow (< 30 m) and deeper (> 40 m) water (Franklin 2021; Tanaka et al. 2022). Habitat suitability model estimates existed at a 55-m horizontal resolution, with release locations set to any grid cell that was estimated to have a greater than 25% probability of occurrence of uku. We chose a 25% probability of occurrence as the threshold to ensure release sites cover the full expanse of Penguin Bank, allowing us to assess the sensitivity of our results to release location within Penguin Bank and account for our uncertainty regarding the exact spawning location of uku on Penguin Bank. We do, however, test the sensitivity of our results to this threshold (see Supporting Information). We acknowledge that the resolution of the release locations is much higher than that of MHI ROMS, but we maintained this high resolution to represent higher relative densities of releases in 4-km grid cells that had a higher density of adult uku habitat.

Three particles were released every other day from each location at midnight, resulting in 223,632 particles released per day of release at 74,544 individual locations (18,785,088 particles released per spawning season). Particles were advected at 10-min time steps from simulated spawning through the end of each particle tracking simulation. For each particle, random diffusion with a constant of $10\,m^2/s$ was imputed to simulate a degree of random movement amongst particles released from the same location. This value represents a moderate degree of diffusion without having diffusivity overwhelming the advective dynamics of the model (Siegel et al. 2003; Paris et al. 2013; Treml et al. 2015).

During each simulation, particles began at the surface for 24 h to reflect buoyant eggs and the approximate hatching time of snapper eggs in temperatures associated with spring and summer temperatures of the MHI (Suzuki and Hioki 1979; Hamamoto et al. 1992). After hatching, particles sank to 20 m at a rate of 10 cm/s, following a mean sinking rate of larvae in laboratory experiments (Hare, Walsh, andWuenschel 2006). Particles then remained at 20 m, the midpoint of uku larval vertical distribution based on historical sampling (Schmidt et al. 2023, and were thus advected in two-dimensional space without further vertical movement or velocities. Historical sampling indicates no evidence of diel vertical migration; thus, diel vertical migration was not included in the model (Schmidt et al. 2023). The lack of evidence for diel vertical migration and lack of study of ontogenetic vertical migration are why larval behaviors were not included in this model. However, we note that future studies may indeed find contradictory results about the vertical migration of uku larvae, especially

if vertical migrating behavior is situationally dependent, and such a finding would warrant updated parameterization of uku larval dispersal models.

We do not know the exact settlement age of uku larvae because of a complete lack of observations of this species during their settlement phase (Schmidt et al. 2023). However, the oldest pelagic larva that has been aged was 26 days old (O'Malley et al. 2021), and thus, settlement may begin after that time period. The upper bound of this larval duration remains unknown, yet a previous study in the MHI found that potential connectivity patterns interisland were not sensitive to larval duration past 45 days posthatch (Wren et al. 2016). Thus, we chose the larval duration estimate for simulated uku larvae to be between 27 and 45 days. Simulations for each particle ended after a 45-day larval duration (see Supporting Information for sensitivity analysis of larval duration). Note that extreme dispersal distances will increase with longer larval duration, even if average interisland potential connectivity does not change. Mortality of larvae would certainly decrease potential connectivity, but we do not incorporate mortality in this model because (1) we do not know the exact reproductive output of uku to accurately scale the number of particles released each day and (2) we do not understand larval mortality rates in Hawai'i generally or for uku in any region.

2.4 | Estimates of Larval Supply and Potential Connectivity

Polygons for settlement habitat were created by generating a 5-km buffer around the 150-m isobath throughout the MHI. The 150-m isobath was chosen as the region at which the probability of adult uku declines rapidly (Figure 1; Franklin 2021). Five kilometers was selected to correspond roughly with the horizontal resolution of MHI ROMS. Keeping this buffer is also important as we did not simulate the final settlement process for uku because of uncertainties in this life stage. Existing studies indicate that larvae may use olfactory and auditory cues for habitat identification (Simpson et al. 2004; Wright et al. 2008). Therefore, we made the assumption that larval behavior plays a significant role within close proximity of settlement habitat (< 5 km). Given our uncertainty in how these settlement behaviors manifest and our lack of knowledge of uku settlement habitat, we focus on larval supply to regions near potential settlement habitats rather than modeling larval uku settlement behavior. Uku settlement habitat may differ from adult habitat, potentially being shallower or deeper than adults, but no settlement stage records exist for this species (Schmidt et al. 2023). However, even if this is the case, the steep bathymetry of MHI means shifting the definition of settlement habitat from 150 to 300 m results in minimal difference in the "settlement" polygons. Shallower settlement habitat could result in a change in settlement polygons. Indeed, other snapper species have been shown to settle in nearshore and estuarine habitats (Nagelkerken et al. 2001; Pollux et al. 2007). However, given the clear waters of Hawai'i, the frequent use of these waters for recreation (including fishing and diving), and the myriad research projects conducted in these nearshore regions, we believe that it is highly unlikely that this area represents settlement habitat for uku as this life stage remains unobserved. It is more likely that uku settle in areas with deeper

habitats that are beyond diving depths (> 30 m), similar to the majority of the adult habitat.

These qualifications result in six settlement areas throughout the MHI: Hawai'i Island, Maui Nui, O'ahu, Kaua'i, Ni'ihau, and Ka'ula (Figure 1). The settlement window for simulated particles was set to 27–45 days posthatch, whereby if a particle entered the 5-km buffer of the 150-m isobath of a settlement area, it was considered settled. We use "settled" for the sake of consistency and brevity, but note that what we really estimated was the delivery of settlement age particles to different areas. There are a number of uncertainties about uku early life history and settlement habitat, differentiating our use of the word "settled" compared with the true biological definition and preventing us from truly simulating settlement.

2.5 | Potential Connectivity Estimates

For each settlement area, the total number of settled particles was assessed annually and collectively throughout the 13 years of runs (i.e., assessment of all particles released throughout the study). For each settlement area, we calculated the proportion of particles delivered to that site within the chosen time window to generate a time series of connections for the six settlement areas, defining this as potential connectivity. We recognize this does not necessarily infer true population connectivity due to the simulation nature of the work and postsettlement process that can regulate survival prior to reproductive age (Pineda, Hare, and Sponaugle 2007; Planque, Bellier, and Lazure 2007), but we use this term to be consistent with other larval dispersal studies throughout the region (Wren et al. 2016; Storlazzi et al. 2017).

Additionally, we assessed the sensitivity of the spatial release location on the potential connectivity to different areas, calculating the mean proportion of released particles from a given release location connected to each of the six settlement areas throughout the full duration of the experiment.

2.6 | Role of Wind Dynamics in Potential Connectivity and Recruitment

We used National Centers for Environmental Information (NCEI) Daily 0.25° Blended Seawinds (v2.0; URL:https://coastwatch.noaa.gov/erddap/griddap/noaacwBlendedWindsDaily.html; Date accessed 2023-08-23) to estimate wind dynamics during the dispersal period of each year. This product was used as opposed to the Weather Regional Forecast because of the longer time span available. For each year during the period spanning the initial release to final settlement (April 15–November 15), the mean daily zonal and meridional winds were averaged from 20 to 22 N and 158 to 156 W, encompassing the region around the Maui Nui complex, including Penguin Bank and immediately upwind of the release locations.

For each year, the mean total windspeed (m/s) and mean meridional wind velocity (V) were calculated. These two wind metrics (mean wind speed and mean V) were compared with the proportion of particles reaching any settlement area within the MHI. Relationships were estimated using beta

regression using a logit link function within the R package betareg (v3.1.4; Zeilies et al. 2016). This approach was chosen because of the proportional nature of the response variable, representing the proportion of particles categorized as having been delivered to potential settlement habitats. To address the impact of wind dynamics on release locations, we estimated correlation coefficients individually for each release point to quantify their relationship with the proportion of particles delivered to potential settlement habitats in the six designated settlement areas. Release locations with correlations that were nonsignificant ($p > 0.05$) or were weakly connected to a given settlement area (< 1% of particles connected) were removed from this analysis.

We examined whether the relationships between wind patterns and the movement of simulated uku larvae could be applied to estimating uku recruitment. Our recruitment and spawning stock biomass estimates were derived from the 2020 Benchmark Uku Stock Assessment (Nadon, Sculley, and Carvalho 2020). We recognize that these estimates, particularly recruitment, are themselves estimates with error, and values of the most recent years may change in future stock assessments (Brooks and Deroba 2015; Palmer et al. 2016). Despite these uncertainties, we used these estimates owing to a lack of data on age-0 fish from surveys. We compared the estimated ratio of recruits per metric ton of spawning stock biomass to both mean wind speed and mean meridional wind velocity during larval occurrences in the Maui Nui region, ranging from 1988 to 2018, using linear regression. The first year of this analysis corresponds to the first full year of the Blended Seawinds product available from NCEI and the final year from the last recruitment class estimated in the stock assessment. The length of this time series suggests that recruitment estimates used in this analysis are likely stable, with the exception being the most recent few years, rendering this analysis to only be sensitive to a stock assessment update if patterns are largely driven by the last few years of the time series (Hare et al. 2015). All statistical analyses were performed using R v. 4.3.2 (R Core Team 2023).

3 | Results

3.1 | Interannual Patterns in Potential Connectivity

The proportion of particles reaching any individual settlement area showed moderate levels of interannual variability, ranging from 0.17 to 0.41 connected to a settlement area within the MHI (mean proportion connected = 0.26; Figure 3). The proportion lost to the system is the reciprocal of the proportion delivered to any site within the MHI (i.e., 1-Pr (MHI)). For most years, retention of particles within the Maui Nui complex was the most common path for settlement age particles, representing 53.8% percent of all particles settled throughout the experiment. O'ahu represented the second most common potential settlement location for simulated particles (26.7%), with fewer particles reaching Kaua'i (8.9%), Ni'ihau (3.5%), Ka'ula (1.8%), and the island of Hawai'i (7.1%). Note that given the long settlement window, multiple particles (~1.6%) would have had the capacity to settle in multiple locations throughout the

27- to 45-day window. Note that the proportion of connected particles released was nearly insensitive to changing the release location threshold of probability of occurrence to 0.5 (Figure S1). Additionally, interannual variability in connections was insensitive to restricting the settlement window to 27–30 days (Figure S2). However, transport to potential settlement locations further from the releases (e.g., Hawai'i island and Kaua'i) did decrease with this shorter larval duration (Figure S2).

Potential connectivity to each settlement area was sensitive to release location throughout Penguin Bank. Releases from the shoals of Penguin Bank (near the center) were highly connected to Maui Nui (mean proportion connected ~0.15; Figure 4B), moderately connected to O'ahu (mean proportion connected ~0.10; Figure 4C), and had minimal relative potential connectivity to other settlement areas. Release locations near the tail of Penguin Bank (the southwestern portions) had higher relative potential connectivity to Hawai'i (Figure 4A), Kaua'i (Figure 4D), Ni'ihau (Figure 4E), and Ka'ula (Figure 4F) compared with release locations further northeast on the bank, though overall potential connectivity to these areas from Penguin Bank was low (< 0.05). The north-northwest flank had high relative potential connectivity to O'ahu.

3.2 | Relationships of Simulated Settlement and Wind Patterns

Total potential connectivity to all areas in the MHI throughout the simulations had a significant negative relationship with mean wind speed during the dispersal period (Slope = −0.54; $R^2 = 0.28$; $p = 0.02$; Figure 5A; Table 1) and positively correlated with mean meridional wind velocity (Slope = 0.64; $R^2 = 0.32$; $p = 0.006$; Figure 5B). Note that the mean meridional wind velocity in the domain was from the north (denoted as negative values; Figure 1); thus, potential connectivity to settlement areas in the MHI was positively correlated with weaker northerly wind components.

Potential connectivity to Maui Nui generally decreased with increased wind speed (Figure 6B), whereas potential connectivity to Kaua'i consistently increased with higher mean wind speeds
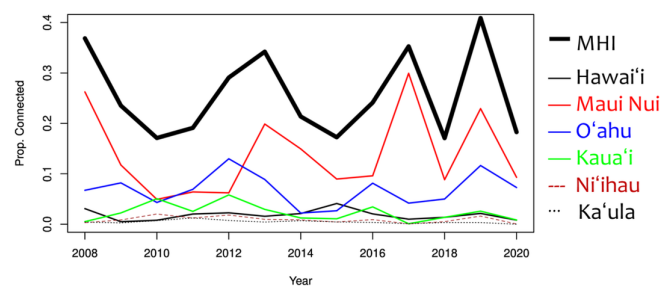

FIGURE 3 | Annual patterns in the proportion of particles released from Penguin Bank, Hawai'i, in a Lagrangian dispersal model that was designed to simulate the advection of uku (*Aprion virescens*) larvae that reached each of six settlement areas adjacent to individual Hawaiian islands, from 2008 through 2020. MHI = main Hawaiian islands. Note that the proportion of particles lost to the system equates to 1-MHI line.
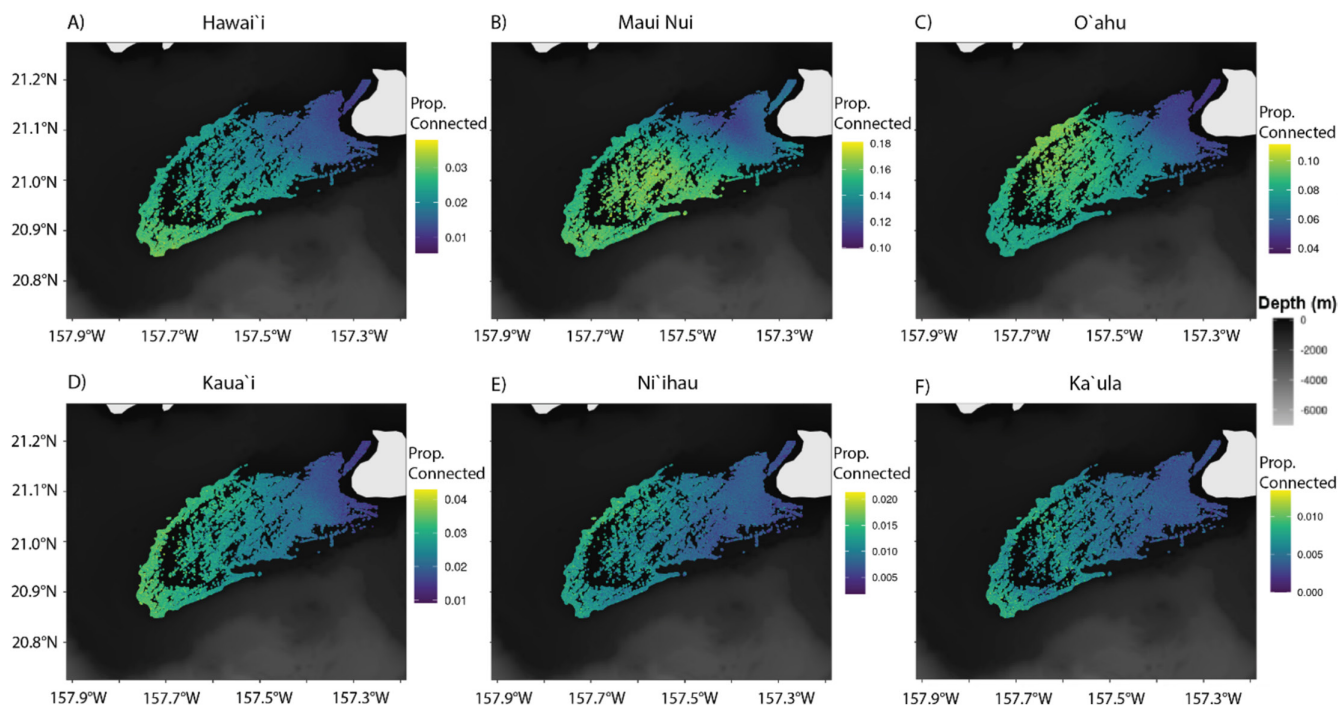
FIGURE 4 | Proportion of particles from a Lagrangian dispersal model that was designed to simulate the advection of uku (*Aprion virescens*) larvae that were delivered to each of the settlement areas (locations in panel titles) based on release location within Penguin Bank, Hawai'i. Note the scale varies by panel to highlight differences within release locations rather than across settlement areas.
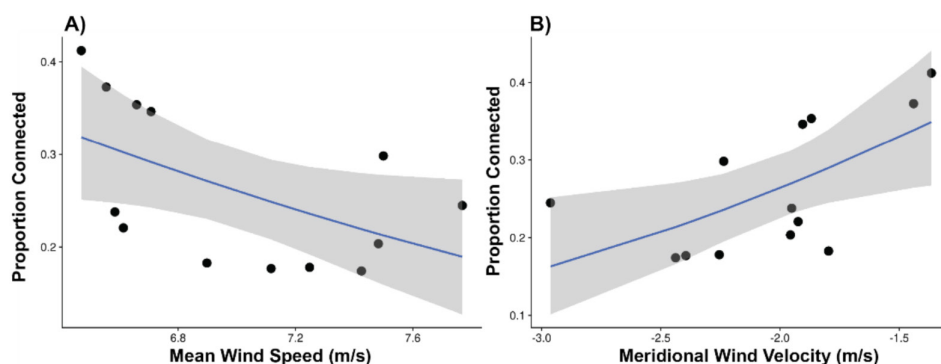

FIGURE 5 | Beta regression between the proportion of particles released from Penguin Bank, Hawai'i, in a Lagrangian dispersal model that was designed to simulate the advection of uku (*Aprion virescens*) larvae that were transported to settlement areas in the main Hawaiian islands by year and (A) mean wind speed and (B) meridional wind velocity in Maui Nui.

(Figure 6D). Relationships of potential connectivity to other settlement areas (Figure 6A–F and Table 1) with wind speed were more location specific, with enhanced potential connectivity to Hawai'i for releases nearest Moloka'i, whereas potential connectivity to Ni'ihau increased with wind speed primarily near the tail of Penguin Bank.

Release and settlement location–specific correlations with meridional wind velocity (Figure 7A–F and Table 1) indicate that potential connectivity to Maui Nui was decreased near Moloka'i and near the tail of Penguin Bank with increased northerly wind velocity (Figure 7B; note that because meridional velocity is net-negative in this domain, positive correlations translate to more potential connectivity with weaker winds). Simulated potential connectivity to O'ahu decreased with increased northerly wind velocity for releases at the eastern portion of Penguin

Bank (Figure 7C). Simulated potential connectivity to Kaua'i (Figure 7D) increased with increased northerly wind velocity throughout most release locations, and potential connectivity to Ni'ihau (Figure 7E) increased with north wind velocity near the tail of Penguin Bank.

Visual assessment of the distribution of particles from a year with strong northerly wind velocity (2016; mean velocity = −2.96 m/s) indicated that particles were distributed nearly evenly throughout the domain, often far from the settlement areas (Figure 8A). During a year with weak northerly winds (2019; mean velocity = −1.37 m/s), particles concentrated near and just north of the settlement areas and were less spread throughout the domain during the settlement window (Figure 8B). Note the increased number of particles near Moloka'i and east O'ahu in 2019 compared with 2016,

TABLE 1 | Summary of the settlement area–specific connectivity responses in the main Hawaiian islands of particles from a Lagrangian dispersal model designed to simulate the advection of uku (*Aprion virescens*) larvae from Penguin Bank, Hawai'i, to increases in mean wind speed and increases in the meridional wind velocity.

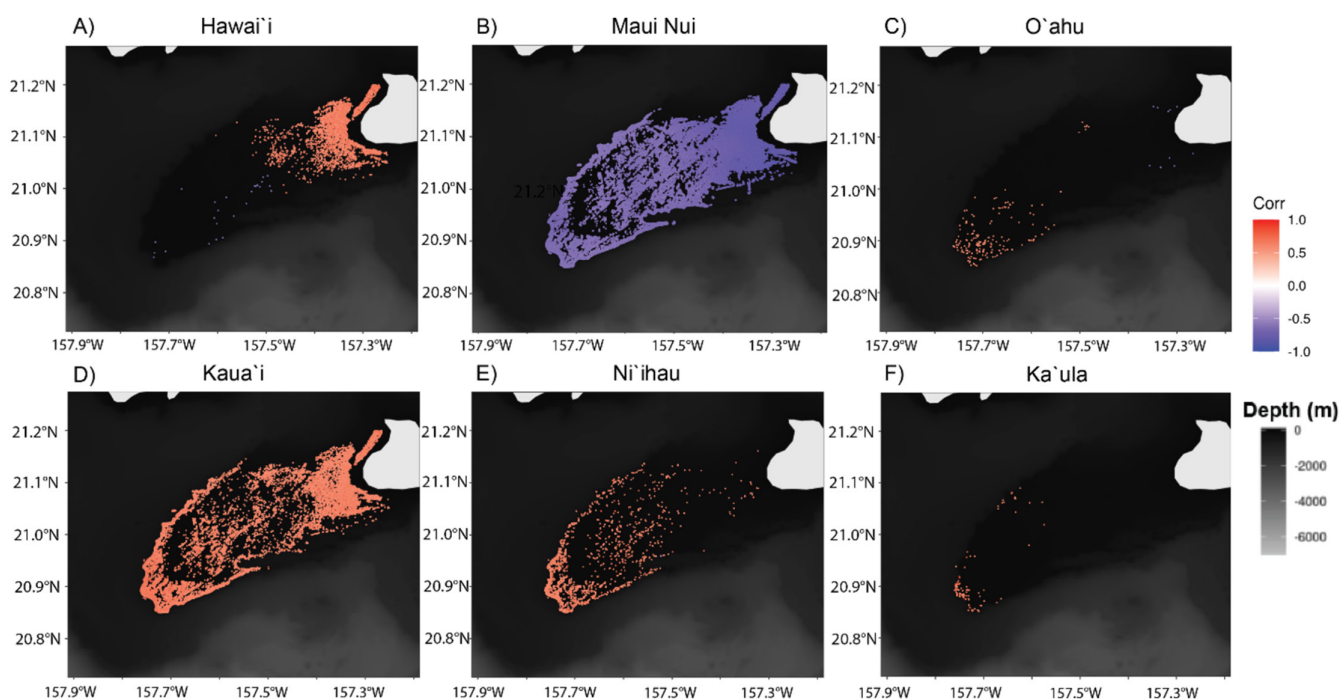| Area	Mean wind speed	Potential connectivity	Meridional wind velocity	Potential connectivity
Hawai'i	+	+	+	—
Maui Nui	+	—	+	+
O'ahu	+	Minimal Difference	+	+ (when particles released from eastern Penguin Bank)
Kaua'i	+	+	+	—
Ni'ihau	+	+ (when released near tail of Penguin Bank)	+	— (when particles released from tail end of Penguin Bank)
Ka'ula	+	Minimal Difference	+	Minimal Difference

FIGURE 6 | Correlation coefficient between the proportion of particles from a Lagrangian dispersal model that was designed to simulate the advection of uku (*Aprion virescens*) larvae that were delivered to each of the settlement areas (locations in panel titles) and mean wind speed in Maui Nui based on release location. Nonsignificant correlations were excluded. Background shading represents bathymetry matching Figure 2.

with a much greater number of particles far from the islands in 2016 (Figure 8C). However, because of the complex mesoscale structure of the advection field, spatial correlations with annual current speed did not reveal clear current structure changes that lead to such patterns (Figure S7).

3.3 | Potential Connectivity and Recruitment

Recruits per metric ton of spawning stock biomass (from Nadon, Sculley, and Carvalho 2020 stock assessment) were not significantly correlated with mean wind speed (Slope = −0.14; $R^2 = 0.02$, $p = 0.292$; Figure 9A) but were significantly correlated with the meridional wind velocity (Slope = 0.48, $R^2 = 0.25$; $p = 0.004$; Figure 9B).

4 | Discussion

Our work indicates a sensitivity in simulated interannual potential connectivity from a known spawning ground of a commercially important species to wind dynamics and that this
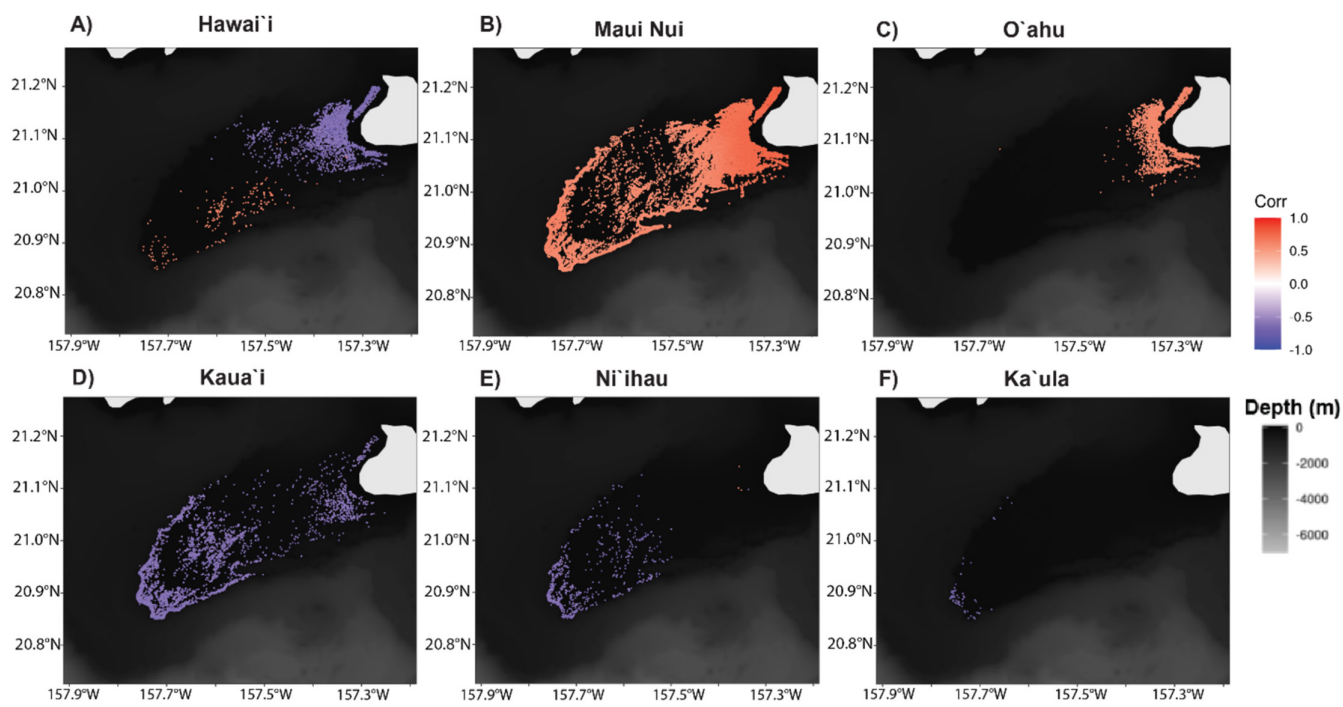
FIGURE 7 | Correlation coefficient between the proportion of particles from a Lagrangian dispersal model that was designed to simulate the advection of uku (*Aprion virescens*) larvae that were delivered to each of the settlement areas (locations in panel titles) and meridional wind velocity in Maui Nui based on release location. Nonsignificant correlations were excluded. Background shading represents bathymetry matching Figure 2.

sensitivity to wind appears to translate to variability in recruitment. Our results show that simulated uku larvae "spawned" on the centrally located Penguin Bank can reach all six major habitat areas throughout the MHI within 45 days. However, most of the particles released were either retained within Maui Nui or reached Oʻahu, indicating that interisland potential connectivity decreases rapidly with distance from the spawning site. This information is important for understanding the potential spatial extent over which the stock that spawns on Penguin Bank is able to deliver their larvae and that further exploration of spawning locations on other islands is likely necessary to advance our understanding of the demographic connectivity of uku within the MHI. Collectively, these results provide a refinement in our understanding of the interisland potential connectivity of a commercially important species and a remotely sensed environmental indicator of their interannual recruitment. These insights are crucial for advancing ecosystem-based management in data-limited regions (Parke et al. 2023).

4.1 | Potential Connectivity at the Genetic and Demographic Scale

To date, no studies have explored the population genetics of uku, both within and across the Hawaiian Archipelago. Consequently, the current understanding of uku population structure remains unknown. Our study provides insights into what this structure may be, with simulated dispersal occurring from the major uku spawning location of Penguin Bank to all of the major island regions within the MHI. Uku may be fairly homogenous in terms of life history characteristics and behavior based on this exchange. Notably, growth rates for this species have been shown to be remarkably similar across their wide Indo-Pacific

range (O'Malley et al. 2021), and they are classified into a far-dispersing predator category compared with other reef fishes (Stier et al. 2014). Other island-associated species have shown population-level connectivity at much greater distances than within the MHI. Considering the presumably moderate to long larval duration of uku, our results support that uku may fall into this category of far-dispersing species (Kamikawa et al. 2023), which likely influences genetic connectivity. However, genetics do not solely govern life history, as environmental conditions, including those that modify metabolism and feeding, can result in pronounced changes in growth and reproduction (Jobling 1997; Persson and De Roos 2006). Ignoring the role of these exogenous environmental influences due to a lack of genetic differences can lead to inappropriately parametrizing life history patterns in stock assessments (Cadrin and Secor 2009). More research is needed to understand the role of environmental conditions on the life history of uku from larval growth through maturation and subsequent spawning.

Population-relevant demographic connectivity, however, is likely more limited than genetic connectivity. Our results suggest that demographic connectivity large and frequent enough to drive population variability may not be pronounced enough between Penguin Bank and more distant islands, such as Hawaiʻi, Kauaʻi, and Niʻihau. The scales of these two different types of connectivity are important for understanding both the management and ecology of this species. Genetic techniques have improved in recent years to come closer to elucidating smaller scale connectivity that is relevant for population fluctuations (Coleman et al. 2023; Toonen et al. 2011). Research within the MHI has indicated fine-scale population structure for species such as manini (*Acanthurus triostegus*), despite their moderately long pelagic larval duration and generalist settlement behavior
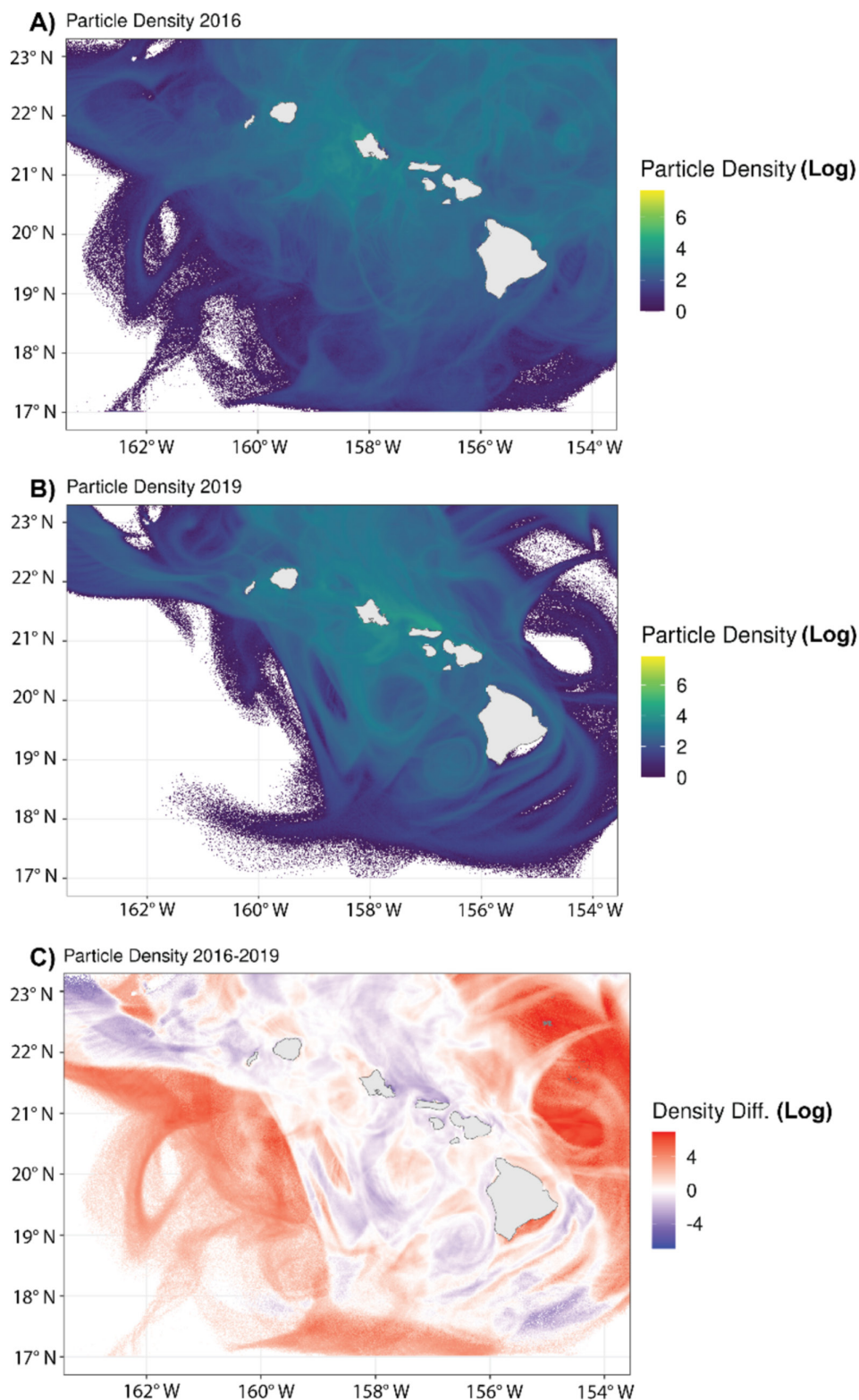
FIGURE 8 | Particle density (log-scale) from a Lagrangian dispersal model that was designed to simulate the advection of uku (*Aprion virescens*) larvae during the settlement period (27–45 days posthatch) during (A) 2016, a year with strong northerly winds, and (B) 2019, a year with weak northerly winds and comparatively higher retention close to the islands. (C) Difference in the log density of particles in each 0.01° bin throughout the domain between 2016 and 2019, with red indicating higher density in 2016 and blue indicating higher density in 2019.

(Coleman et al. 2023). As modern genetic techniques can provide unexpected results, such as those for manini, future work targeted at population genetics of uku within the Hawaiian archipelago could complement our larval dispersal results. Such a population genetics study could provide a form of model validation for our dispersal simulations. However, it is important to note that if our dispersal simulations are indeed representative of larval transport of uku across the MHI, population genetics
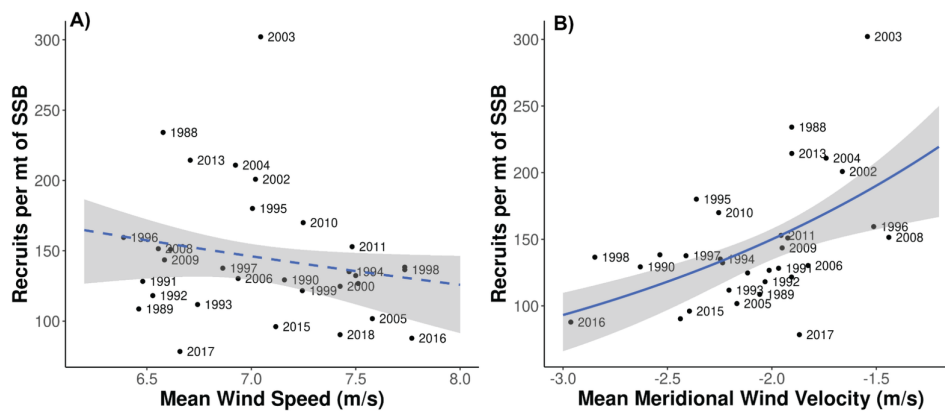
FIGURE 9 | Linear regressions between estimated annual recruits per metric ton of spawning stock biomass of uku in the main Hawaiian islands and annual mean wind speed (A) and annual mean meridional wind velocity (B) in Maui Nui from 1988–2018. Each point represents 1 year. Dashed lines indicate a statistically nonsignificant relationship ($\alpha = 0.05$), and solid lines indicate a significant relationship.

may not identify much, if any, genetic structure within the MHI due to the occasional exchange of larvae from Penguin Bank to each habitat area. Although genetic techniques have indeed improved over time, caution is needed when using methods that may overestimate demographic connectivity of stocks, as this has led to serial depletion of fisheries throughout the globe (Armstrong, Armstrong, and Hilborn 1998; Cardinale, Nugroho, and Jonson 2011).

4.2 | Role of Tradewinds in Dispersal and Retention

Our results indicate that both the direction and strength of the wind were important factors that contributed to variations in simulated larval transport from Penguin Bank. Increased wind speeds did correspond with a higher loss of particles from settlement areas, yet this did not correlate strongly with decreases in estimated recruitment. One of the most likely causes of this seemingly confounding result is the singular release area in this study. Although Penguin Bank is the only documented spawning site for uku in the MHI by western science, anecdotal information from fishers suggests that uku spawning is likely to occur in other areas throughout the MHI (Barlow, per. comm.). If this is indeed the case, then increased wind speeds may enhance interisland potential connectivity from these locations as well, offsetting the losses from Penguin Bank by the supplement of larvae from other spawning locations. Our results did indicate that the potential connectivity to areas far from Penguin Bank did correlate with stronger wind speeds, supporting the hypothesis that increased wind speed may enhance interisland potential connectivity.

Meridional wind velocity near Maui Nui correlated both with the degree of potential connectivity to settlement areas for simulated uku larvae and the recruitment estimates (Figures 7 and 9). This sensitivity to wind direction is a key component for forecasting uku recruitment in coming years, as the direction and speed of tradewinds have oscillated over decades (Garza et al. 2012; Nan et al. 2020). From the 1970s through the mid-2000s, tradewind speeds increased and generally became more easterly (Garza et al. 2012). This pattern of increased overall wind speed suggests interisland potential connectivity of uku

spawned on Penguin Bank may have increased during that time. However, in more recent years, the tradewind frequency has decreased again, leading to uncertainty about the fate of tradewind frequency with climate change (Nan et al. 2020). Climate simulations have indicated that tradewinds may increase in frequency and moderately in strength, though directional changes are not often discussed (Takahashi and Watanabe 2016). The sensitivity of estimated uku recruitment to wind direction supports the need for understanding this nuance of tradewind patterns in a changing climate. It is important to note that the relationship of recruitment with overall wind speed and northerly wind velocity may change in coming years as recruitment estimates from the stock assessment are updated. The most recent 2 years (2017 and 2018) were not years with impacts on the significance of the relationship between wind speed and direction and recruitment. However, 2016 is a notable year with low recruitment estimates and strong northerly winds, leaving some sensitivity of our results to updated recruitment estimates. Additionally, 75% of recruitment variability remained unexplained by meridional wind velocity, indicating that other processes are important for uku recruitment in the MHI. For a species that is moderately long-lived and becomes mature near 4 years (Nadon, Sculley, and Carvalho 2020; O'Malley et al. 2021), year-to-year recruitment variations connected with wind are unlikely to have pronounced effects on stock size unless several successive years of weak or strong northerly winds occur. Although there is no clear evidence of such a situation occurring in the recent past, understanding how climate change will modulate wind dynamics will be important for knowing whether wind-driven loss of larvae and thus recruitment are likely to affect uku stock size within the MHI. However, the low to moderate amount of recruitment variance attributed to wind dynamics suggests that other factors could mask or enhance recruitment variability in the future. Several factors likely led to 75% of uku recruitment variations remaining unexplained by wind forcing. We did not incorporate larval feeding or mortality in our model, which are both important for larval survival and thus uku recruitment (Hjort 1914; Pepin et al. 2014). Further, postsettlement processes may play important roles in modulating recruitment. As a bottomfish, habitat can be limited if the "over-supply" of larvae to settlement grounds occurs, leading to density dependence as individuals compete for limited resources and space

(Fromentin et al. 2001; Johnson 2007). Postsettlement predation can also be pronounced for bottomfishes, particularly reef fishes (Carr and Hixon 1995; Steele 1997; Webster 2002). Once uku settlement habitats are identified, elucidating the potential role for postsettlement bottlenecks to population size will be helpful for better understanding recruitment and uku stock size in the MHI.

4.3 | Limitations and Future Considerations

Although our study offers simulation-based insights and hypotheses for variability in interisland potential connectivity of uku recruitment, much remains uncertain regarding the mechanisms by which the wind modulates the current structure in the region. Detailed analysis of the dynamics of the eddies in the lee of the islands and current reversals through channels is needed to better understand how tradewind variability directly leads to dispersal changes. Understanding these current mechanisms may become especially important as we attempt to forecast how winds will change in a warming climate. Though tradewinds drive the North Hawaiian Ridge Current and the Hawaiian Lee Countercurrent, the latter often lacks a clear structure and much more remains to be understood about its dynamics (Yoshida, Qiu, and Hacker 2010). The remaining recruitment variability not explained by meridional wind velocity may be better understood with a more direct measurement of how current structure varies with wind and thus how loss of larvae may be manifesting.

Although we have improved our knowledge of uku life history in the MHI in recent years, we still lack key information about this species. We need to better refine our understanding of specific spawning locations on Penguin Bank and throughout other islands, the drivers of spawning initiation and duration, the specific age of settlement for this species, and the location and qualities of uku settlement habitat. To address spawning location, we used a species distribution model based on data from across the seasonal cycle. Lacking seasonal data within the distribution model is a notable limitation given the documented movements of uku during spawning season (Meyer, Papastamatiou, and Holland 2007). Improved characterization of uku spatial abundance and fecundity during the spawning season would resolve this but will require additional data collection either through enhanced survey effort or tagging studies. The interannual patterns in simulated uku larval potential connectivity across the MHI in our study were not sensitive to the estimated suitability of release location across Penguin Bank, yet the ability of larvae to be connected to distant locations declines with limited release locations (Figure S2), and potential connectivity to these locations was largely sourced from releases around the edge of Penguin Bank (Figure 4). Therefore, genetic and demographic connectivity among islands is likely to be sensitive to release location, furthering the need for more information on spawning locations. Spawning timing and duration, including its triggers, will also be important next steps in understanding uku ecology. We used the full window of the documented uku spawning season for our releases that we lacked further information on interannual variability (Everson, Williams, and Ito 1989). However, it is likely that uku spawning varies year to year both in timing and duration. Shifts in spawning timing and duration may serve to either enhance or mitigate interannual variability in connectivity.

The timing of juvenile uku settlement is presently unknown and could aid in our understanding of their life history and protection of such habitats. We used a combination of information based on aging data of pelagic phase juveniles and past simulations of larval transport to set our settlement window. However, the exact age of uku settlement may lie within the 27- to 45-day window, which would affect dispersal distances and potential connectivity from Penguin Bank to more distant settlement areas such as Kaua'i and Ni'ihau. Interannual patterns in potential connectivity to collective settlement areas (i.e., anywhere in the MHI) were not sensitive to settlement timing, but shorter estimated settlement windows did decrease overall potential connectivity, and thus, refining this estimate is an important future step. The modeled larval supply to possible settlement habitat may be sensitive to the vertical migrating behavior of these larvae. Although an analysis of historical samples of uku larvae throughout the MHI did not show any evidence of diel vertical migration, it is indeed possible that uku larvae undergo diel vertical migration in specific situations that a historical review would be unable to identify. Ontogenetic vertical migration may also occur, but we lack this information because of larger uku larvae being rarely sampled. Collectively, it is possible vertical migrating behavior could limit larval uku dispersal distances, and more studies on this aspect of uku early life history are warranted.

Settlement habitat remains unknown for uku throughout the globe, with no individuals having been identified between 26 and 90 days old (O'Malley et al. 2021; Schmidt et al. 2023). Settlement habitat for snappers often occurs in nearshore and estuarine waters (Nagelkerken et al. 2001; Pollux et al. 2007). However, we doubt this is the case for uku given the large amount of sampling and fishing effort in this region. Some snappers, such as 'ōpakapaka (*Pristipomoides filamentosus*), settle on deeper (~40–70 m) featureless habitat (Parrish, DeMartini, and Ellis 1997). Uku may settle in similar, or deeper, regions that warrant further exploration to be able to define this habitat and understand when movement to adult habitat occurs. Defining uku settlement habitat will not only be important for improving studies like ours, rather it can also improve growth parametrization for stock assessments and refine designation of essential fish habitats for this life stage.

Finally, our use of Lagrangian particle tracking models is itself a limitation in our ability to elucidate stock structure and potential connectivity for uku. A number of past studies have found mixed agreement between observed dispersal and simulations (Levin 2006; Bode et al. 2019; Swearer, Treml, and Shima 2019). Our dispersal simulations are unable to refine whether connectivity is primarily genetic or demographic from Penguin Bank throughout the MHI and if our estimated connectivity from Penguin Bank to further islands truly manifests. Genetic studies assessing the degree of structure among islands may either serve to support the hypothesized connections from our study or refine the degree of potential connectivity we presently estimate to better understand the stock structure of this important species. Genetics studies do come with their limitations, however, as the dispersal modeling

presented here primarily focuses on shorter time scales similar to the time scales of active fisheries management (approximately interannual) compared with genetic time scales (decades to millennia).

5 | Conclusion

Our results indicate that transport of simulated uku larvae from Penguin Bank can reach the full domain of MHI uku settlement areas, spanning Hawaiʻi island to Kaʻula. However, most simulated larvae remained within Maui Nui or Oʻahu. Furthermore, tradewind dynamics significantly affected the simulated interannual variability in potential connectivity to settlement areas in the MHI. Stronger tradewinds enhanced simulated potential connectivity to more distant settlement areas, whereas both increases in mean wind speed and northerly wind strength led to decreases in the overall number of connections of simulated larvae from Penguin Bank to settlement areas. The pattern of decreased connection to settlement areas with stronger northerly winds was supported by the decreases in estimated recruitment during these years, providing both an external validation of this pattern and an ecosystem-based indicator of uku recruitment in the MHI. Much more work remains to fully elucidate the connectivity of uku populations in the MHI and their recruitment, yet our work contributes an important step toward understanding uku ecology in the region.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available in Github at https://github.com/jsuca18/Uku_Dispersal. These data were derived from the following resources available in the public domain:

– PacIOOS, https://pae-paha.pacioos.hawaii.edu/erddap/griddap/roms_hiig_reanalysis.html

– NCEI WInds, https://coastwatch.noaa.gov/erddap/griddap/noaacwBlendedWindsDaily.html

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.