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Research Article

Modeling the dispersal of the cryptogenic alga *Chondria tumulosa* (Rhodophyta, Ceramiales) in the Papahānaumokuākea Marine National Monument

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Abstract

The cryptogenic nuisance alga *Chondria tumulosa* was first observed in 2016 at Manawai (Pearl and Hermes Atoll) in the Papahānaumokuākea Marine National Monument. It has since spread across the atoll, growing in thick mats and smothering benthic habitat. In September 2021 the species was observed at Kuaihelani (Midway Atoll), ~130 km to the northwest. Due to its growth habit and recent spread, considerable concern has been raised and management of the species may be warranted. We used publicly available oceanographic data and the Connectivity Modeling System software to assess how the potential for successful dispersal of *C. tumulosa* is affected by particle properties and oceanographic conditions. We found the likelihood of successful transit to be linked to particle density, oceanographic conditions at the time of release, and release location. Further modeling explicitly targeted the capacity of both reproductive tetraspores as well as drifting fragments to disperse. Model results indicated tetraspores of *C. tumulosa* are unlikely to survive the transit from Manawai to Kuaihelani, as none arrived at Kuaihelani above the depth limit of the species and those arriving below successfully settled at a rate of only 0.02%. In contrast, fragments modeled as rafting on marine flotsam such as macroalgae and marine debris settled at a rate of 3.85%. Rafting fragments also settled ~600 km further to the southeast (towards the Main Hawaiian Islands) than tetraspores. This study identified oceanographic conditions and particle properties likely to aid dispersal of *C. tumulosa* to Kuaihelani and suggests that fragments rafting on marine flotsam may accelerate its spread.

Key words: flotsam, Hawai'i, marine debris, marine protected areas, phycology, rafting, tetraspores

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Introduction

The red alga *Chondria tumulosa* A.R.Sherwood & Huisman, 2020 was first observed in 2016 at Manawai in the Papahānaumokuākea Marine National Monument (PMNM) (Sherwood et al. 2020). The species is cryptogenic, it exhibits qualities of invasiveness but has yet to be demonstrated as being introduced from elsewhere or a native species that has undergone a recent population expansion. Thalli of the alga interweave to form large mounds of several square meters with mats growing sufficiently thick to stifle or kill overtaken benthos (Sherwood et al. 2020; Williams et al. 2024). Due to the remote nature of the PMNM, studying the physiological properties and ecological impacts of *C. tumulosa* remain challenging. The alga appears to have no natural herbivory pressure in Hawai'i, allowing it to reach a mat thickness of up to 18 cm, though herbivory by microherbivores has not been assessed (Sherwood et al. 2020; Lopes et al. 2023). Depths from 1–19 m are affected, both in the lagoon as well as on the northern, western, and eastern sides of the atoll (Sherwood et al. 2020). Despite closed circuit rebreather surveys from 30–100 m, *C. tumulosa* has not been observed beyond this depth limit. The mechanism of this limitation remains untested. Remote sensing indicates *C. tumulosa* has exhibited rapid expansion, increasing 115-fold in area from 2015 to 2021 (Lopes et al. 2023). The growth habit of the species and its presence on a remote reef in one of the largest fully protected marine areas is of considerable cause for concern.

The main mechanism of expansion for *C. tumulosa* across Manawai appears to be vegetative fragmentation based both on field observations and genetic diversity information (Sherwood et al. 2020; Lopes et al. 2023; Williams et al. 2024). The species exhibits a "tumbleweed" morphology, breaking off in mats of various sizes and tumbling along the benthos until becoming lodged in other growth locations (Sherwood et al. 2020; Lopes et al. 2023). In 2022, *C. tumulosa* was confirmed on Kuaihelani ~130 km to the west-northwest of Manawai in the first observed range expansion of the species (Lopes et al. 2023). Dislodgement and tumbling of negatively buoyant *C. tumulosa* mats is effective for dispersal across continuous suitable benthic habitat such as the majority of Manawai, but is unlikely to account for dispersal to another atoll or island. Although an apparent majority of dislodged mats or tufts are negatively buoyant, rafting mats of *C. tumulosa* have been observed (Lopes et al. 2023). These floating rafts may be kept buoyant by air entrapment, entanglement with other rafting macroalgae, or attachment to marine debris acting as a mechanism for inter-island dispersal (Martinez et al. 2007; Selkoe et al. 2008). Marine debris in PMNM is abundant and considered to be a top threat in the region (Selkoe et al. 2008). Surveys on Sand Island at Kuaihelani found an average of 32 kg of marine debris across 150 m transects after a single month of accumulation (Ribic et al. 2012). Surveys of plastic debris on beaches of the Main Hawaiian Islands (MHI) suggest the density of these items can be as low as 850 kg/m^3 and as high as 1450 kg/m^3 with those objects denser than seawater exhibiting flotation via entrapped air (Brignac et al. 2019). Further, rafting as a means of dispersal across ocean basins is often facilitated by marine debris (Carlton et al. 2018; Chong et al. 2023; Haram et al. 2023). Dispersal may also be accomplished through sexual reproduction though there are several biological constraints limiting long distance settlement in the Rhodophyta. The dispersal characteristics of *C. tumulosa* spores remain unknown due to the remote location of the PMNM and the biosecurity constraints that prevent the transport of live specimens to the MHI for laboratory studies. Despite this absence of species-specific data, existing literature generally suggests that Rhodophyta exhibit a relatively narrow range of spore dispersal characteristics. Spores are short lived (Hoffman

and Camus 1989), negatively buoyant (Okuda and Neushul 1981; Hoffman and Camus 1989), and attach rapidly to nearby substrata when released (Okuda and Neushul 1981; Fletcher and Callow 1992; Maggs and Callow 2002). The density of red algal tetraspores ranges from 1060–1150 kg/m^3, which is approximately 5–10% denser than seawater, resulting in a sinking rate of 5.95–104.33 µm/s (Okuda and Neushul 1981; Maggs and Callow 2002). These limitations imply there may be major differences in dispersal patterns between macroalgal and animal groups, the latter of which generally exhibit long pelagic larval durations, the capacity to actively swim and to select settlement habitat (Kinlan and Gaines 2003). Instances of long range macroalgal dispersal are regularly missed during field surveys, implying the use of modeling may be advantageous to monitor the spread of macroalgae (Gaylord et al. 2002). Macroalgal dispersal is generally localized, with occasional instances of broader-scale spread occurring less frequently. Migrants are most likely to be exchanged between neighboring populations while the tails of dispersal distribution can be large (Gaylord et al. 2002; Brennan et al. 2014). Stochastic factors complicate global predictions of macroalgal spread, requiring case-by-case studies to accurately assess dispersal patterns. During macroalgal invasion range size typically increases linearly after an initial lag yet range expansion rates can vary between different species in the same region and even within the same species across different regions (Lyons and Scheibling 2009). Modeling of the dispersal of buoyant fragments of *Codium fragile* subsp. *fragile* (Suringar) Hariot 1889 along a straight continental coastline successfully predicted the rate of spread (Gagnon et al. 2015) however the complex physical structure of an archipelago complicates this understanding. Further, increased ocean temperatures have caused an acceleration of spread rates among introduced macroalgae in the Mediterranean basin (Wesselmann et al. 2024) and anthropogenic vectors play a key role in macroalgal spread at regional scales (Lyon and Scheibling 2009).

The Hawaiian archipelago lies in the North Pacific Subtropical Gyre with the islands themselves complicating flow (Lumpkin 1998; Lindo-Atichati et al. 2020). The region is characterized by deep channels and swift-water currents and is rich in both cyclonic and anticyclonic eddies (Lindo-Atichati et al. 2020). The primary direction for inter-island connectivity is towards the northwest with localized complexities driving dispersal towards the southeast and nearer to the MHI (Lumpkin 1998; Firing et al. 1999; Vaz 2012; Lindo-Atichati et al. 2020). Population genetic studies on marine animals as well as oceanographic modeling work align in identifying several breaks in the archipelago with limited biological connectivity. Further, these studies find a break between the central and northern PMNM, placing this barrier immediately to the south of Manawai (Toonen et al. 2011; Selkoe et al. 2014; Wren 2016). Despite several examples using animal models, phylogeographic study of marine macroalgae in the region is limited, and no studies have explicitly modeled macroalgal dispersal. Population genetic work assessing the connectivity of macroalgal groups is limited by the remote nature of the PMNM and slowed by the pace of data generation. *Amansia glomerata* C.Agardh, 1822 and *Asparagopsis taxiformis* (Delile) Trevisan 1845 are exceptions, as phylogeographic studies have assessed connectivity boundaries in Hawai‘i (Sherwood 2008; Sherwood et al. 2011; Fumo and Sherwood 2023). Both species are split into several lineages across the archipelago with F_{st} values in *A. glomerata* generally supporting those barriers identified for animal groups in the MHI (Fumo and Sherwood 2023). The entirety of the PMNM, however, is represented by a single lineage in both cases yet insufficient inter-island sampling in the northern PMNM limits the reliability of F_{st} calculations there.

The recent spread of *C. tumulosa*, the lack of macroalgal comparative examples, and the challenges in holistically assessing connectivity necessitates modeling techniques as a meaningful addition to our integrated understanding of dispersal in the species. The Connectivity Modeling System (CMS) is an individual-based biophysical stochastic lagrangian dispersal simulator (Paris et al. 2013). CMS relies on oceanographic data, particle properties, and flexible user options to estimate connectivity between populations of marine organisms. Though there are several ocean models offering higher spatial and temporal resolution in the MHI, CMS must rely on the globally resolved HYbrid Coordinate Ocean Model (HYCOM), the only available ocean model in the PMNM (Cummings 2005; Cummings and Smedstad 2013; Helber et al. 2013). HYCOM is a 3-dimensional assimilation of oceanographic data incorporating vector velocity, temperature, and salinity at a grid resolution of 1/12 of a degree and depth to 5000 m (Cummings 2005; Cummings and Smedstad 2013; Helber et al. 2013). HYCOM GLBy0.08 data incorporates 10 m wind velocities to calculate wind stress. In Hawai'i, models utilizing HYCOM have been shown to be in agreement with field surveys of coral-dwelling fish and as the basis for dispersal modeling in the deep-dwelling fish *Pristipomoides filamentosus* (Valenciennes, 1830) (Vaz 2012; DeMartini et al. 2013). Drifter deployments validating HYCOM measurements in PMNM have not been conducted due to the protected and restricted status of the area. Global resolution and regional resolution HYCOM in Hawai'i generally agree and dispersal barriers are recovered in both models despite certain features, most notably eddy strength, being misrepresented in the global data (Vaz 2012; Wren et al. 2016). HYCOM temperature and salinity data are used by CMS to calculate grid and time specific densities of seawater through which particles disperse. CMS has been used across ocean basins to understand the dispersal and connectivity of everything from oil spills to fish larvae (Le Corre et al. 2020; Lima et al. 2020; Paris et al. 2020). In Hawai'i, CMS has been used to model *Thunnus albacares* (Bonnaterre, 1788) spawning retention and *Acanthurus triostegus* (Linnaeus, 1758) population connectivity (Vaz 2012; Counsell et al. 2022). Enhancing our comprehension of the dispersal of *C. tumulosa* and identifying dispersal barriers or bottlenecks can be achieved more economically and efficiently by modeling the connectivity of macroalgal populations. This approach serves as a vital first step, while genetic analyses will complement our findings over time. The aim of this study is to investigate the particle and oceanographic properties which may have led to successful dispersal of *C. tumulosa* from Manawai to Kuaihelani.

Methods

Global HYCOM (Cummings 2005; Cummings and Smedstad 2013; Helber et al. 2013) GLBy0.08 temperature, salinity, and vector velocities were acquired for the dates Jan. 1, 2019–Jan. 1, 2023 at 3 h (10800 s) intervals from 177°E-150°W and from 18–30°N, encompassing the entire Hawaiian Archipelago and ~500 km beyond. Vector velocities, salinities, and temperatures were acquired for vertical layers spanning 0–100 m. Global HYCOM is depth resolved to 2 m intervals from 0 to 12 m depth, 5 m intervals to 50 m, and 10 m intervals to 100 m for a total of 20 depth bins. Biologically speaking, it may be possible for *C. tumulosa* fragments or spores to sink below 19 m, survive, vertically advect, and successfully settle. The inclusion of all HYCOM vertical layers to 100 m depth allows this mechanism to occur to ~5× the maximum observed depth of species (Sherwood et al. 2020) while additional coverage beyond the archipelago allows for eddy entrapment

and transport to atolls of interest. All HYCOM downloads were conducted and stored on the University of Hawai'i High Performance Computing (HPC) cluster (https://datascience.hawaii.edu/hpc) using the getdata function from CMS software (Paris et al. 2013).

CMS simulated the release of 100 particles at each 3-hour interval, resulting in a cumulative total of 1,168,900 releases over the duration of the study period. Random release points were sampled from a region centered over Manawai with a latitudinal range of 27.740°N to 27.970°N and longitudes from 176.000°W to 175.700°W. Random particle release locations were selected at 0.001 degree intervals with replacement. Depths were sampled from 1–19 m at 0.1 m intervals with replacement. Release depth, latitude, and longitude were generated in R (R Core Team 2021) and collectively used to create the release file passed to CMS. Particle properties were generated as random numbers by turning on the buoyancy module in CMS. Density of each particle was selected from the range 850 to 1150 kg/m^3 and diameter from 120 μm to 5 m, capturing the feasible range for both tetraspores and rafting fragments (Okuda and Neushul 1981; Brignac et al. 2019; Ribic et al. 2019; Sherwood et al. 2020). Polygons of islands and atolls were extracted using QGIS (QGIS Association http://www.qgis.org) on NOAA bathymetric data (https://www.ncei.noaa.gov/maps/bathymetry/) for the entire Hawaiian Archipelago to create settlement areas at the 25 m depth contour. The selection of a 25 m depth contour allows particles to settle at or near the observed maximum depth in the region. Multiple polygons for a single atoll or island were extracted to account for varied bathymetry. The potential settlement areas for Manawai were not included in the polygon files to allow particles to disperse to other settlement areas without settling on their island of origin. A turbulence was generated for each particle every 3 h (10800 s) at 2.5 m^2/s in the horizontal direction and vertical to 0.001 m^2/s (Okubo 1971). Modules for mortality rate, mass spawning, vertical migration, and stream transport were excluded from CMS to optimize the model for macroalgal dispersal. All parameters entered into CMS are available in Table 1. Particles were considered to have settled if at any point they contacted a settlement polygon or were removed from the simulation by leaving the bounds of the study region or by sinking below 100 m depth. A summary file consisting of the release and settlement locations, particle properties, drift duration and distance, and oceanographic conditions at the time of release was constructed from the raw model output information (Suppl. material 1).

A Generalized Additive Model (GAM) was implemented in R using the mgcv package to determine the impact of relevant variables on settlement success (Wood 2011; R Core Team 2021; Suppl. material 2). Settlement was treated as a binomial response variable with a successful transit to Kuaihelani assigned a positive outcome under the negative log restricted likelihood model. Tested explanatory variables were the two dimensional release position (latitude and longitude), particle density, particle diameter, release depth, and the two dimensional oceanographic condition (current direction and speed at the time of release). Current speed and direction were calculated as the mean of the vector velocities from within the bounds of the release area at the time of release. The mgcv gam.check and concurvity functions were used to ensure convergence, adequate basis function values, normal residual distribution, and the absence of concurvity (Wood 2011). Significance was assessed with the parameter and smooth significance terms of the summary.gam function (Wood 2011). As significance values are approximate, explanatory terms were considered significant only at a threshold of $p < 0.0001$ (Wood 2013a, b). Partial effect plotting was conducted in R using the plot.gam function on a probability scale with intercept offset.

Table 1. Parameters used in the Connectivity Modeling System.

	General model	Tetraspores only	Fragments only
Release number	1,168,900	116,890	116,890
Release rate	100 particles per time step	10 particles per time step	10 particles per time step
Particle size	120 µm–5 m	120–185 µm	1 cm–5 m
Particle density	850–1150 kg/m^3	1060–1150 kg/m^3	850–1010 kg/m^3
Release latitude	27.740–27.970°N	27.740–27.970°N	27.740–27.970°N
Release longitude	176.000–175.700°W	176.000–175.700°W	176.000–175.700°W
Release depth	1–19 m	1–19 m	1–19 m
Settlement polygons	25 m depth contour	25 m depth contour	25 m depth contour
Horizontal diffusivity	2.5 m/s^2	2.5 m/s^2	2.5 m/s^2
Vertical diffusivity	0.5 m/s^2	0.5 m/s^2	0.5 m/s^2
Time step	10800 s	10800 s	10800 s

Further CMS modeling runs focused more specifically on tetraspore and fragment dispersal in order to compare the number of successful settlements directly under an equal number of releases in each case. Modifications to the parameters used for the general CMS model were necessary. Tetraspore density was restricted to 1060–1150 kg/m^3 (Okuda and Neushul 1981) and diameter to 120–185 µm (Sherwood et al. 2020). Rafting fragments were restricted to 1 cm–5 m (Ribic et al. 2012; Brignac et al. 2019) and to 850–1010 kg/m^3, ensuring positive buoyancy and consistent with the finding that 91% of marine debris on Kuaihelani's Sand Island is plastic (Ribic et al. 2012). Tetraspore and fragment modeling runs released 10 particles at 3 h intervals for a total of 116,890 releases each (Table 1). The number of successful landings at each settlement area for rafting fragments and tetraspores was assessed and plotted in R (R Core Team 2021).

Results

Of the 1,168,900 particles released from Manawai in the general model, 23,989 (2.05%) successfully settled at Kuaihelani. Settlement success of a particle at Kuaihelani was functionally linked to its density ($p < 0.0001$), the direction and strength of the currents at the time of release ($p < 0.0001$), and the location of release ($p < 0.0001$), according to the implemented GAM (Suppl. material 3). Particle diameter ($p = 0.6$) and release depth ($p = 1.0$) were not functionally important for settlement success. Particle density ranging from 850–1010 kg/m^3 exhibited increased likelihood of settlement and a peak in settlement probability at 1010 kg/m^3. Particles denser than 1020 kg/m^3 had a lower likelihood of successful settlement with a steep transition in settlement success between more and less dense particles (Fig. 1A). Successful particle settlement is tied to the direction and intensity of ocean currents at the moment of release. Higher success rates are observed when particles were directed toward Kuaihelani, while success diminishes as the direction deviates further from a near-direct trajectory especially when faced with swifter ocean currents (Fig. 1B). Settlement success was relatively low when the release direction was east (90°) or nearly so. The maximum likelihood of settlement occurred when current heading was 299° (~NW), just north of the direct heading from Manawai to Kuaihelani (283 degrees). The headings ~200° and ~250° also exhibited peaks in settlement probability (Fig. 1B). Release position was most favorable for settlement from the north-central portion of the atoll with less favorable locations

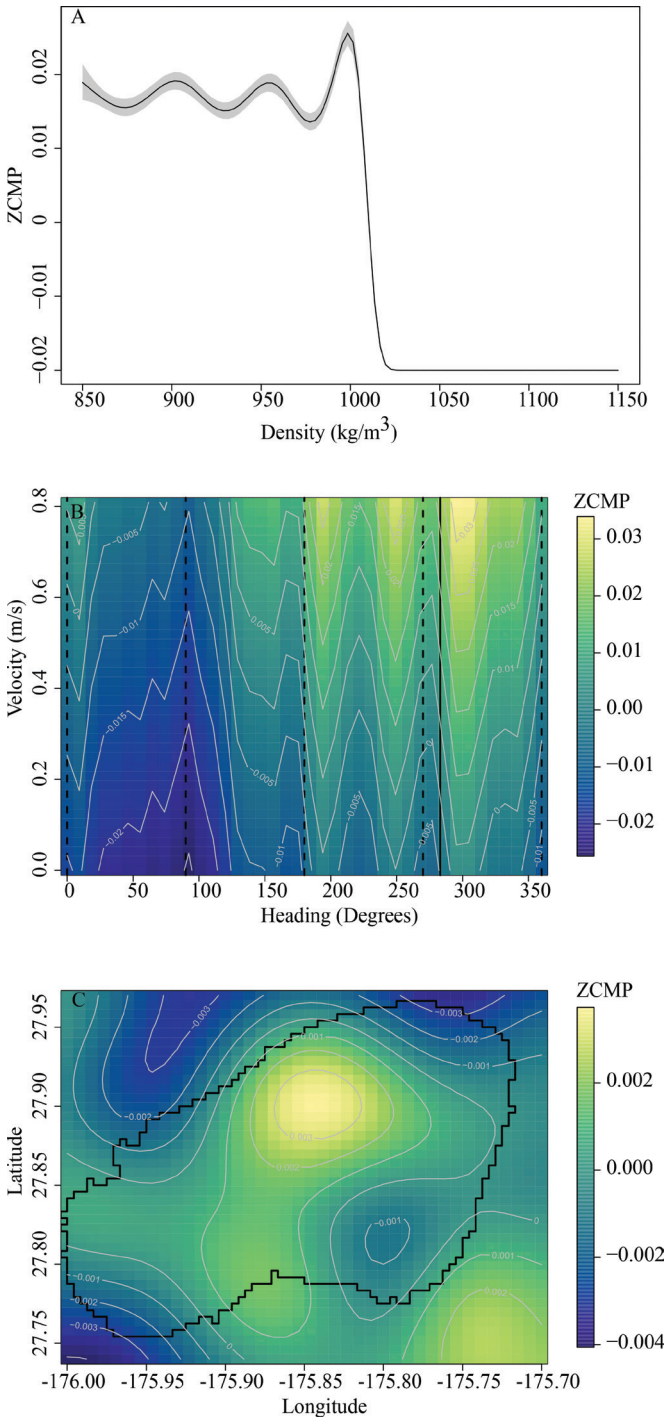

Figure 1. Generalized Additive Model (GAM) summary plots showing the zero-centered model predictions (ZCMP) for significant smooth terms. In panel (**A**) lower density is linked to higher settlement probability. Interactive effects of related terms as a contour are displayed for current velocity and direction (**B**) and release location (**C**). Dashed vertical lines in panel **B** represent the cardinal directions (N, E, S, W) and the solid vertical line represents the direct heading from Manawai to Kuaihelani (283 degrees). The black outline in panel (**C**) represents the 19 m depth contour of Manawai. The ZCMP are represented by the y-axis in (**A**) and by the color scale bars in (**B, C**).

including the southwestern and northern ends of the release area. Differences in explanatory variable partial effect size for release location showed a relationship to successful settlement that was an order of magnitude lower than those of density and ocean currents (Fig. 1).

Targeted model runs revealed that tetraspores released from Manawai successfully settled at Kuaihelani at a lower rate (0.02%) than rafting fragments (3.85%). None of the successful tetraspores (n = 29) settling at Kuaihelani did so within the observed depth range of the species. The percentage of tetraspores sinking below 100 m and 19 m after 5 days was 64.5% and 99.9%, respectively. Drift duration of successfully settling tetraspores ranged from 8.3 to 40.4 days. The same number of rafting fragments released from Manawai (n = 116,890) yielded 4,495 successful landings (Fig. 2). Both the tetraspore and fragment models yielded landings beyond Kuaihelani to the northwest at Hōlanikū (n = 1 and 2220, respectively) and to the southeast at Kapou (n = 2 and 2452). Fragments successfully settled further southeast than tetraspores, reaching Kamole (n = 98), Kamokuokamohoali'i (n = 264), and 'Ōnūnui/'Ōnūiki (n = 16) during the study period (Fig. 2). The timing of arrival for tetraspores was restricted to several months in the spring and summer of 2021 while rafting fragments released from Manawai successfully settled at Kuaihelani throughout the study period (Fig. 3; Suppl. materials 4, 5).

Discussion

Overall, the particles most likely to successfully settle at Kuaihelani from Manawai are those with a density of less than 1010 kg/m^3 released from the north-central portion of the atoll while swift northwest-bound currents occur over the release area. Particles with low densities drift for extended periods along the surface of the ocean while dense particles sink rapidly out of the modeled region. An apparent peak in dispersal likelihood at a density of ~1010 kg/m^3 may be related to an avoidance of surface entrapment while sinking slowly enough to avoid export from the modeled region and a corresponding improvement in along-wind and cross-wind dispersion (Thoman et al. 2021). Particles with very low densities experience a reduction in dispersal capability due to an increased exposure to surface turbulence, while those with high densities sink rapidly out of the surface ocean (Thoman et al. 2021). Increased settlement probability in multiple bands centered around ~200°, 250°, and 300° may be driven by eddy entrainment and subsequent transport. The Hawaiian Archipelago is a region of high eddy activity with higher latitude eddies tending to be long lived, low amplitude, westward propagating, and predominantly anticyclonic (Lindo-Atichati et al. 2020). A westward propagating long lived anticyclonic eddy would transport particles initially towards the northwest with subsequent eddy entrainment then driving particles towards the target destination, explaining the peak in settlement probability that is slightly more northwest than the direct heading from Manawai to Kuaihelani. Higher vector velocities allow denser particles to travel farther before sinking out of the modeled region. The release location with the highest likelihood for settlement is the north-central portion of the atoll. Targeted marine debris removal should focus on this region which exhibits the highest likelihood for exporting particles that will successfully transit to other atolls. The distribution of *C. tumulosa* is not restricted to the forereef and backreef of Manawai but extends into the central atoll where densities can be high. HYCOM does not resolve the islands of the PMNM, however, and the polygons provided to CMS do not include Manawai, which includes shallow water regions surrounding the central portion of the atoll and even several small islands. The ability of particles to escape the central portion of the atoll may therefore be over represented in this study. Further, despite the apparent peak in settlement probability from the central portion of the atoll, the effect on success is an order of magnitude less than both particle density and currents at the time of release. Nevertheless, this study demonstrates that the capacity to disperse from

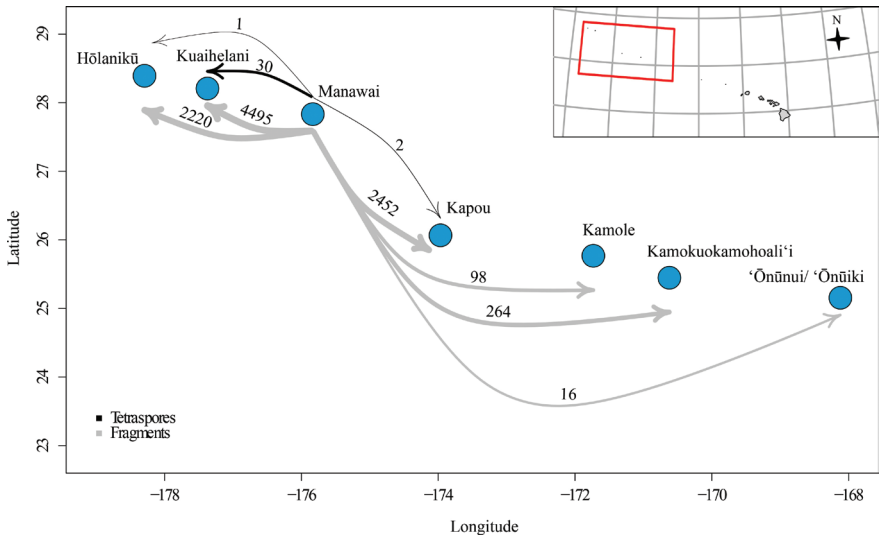

Figure 2. Total number of successfully settled particles released from Manawai. Islands are represented as blue dots with tetraspores shown above in black and fragments below in gray. Arrow width and associated numbers correspond to the number of successful settlements from Manawai to the settlement location of interest. The red box in the inset map in the top right corner shows the location of the study region with respect to the remainder of the Hawaiian Archipelago.

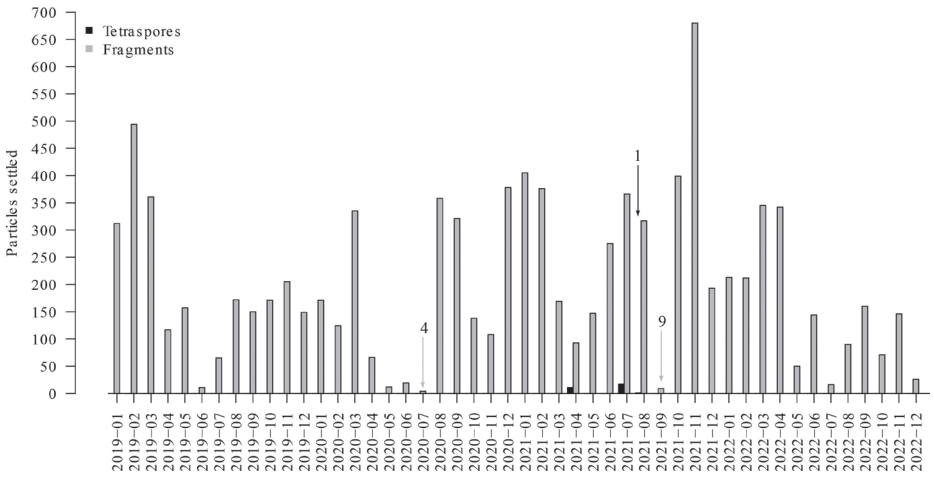

Figure 3. Number of successful landings of tetraspores and fragments released from Manawai and settling at Kuaihelani by month throughout the study period. All non-zero monthly settlement totals below 10 are labeled directly and the indicating arrow is colored by particle type.

Manawai to Kuaihelani is linked largely to particle density as well as the oceanographic conditions at the time of release.

Tetraspores exist in a narrow range of physical properties in comparison to the range of particles included in the general model. While the particles are putatively negatively buoyant, with a density range of 1060–1150 kg/m^3 (Okuda and Neushul 1981), CMS indicated that tetraspores can still disperse to Kuaihelani, albeit with limited efficacy (Figs 2, 3). The range of depths at which tetraspores arrive at Kuaihelani (50–89 m) is deeper than the 19 m depth limit of the species (Sherwood et al. 2020). Though these particles settle below the depth limit, they may still manage to survive. As HYCOM does not consider the presence of islands in PMNM there may be small scale processes in near-shore regions allowing upward recruitment while approaching islands (Cummings 2005; Vroom and Braun 2010; Cummings and Smedstad 2013; Helber et al. 2013).

The detectability of the species beyond the current depth limit may be constrained due to the cryptic nature of *C. tumulosa* in specific locations, the challenges posed by the remote nature of the islands, and the ongoing uncertainty regarding the abiotic or biotic factors influencing the depth limit of the species. Thus the depth at which tetraspores can survive may not be constrained to 19 m, increasing their likelihood of surviving transit to Kuaihelani.

Fragments were modeled identically to tetraspores with the exception of particle diameter and density, which were chosen to include a range of flotsam objects such as rafting mats, other macroalgae and marine debris, as these objects may aid in dispersal of marine organisms (Martinez et al. 2007; Carlton et al. 2018; Brignac et al. 2019). The successful settlement rate to Kuaihelani (3.85%) for these particles is two orders of magnitude greater than that of tetraspores (0.03%). The divergences between tetraspore and fragment settlement potential are driven by the difference in density between modeled particles as denser particles sink out of the surface ocean rapidly while rafting fragments remain in the system until leaving the modeled region. Further, upon settlement, rafting fragments are likely to survive at higher rates than their tetraspore counterparts and initiate additional spread more rapidly, as tetraspores must settle in suitable habitat and grow to a sufficiently large size prior to fragmentation or tetraspore development (Fletcher and Callow 1992; Maggs and Callow 2002).

In both the tetraspore and fragment model runs, landings occurred beyond Kuaihelani with the two mechanisms exhibiting substantial divergences in maximum colonized distance. Fragments reached as far south as ʻŌnūnui/ ʻŌnūiki, ~600 km further than Kapou, the maximum extent of modeled tetraspore landings. The channel between Manawai and Kapou is considered a strong break point for the dispersal of marine organisms in the Hawaiian Archipelago and is reflected in both studies on oceanographic connectivity and population genetics (Toonen et al. 2011; Vaz 2012; Selkoe et al. 2014; Wren 2016). However, this study suggests substantial amounts of flotsam traversing this boundary. Early Detection and Rapid Response (EDRR) efforts should be concentrated on the windward (northeastern) sides of the islands, specifically from Kapou to ʻŌnūnui/ʻŌnūiki, to enhance the effectiveness of these surveys. Further population genetic work assessing the strength of the barriers outlined by Toonen et al. (2011) remains essential for comparing macroalgal dispersal to that of animal groups (Fumo and Sherwood 2023). The modeled number of landings on Kapou is concerning in that available studies of animal groups suggest the islands of the central PMNM are well mixed (Toonen et al. 2011; Vaz 2012). Should *C. tumulosa* settle on Kapou it may be capable of dispersing more readily to the southeast and towards the Main Hawaiian Islands. Extreme events such as tsunami-driven rafting may be capable of dispersing the species far beyond the suggested extent in these model runs (Carlton et al. 2018; McCuller et al. 2018; Ta et al. 2018).

While unable to unequivocally explain the dispersal of *C. tumulosa* in the PMNM, modeling provides a useful, timely, and economically feasible addition to our holistic understanding of this species of growing concern. Management actions suggested by these findings include the continuation of marine debris removal efforts especially in the north-central portion of Manawai, directing future aquatic invasive species monitoring surveys and eDNA work towards potential landing destinations, namely the windward (northeastern) sides of the atolls between and including Kapou and ʻŌnūnui/ʻŌnūiki, and rigorously testing the dispersal potential of both native and invasive macroalgae, especially *C. tumulosa*. Although other algal outbreaks have been observed in PMNM these have been short lived and are not considered to have been

invasive (Vroom et al. 2009; Tsuda et al. 2015). Algal introductions in the MHI, in contrast, are numerous and are associated with coral overgrowth that facilitates a phase shift towards algal dominance, leading to a loss of biodiversity through shifts in community structure (Smith et al. 2002). As the Hawaiian archipelago has a robust history of algal invasions causing damage to nearshore reefs it is of great importance to limit the spread of *C. tumulosa* and prevent its introduction to the MHI.

Authors' contribution

All authors conceptualized the research, assisted in study design and methodology, interpreted results, and reviewed and edited the manuscript. J.T.F. conducted the investigation, data collection, data analysis, and wrote the original draft.

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Data availability statement

The datasets generated and analyzed in the current study, along with the R scripts and statistical model outputs, are included in the supplementary material of this paper. For further inquiries or additional data requests, please contact the corresponding author.

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Supplementary material 1

Summary data frame

Authors: James T. Fumo, Brian S. Powell, Randall K. Kosaki, Alison R. Sherwood

Data type: txt

Explanation note: Summary data frame in .csv format consisting of the release and settlement locations, particle properties, drift duration and distance, and oceanographic conditions at the time of release constructed from the raw CMS model output information.

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Link: https://doi.org/10.3391/ai.2024.19.3.135377.suppl1

Supplementary material 2

R script implemented using S1 to produce S3

Authors: James T. Fumo, Brian S. Powell, Randall K. Kosaki, Alison R. Sherwood
Data type: R file
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Link: https://doi.org/10.3391/ai.2024.19.3.135377.suppl2

Supplementary material 3

Raw output statistics from the summary(), concurvity(), and gam.check() functions in R on the Generalized Additive Model (GAM) implemented in R using the mgcv package

Authors: James T. Fumo, Brian S. Powell, Randall K. Kosaki, Alison R. Sherwood
Data type: docx
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Supplementary material 4

Raw connectivity output file resulting from a targeted CMS run releasing tetraspores from Manawai

Authors: James T. Fumo, Brian S. Powell, Randall K. Kosaki, Alison R. Sherwood
Data type: cms
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Supplementary material 5

Raw connectivity output file resulting from a targeted CMS run releasing rafting fragments from Manawai

Authors: James T. Fumo, Brian S. Powell, Randall K. Kosaki, Alison R. Sherwood
Data type: cms
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