Coral Reefs
https://doi.org/10.1007/s00338-025-02712-y

RESEARCH

Depth affects the population dynamics on a soft coral-dominated reef on the Great White Wall, Fiji

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Received: 2 November 2024 / Accepted: 5 July 2025

Abstract Soft corals (order Alcyonacea) are an important component of tropical coral reefs, and often form locally abundance dense carpets. Some soft coral species are prone to bleaching and heat stress like scleractinian, reef-forming corals, but others appear resistant to bleaching stressors. Despite the importance of soft corals in tropical reefs, there is limited knowledge regarding their demographic ecology. Spatial point process analysis (SPPA) enables inference of ecological processes underlying spatial distributions of individuals in a community by investigating the fit of models of known processes to observed spatial patterns. SPPA can also quantify how these underlying ecological processes change with environmental gradients (such as depth). We used SPPA to investigate the population ecology on the Great White Wall (GWW), Fiji—a vertical reef dominated by Nephtheidae soft corals alongside other filter feeders and algae. We found that a combination of reproductive and habitat association processes best explained the spatial patterns on the GWW. We found that the best-fit underlying ecological processes changed with depth, and that Nephtheidae soft corals became more dominant on deeper parts of the wall, likely due to a combination of reproductive lability, fast growth rates, and increasing suitable habitat associated with filter-feeding. Even where the Nephtheidae were most dominant, other filter feeders were able to persist. This mixed community composition could be because the Nephtheidae feed in periods of high current, and temporal niche partitioning in feeding could be permitting biodiversity on the GWW, allowing for hydroids and sponges to coexist with the Nephtheidae.

Keywords Soft coral · Spatial analysis · Population ecology · Trophic niche · Reproductive ecology

Introduction

Tropical coral reefs are major contributors to marine biodiversity (Roberts et al. 2002), and provide economically important ecosystem services, such as reducing wave action and erosion, tsunami protection, ecotourism, and subsistence fishing (Costanza et al. 2014). Tropical coral reefs are experiencing dramatic ecological collapses due to anthropogenic climate change (via increased storm frequency, ocean warming, and acidification), destructive fishing techniques, and overharvesting, leading to a decline in hard coral populations, and consequentially, those ecosystem services provided by hard corals (Hughes et al. 2017, 2018; Reimer et al. 2024). A major component of the benthic community within tropical coral reefs are the soft corals (order Alcyonacea) (Maucieri and Baum 2021; Putnam et al. 2017)—soft bodied octocorals with an internal skeleton composed of sclerites (Fabricius and Alderslade 2001). Similarly to hard corals, soft corals are primary consumers (Corry et al. 2018), promoting biodiversity via mutualistic benefits to a range of species (Lalas et al. 2024), produce economically important

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00338-025-02712-y.

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biocompounds (Conte et al. 2020), and support fish biodiversity (Epstein and Kingsford 2019). In contrast to hard corals, some soft coral taxa, such as those in the family Nephtheidae, retract when not feeding (Hellström and Benzie 2011) and so do not provide the same coastline protection via disruption of wave action. However, certain soft coral taxa (e.g., *Sclerophytum, Lobophytum,* and *Sarcophyton*) are resistant to many of the stressors prevalent in the decline of hard coral reefs, such as pollution and sedimentation (McClanahan and Obura 1997; Lalas et al. 2024;although see Larkin et al. 2021), temperature-related bleaching (e.g., *Veretillum*) (Coffroth et al. 2023; Lopes et al. 2018), ocean acidification (e.g., *Sarcophyton*) (Inoue et al. 2013), and storm damage (Lalas et al. 2023; Lasker et al. 2020). This resistance has led to persistence or even dominance of soft corals in some areas where hard corals are declining (Bastidas et al. 2004; Fox et al. 2003; Lalas et al. 2024; Ruzicka et al. 2013). Conversely, some soft coral populations bleach and experience population declines congruent with those of hard corals in response to climate change (Larkin et al. 2021, 2024; Madin et al. 2018; Maucieri and Baum 2021).

Some soft coral species have been designated as invasive or range shifters in the Atlantic (Lolis et al. 2023), Caribbean (Toledo-Rodriguez et al. 2025), and recently in the Mediterranean Sea (Shlesinger et al. 2024). This designation is due to rapid substrate colonisation arising from fast growth rates (particularly in nephtheids and xeniids) (Benayahu and Loya 1977; Fabricius 1995), high competitive capacity through allelopathy, removal via colony migration permitting overgrowth of hard corals (Fabricius 1995; Sammarco 1985), and lability of reproductive mode (Bastidas et al. 2004). Therefore, soft coral-dominated communities have the potential to be an end point of phase-shifts for tropical coral reefs as hard corals decline due to anthropogenic stressors which soft corals can tolerate, leading to potential domination of soft corals in some reef communities (Graham et al. 2013; Inoue et al. 2013; Roff and Mumby 2012). However, soft coral reefs would likely provide a different set of ecosystem services compared to hard corals (Lalas et al. 2023). It is therefore important to understand underlying ecological processes contributing to soft coral demographic ecology in areas where they are dominant in order to inform conservation and management strategies for tropical coral reefs.

The demographic ecology of sessile organisms can be determined through analyses of the spatial pattern of individuals in a population. The spatial patterns of organisms within communities reflects underlying ecological processes that have occurred throughout an organisms' life. Four sets of processes are known to determine the patterns of sessile organisms: (1) interactions with the environment; (2) reproductive processes; (3) interactions within and between species (e.g., competition, facilitation); and (4) density-dependent mortality processes (Illian et al. 2008; Wiegand and Moloney 2014). Spatial point process analysis (SPPA) is the analysis of patterns of points (here, each representing a single organism), revealing the most likely ecological processes underpinning the observed spatial pattern. For instance, reproductive aggregations can be modelled by Thomas cluster (TC) processes (Thomas 1949), while aggregations due to associations with local habitat heterogeneities by heterogeneous Poisson (HP) processes (Wiegand and Moloney 2014). SPPA has been used to reveal mortality processes (Gibbs and Hay 2015), habitat interactions (Hu et al. 2020), and competition (Muko et al. 2014) in hard coral communities, as well as density-dependent mortality processes and facilitation in deep-sea soft corals (Mitchell and Harris 2020), and reproductive aggregations in gorgonians (Gori et al. 2011; Prado et al. 2019). However, SPPA has not, to our knowledge, been applied to tropical soft corals to date. Within the SPPA framework, spatial patterns are summarised using distance measures, which describe how patterns change over different spatial scales, enabling comparison to known models and thus the inference of underlying processes (Illian et al. 2008).

Underlying ecological processes that determine the spatial patterns of sessile organisms are likely to change in response to environmental gradients. Depth in the water column represents one such gradient; in shallow areas, planktonic food particles may be more limited relative to light and so transitions in dominance from photosynthesisers to filter feeders are expected with increasing depth (Lesser 2006; López-Londoño et al. 2022). Suspended food is associated with current speed, and both current speed and light availability are associated with habitat features such as topography and environmental complexity (Lesser et al. 2021). Therefore, habitat preferences (modelled by HP processes) are likely to be important where food and light availability are underlying drivers of spatial patterns. Conversely, in environments where these resources are not limiting, and density-dependent mortality is therefore weaker (Jacquemyn et al. 2010), spatial patterns may be influenced by reproductive processes because organisms can allocate more resources towards reproduction, leading to the dominance of reproductive cluster patterns in sessile taxa (modelled by TC processes) (Wiegand and Moloney 2014). The power in SPPA lies in being able to test the fit of observed patterns to patterns generated by known underlying processes (McFadden et al. 2019; Mitchell et al. 2019; Mitchell and Harris 2020; Wiegand and Moloney 2014). In this study, we applied SPPA to populations of soft corals, sponges, hydroids, hard corals, and algae on the Great White Wall (GWW) in Fiji, a vertical wall reef in the Somosomo Strait. The GWW was chosen because it contains a large, locally-dominant population of Nephtheidae soft corals, making it ideal to describe the ecological processes of these soft corals alongside the other taxa in this community.

Methods

Field site

In this study, we focussed on the GWW, a vertical section of a barrier reef in the southwest of the Somosomo Strait which runs between Vanua Levu and Taveuni Islands, Fiji (Fig. 1a), and is dominated by white Nephtheidae soft corals that give the site its name. The GWW is the ideal site to try to understand soft coral population dynamics because it is a well-known, accessible reef with high densities of soft corals within safe diving limits. We accessed the site by scuba diving and used video to map between the top of the wall at 17 m to a depth of 33.5 m. Alongside, the white Nephtheidae soft corals, other abundant morphospecies were a species of colonial hydroid (visually similar to *Myriopathes*), lemon sponges (*Leucetta chagosensis*), colourful *Dendronephthya* soft corals, algae (possibly *Halimeda* spp.), and

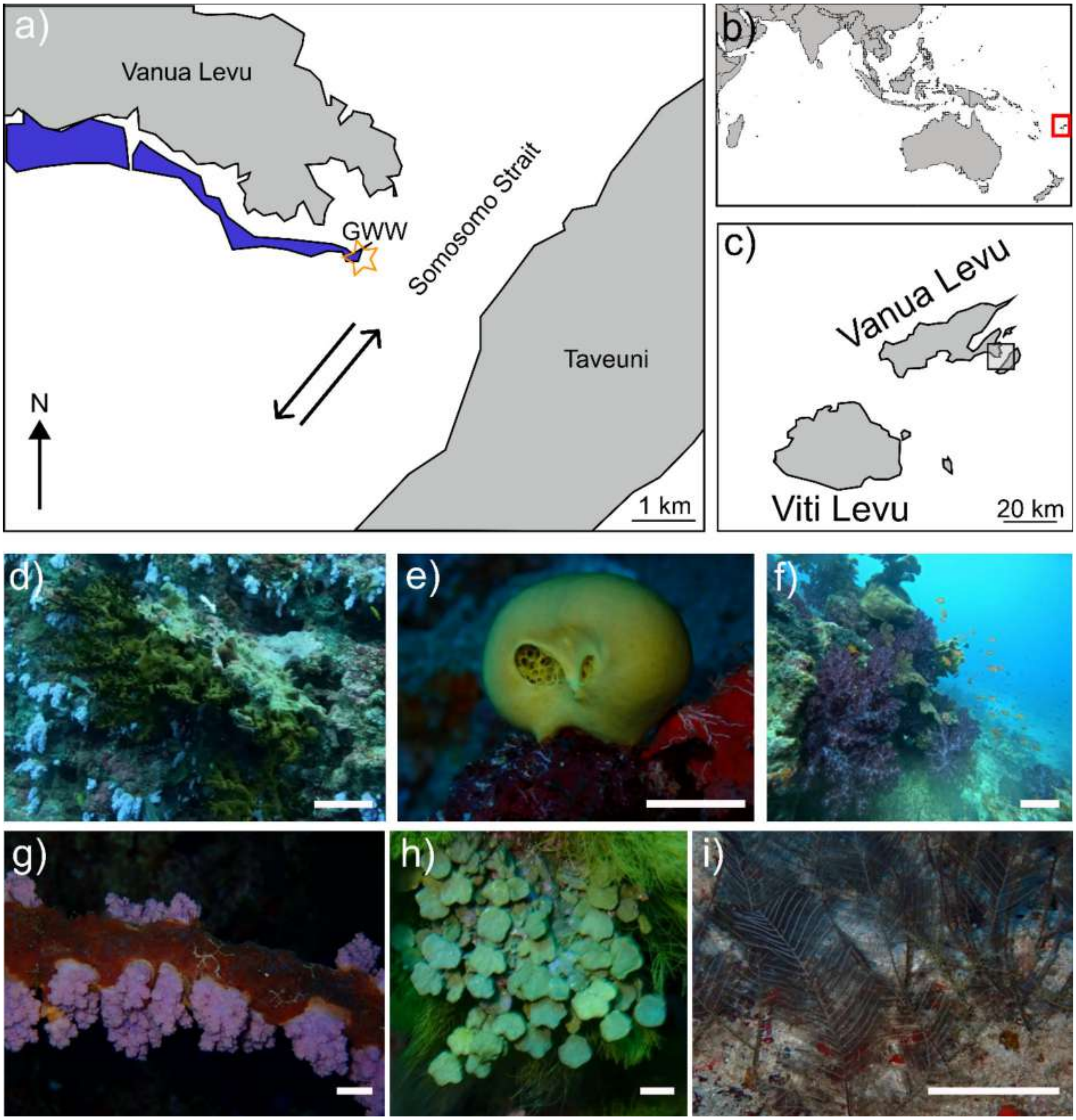

Fig. 1 **a** Location of the Great White Wall (GWW; orange star). **b** zoomed out map of Vanua Levu and Viti Levu islands, Fiji, and **c** broader geographical context of Fiji. Arrows in **a** indicate current direction depending on tides. Blue area indicates barrier reef. **d** Tubastraea on the GWW, **e** Lemon sponge, **f** *Dendronephthya*, **g** white Nephtheidae on the GWW, **h** algae, **i** hydroid colonies. Scale bars for e, **g**, **h**, and **i** ~ 1 cm; scale bars for **d** and **f** ~ 10 cm.

adult *Tubastraea* sp. (an azooxanthellate hexacoral with a hard skeleton) (Fig. 1b–g). All these morphospecies except the algae are filter feeders. Further taxa were found within the study area but not in sufficient abundance ($n < 100$) for the analyses used in this study included: endolithic sponges (*Siphonodictyon maldiviense*), alongside *Stylissa* and *Calyspongia* sponges; *Sarcophyton* sp., *Cladiella* sp., and *Chironephthya* spp. (soft corals), *Acropora* spp. (branching and tabulate), *Pocillopora* spp., *Mussidae* sp., and *Plerogyra* sp. (hard corals), Ellisellidids (whip gorgonians and sea fans) (possibly *Annela, Melithaea, Subergorgia,* and *Acanthogorgia*) as representatives of Cnidaria; *Polyandrocarpa* and *Didemnum* (tunicates); and *Anneissia* (crinoids). In this study, we identified organisms to a morphospecies level due to the high level of cryptic diversity present in soft corals (McFadden et al. 2022; Otis et al. 2024), and because collection of biological materials to aid finer resolution identification was not possible.

Data collection

We used structure-from-motion photogrammetry derived from video footage of the GWW in Agisoft Metashape (v2.1.1) to reconstruct the GWW community following (Mitchell and Harris 2020):

1. Video footage comprising 20 videos (total length = 4251 s, mean length ± standard deviation = 236.2 s ± 245.8 s, resolution = 120 frames/second) and photographs (64 images) were collected by scuba divers moving in a boustrophedonic, lawnmower pattern from the deepest section to the top of the wall. Footage could only be collected in periods of low current.
2. Video footage was segmented at a capture rate of 1 frame/second using ffmpeg (*cf* Mitchell and Harris 2020) yielding a total of 4,348 frames.
3. Blurred, obstructed, and out of focus frames (17%, 747 frames) were removed, then remaining photos (3,601 frames) were imported into Agisoft Metashape.
4. Photos were aligned to form a point cloud, which was then used to produce a 3D model from resultant depth maps.
5. The model was scaled using a combination of spaced laser dots projected by divers during video capture and objects of known size captured in footage.
6. A 2D orthomosaic (photomap; Fig. 2a) was then produced and exported into vector software Inkscape (v 1.3.2).
7. Individual organisms were outlined and identified on the 2D map to a morphospecies level, using visual anatomical characters as identifiers (e.g., colour, shape), and IDs were checked using original video footage. We only marked up to morphospecies level and were as conservative as possible with IDs due to the known widespread cryptic diversity in colonial cnidaria in the Indo-Pacific (McFadden et al. 2022).
8. The marked-up map was then extracted using a custom script in R (https://github.com/nis38/GWW_pop_ecol, adapted from Delahooke et al. (2024) resulting in a final digital dataset of the spatial position and morphospecies ID for each specimen on the GWW.

In order to investigate if morphospecies were responding to broad-scale background topography, we constructed a digital elevation model (DEM) from the 3D mesh recovered in Agisoft Metashape (step 4 above). To make this DEM, we decimated the mesh in GeoMagic Wrap (v2021) to 1% of the original points which was a level which balanced resolution with computational speed for generating the mesh. We then smoothed the mesh in order to remove any topography caused by the corals themselves, visually assessing where corals were still visible. We then imported the mesh into Agisoft Metashape and produced a DEM, which reflected the coarse (decimetre-scale) topography of the GWW.

Because our DEM of the GWW also contained information on the overall (global) curvature of the wall, but we were interested in topographic changes over a smaller spatial scale, we removed this global curvature by subtracting a smoothed image, created by aggregating the original image by a factor of 500 followed by gaussian smoothing (kernel bandwidth = 2) in the package SpatialEco (*cf* Evans 2023) in R (v4.3.2) (R Core Team 2023). This process generated a height map of the GWW with the global curvature removed, preserving only the finer 3D topological structure (e.g., shallow caves and crevices), as this smaller-scale topology may be influencing the population dynamics of the morphospecies present (Fig. 2b).

Broad ecological patterns on the GWW

In order to assess broad ecological patterns in the GWW community, we used Berman–Lawson–Waller (Berman 1986; Lawson 1993; Waller et al. 1992) tests to investigate the relationship between depth and density for all organisms collectively and for morphospecies individually. Berman–Lawson–Waller tests consider the null hypothesis that density of a point process (e.g., corals) is constant against an alternative hypothesis that the density depends on a specified covariate (here, depth), and assumes a Poisson process with density (Baddeley 2015; Berman 1986). Accordingly, we used this test to compare heterogeneous Poisson models with depth as a predictor against a null model.

We did not conduct any size-based analyses because Nephtheidae soft corals change size with respect to current (Hellström and Benzie 2011), so accurate size measures

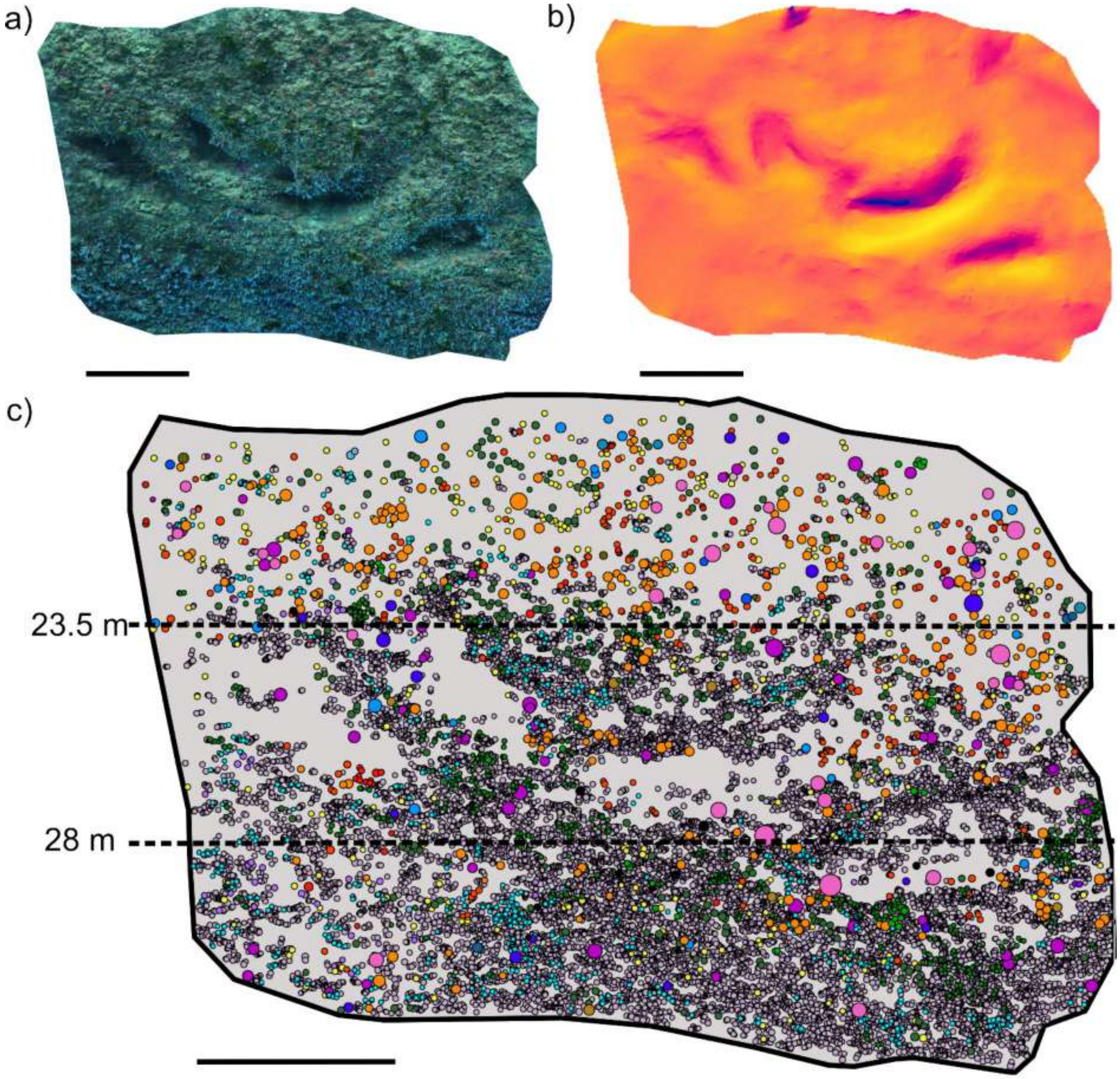

Fig. 2 . **a** Orthomosaic of the Great White Wall (GWW; Fig S1. Higher resolution map); **b** Digital elevation model of the GWW produced from a smoothed and decimated orthomosaic; **c** specimen map of the GWW. Colour of point indicates morphospecies (lilac = white Nephtheidae, yellow = lemon sponges, purples = sea fans; pink = endolithic sponges, light blue = hydroids, dark green = algae, oranges = other sponges, dark blues = scleractinian corals (including *Tubastraea*), browns = crinoids, reds = other soft corals (including *Dendronephthya*), grey = other, rare morphospecies (including singletons)). Scale bars = 5 m. Note that we changed the size of the circles to aid with visibility and so the circles are not to scale.

for soft coral colonies from videos of the GWW were not possible.

Univariate spatial analysis of common morphospecies

In this study, we investigated the population ecology of the six abundant morphospecies on the GWW by means of univariate spatial point process analyses (SPPA). To do this, we used the pair correlation function (PCF) distance measure to investigate model fits between the observed point pattern of each taxon against known spatial patterns. PCFs represent how the density of points (i.e., corals) at a given distance r from a given point change as a function of distance from that point. While inferring these processes from patterns is difficult because of the possible superposition of multiple processes (i.e., the overlaying of intra- and interspecific interactions or variable environmental preferences) and equifinality (where different processes generate similar spatial patterns) (Brown et al. 2011; May et al. 2015; Wiegand and Moloney 2014), the application of complimentary statistical techniques can disentangle processes underpinning different ecological patterns, particularly across differing spatial scales (May et al. 2015; Mitchell et al. 2015; Wiegand and Moloney 2014).

The simplest spatial pattern is that of complete spatial randomness (CSR), which can be modelled as a homogeneous Poisson process (Illian et al. 2008). A CSR pattern ($PCF = 1$) would reflect that no biotic or abiotic interactions are observed at the spatial scales considered (Illian et al. 2008; Velázquez et al. 2016). In the case where spatial patterns are non-CSR, they can be aggregated ($PCF > 1$) or segregated ($PCF < 1$), and these patterns can be detected at a range of spatial scales (Illian et al. 2008). Aggregation within a population can be caused by habitat associations, whereby organisms cluster within an area of preferable resources (*cf* Shen et al. 2009; Mitchell et al. 2020), by the spatial positioning of reproductive offspring yielded by dispersal-limited processes (*cf* Mitchell et al. 2015; Jácome-Flores et al., 2016; McFadden et al. 2019; Mitchell and Harris 2020), or by both processes (Velázquez et al. 2016; Wiegand and Moloney 2014). Habitat-associated aggregation processes can be modelled by heterogeneous Poisson (HP) processes (Wiegand and Moloney 2014), whereas reproductive aggregation can be modelled by single or double Thomas cluster (TC) processes (representing two or three generations, respectively) (Mitchell et al. 2015; Thomas 1949; Wiegand and Moloney 2014). Reproductive- and habitat-associated processes combined would thus be best modelled by Thomas clustering processes over a heterogeneous background—inhomogeneous Thomas clusters (ITC) (Illian et al. 2008), whereas reproductive processes alone would be modelled on a homogeneous background (TC). Segregation within a population can be caused by intraspecific resource competition whereby individuals that are too close to each other incur mortality as a consequence of obtaining fewer resources in patches of higher density (Gray and He 2009; Raventós et al. 2010). Density-dependent processes, such as disease dynamics, can also generate density-dependent mortality (Janzen-Connell processes (Brown et al. 2011; Connell 1970; Janzen 1970)), and can be detected with a record of recently dead organisms within a population, which were not observed on the GWW (in contrast to other benthic systems, e.g., (Mitchell and Harris 2020)). Model-fitting techniques are then used to assess the most likely underlying processes (Diggle 2003; Loosmore and Ford 2006; Wiegand and Moloney 2014).

SPPA were performed in R (v4.3.2) using the spatial analysis package spatstat (Baddeley 2015, 2024). In order to investigate the effect of depth on population dynamics of the white Nephtheidae, hydroids, lemon sponges, algae, *Tubastraea*, and *Dendronephthya*, we divided our study area into three depth bins: shallow (17–23.5 m), intermediate (23.5–28 m), and deep (28–33.5 m). Division by depth bins was dictated by variation in the topography of the GWW; the intermediate depth bin contains four shallow caves (Fig. 2), which are areas that interact with fluid flow (and thus food availability) and light availability, whereas these caves were absent from shallow and deep depth bins. The following analyses were performed on all abundant ($n > 100$) morphospecies at each depth bin resulting in white Nephtheidae, lemon sponges ($n = 94$ for intermediate), hydroids, and algae at all depth bins, and *Dendronephthya* and *Tubastraea* in the shallow depth bin only.

CSR and HP models were fitted by maximum likelihood because these models are tractable for use of a Poisson process with constant intensity (Baddeley 2015; Baddeley and Turner 2000), whereas TC and ITC models were fitted by minimum contrast because these methods can account for inter-point interactions (Baddeley 2015; Diggle and Gratton 1984). To test whether a morphospecies' PCF was best fit to a given theoretical model PCF, 9,984 Monte Carlo simulations were run for CSR, TC, HP, and ITC processes, and the simulation envelopes chosen to be between the 5% highest and lowest values (Baddeley 2015). 9984 (rather than 9999) was chosen so that simulations could be run evenly across 48 computer cores to aid with the speed of processing. CSR and TC models were tested in this way with a homogeneous background, and for HP and ITC models, a heterogeneous background generated from the DEM of the GWW was used (Fig. 2b).

A goodness-of-fit test was then used to quantitatively assess differences between the observed pattern PCFs and simulated PCFs. Goodness-of-fit tests provide a hypothesis test, with the null hypothesis being that the measured process (here, PCF for each morphospecies' point pattern) departs from the simulation envelope over a specified distance interval. Here, we used Diggle's goodness-of-fit test (p_d) (Diggle 2003), with high p_d (i.e., closer to 1) interpreted to be a good model fit, alongside visual inspection of the morphospecies' PCF plot (Fedriani et al. 2010; Illian et al. 2008). In order to test whether processes only occurred at specific spatial scales, the model fitting process was repeated over the same intervals that matched excursions from simulation envelopes. If two models both had high p_d values over the same spatial range, then the model with the highest p_d value was determined to be the best-fit model. If a TC process was the best-fit model, but there were good fits over multiple spatial scales (instead of a single spatial scale, e.g. 3–6 cm and 6–10 cm both produce good fits whereas 3–10 cm did not), a double Thomas cluster (DTC) model was fit to the data (with an inhomogeneous background if an ITC process was the best-fit process) in Programita (v November 2018) (Wiegand 2018).

Assessment of clustering parameters

Once the best-fit model for each taxon at each depth bin was found, if the best fit indicated a (in)homogeneous Thomas cluster process, the standard deviation of the distance between offspring point to the parent point (scale; 2*σ, cluster radius hereafter), mean density of parent points (κ), and mean number of individuals per cluster (μ) were determined. In order to investigate the nature of clustering across the GWW, σ, κ, and μ were qualitatively inspected for each taxon across depth bins. We could not assess relationships in these metrics quantitatively due to only sampling three depth bins on the GWW.

Results

The mapped GWW community consisted of 25,496 specimens over 377.74 m^2 (Fig. 3). The community was dominated by white Nephtheidae (20,978 colonies; 85.82% relative abundance), with an increase in abundance from shallow (1,252) to intermediate (9,304) to deep (11,165) depth bins. Hydroids (1,037 colonies; 4.24%), lemon sponges (437 individuals; 1.79%), and algae (possibly *Halimeda*) (885 individuals; 3.62%) were the other most dominant morphospecies. *Tubastraea* (288 colonies; 1.18%) and *Dendronephthya* (258 colonies; 1.06%) were abundant in the shallow depth bin but hardly present at the deeper depth bins. Berman–Lawson–Waller tests revealed that density of all morphospecies together ($df = 1$, Rao = 5,956.1, $p > 0.001$) and of each of white Nephtheidae ($df = 1$, Rao = 7205.8, $p < 0.001$), lemon sponges ($df = 1$, Rao = 93.308, $p < 0.001$), hydroids ($df = 1$, Rao = 287.860, $p < 0.001$), algae ($df = 1$, Rao = 78.322, $p < 0.001$), *Tubastraea* ($df = 1$, Rao = 17.586, $p < 0.001$), and *Dendronephthya* ($df = 1$, Rao = 75.030, $p < 0.001$), significantly depended on depth (Table S1).

No morphospecies exhibited a best fit model to CSR at any depth bin. The white Nephtheidae and hydroid populations at each depth bin were best fit by a TC model at smaller spatial scales (centimetre-scale) and an ITC model at larger spatial scales (metre-scale) (Table 1 and S2, Fig. 3a, e, respectively). In the shallow and intermediate depth bins, lemon sponges were best fit by HP and ITC at larger spatial scales and TC in the intermediate and deep depth bins at smaller spatial scales (Table 1 and S2, Fig. 3b). The algae spatial pattern was best fit by an ITC model at the shallow depth bin and a TC and ITC model for intermediate and deep depth bins at similar spatial scales (Table 1 and S2, Fig. 3c). We also found a good fit to an inhomogeneous DTC model for algae in the deep depth bin (Table S2). In the shallow depth bin, *Dendronephthya* were best fit by all three models, with TC having the best fit (Table 1 and S2, Fig. 3f). *Tubastraea* were best fit by TC and ITC models, with TC having the best fit (Table 1 and S2, Fig. 3d).

In terms of clustering parameters extracted from best fit TC models, all four abundant morphospecies increased in the density of parent points (κ) with depth, but the white Nephtheidae exhibited a disproportionately greater response

Table 1 Summary of univariate PCF analyses for abundant morphospecies on the Great White Wall, with the best fit spatial scales and clustering parameters for cluster models

Morpho species	Depth bin	n	Dens (m^{-2})	p_d CSR	p_d HP	p_d TC	p_d ITC	Best-fit spatial scale (m)	Best-fit σ (m)	Best-fit κ (m^{-2})	Best-fit μ (cluster^{-1})
Nephtheidae	S	1,252	9.67	0.000	0.000	0.136	0.534	0.1–1.5	0.52	0.07	145.63
	I	9,304	66.46	0.000	0.000	0.100	0.654	0.3–1.5	0.57	0.53	125.02
	D	11,165	95.17	0.000	0.000	0.209	0.348	0.1–1.5	0.80	0.54	174.72
Lemon sponge	S	288	2.22	0.000	0.193	0.000	0.505	0.3–1.5	0.23	5.43	0.41
	I	96	0.67	0.000	0.057	0.951	0.801	0–0.3	0.07	1.27	0.53
	D	107	0.91	0.000	0.000	0.985	0.757	0–0.3	0.06	2.68	0.41
Hydroid	S	176	1.36	0.000	0.000	0.291	0.609	0.3–1.5	0.29	0.19	7.05
	I	343	2.45	0.000	0.000	0.234	0.564	0–0.2	0.05	0.66	3.73
	D	647	5.52	0.000	0.000	0.413	0.713	0–0.1	0.03	2.03	2.72
Algae	S	145	2.34	0.000	0.000	0.875	0.001	0–1.50	0.14	0.06	18.99
	I	474	1.12	0.000	0.000	0.299	0.339	0–0.3	0.01	0.31	10.86
	D	347	3.39	0.000	0.000	0.481	0.258	0–0.1	0.04	1.04	2.84
Tubastraea	S	129	1.00	0.000	0.000	0.330	0.156	0–1.5	0.19	0.44	2.28
Dendronephthya	S	164	1.27	0.000	0.175	0.917	0.797	0–0.3	0.06	2.41	0.53

S, shallow; I, intermediate; D, deep; CSR, complete spatial randomness; HP, heterogeneous Poisson; TC, Thomas cluster; ITC, inhomogeneous Thomas cluster; σ, standard deviation of distance between parent and offspring point; κ, density of parent points; μ, mean number of points per cluster.

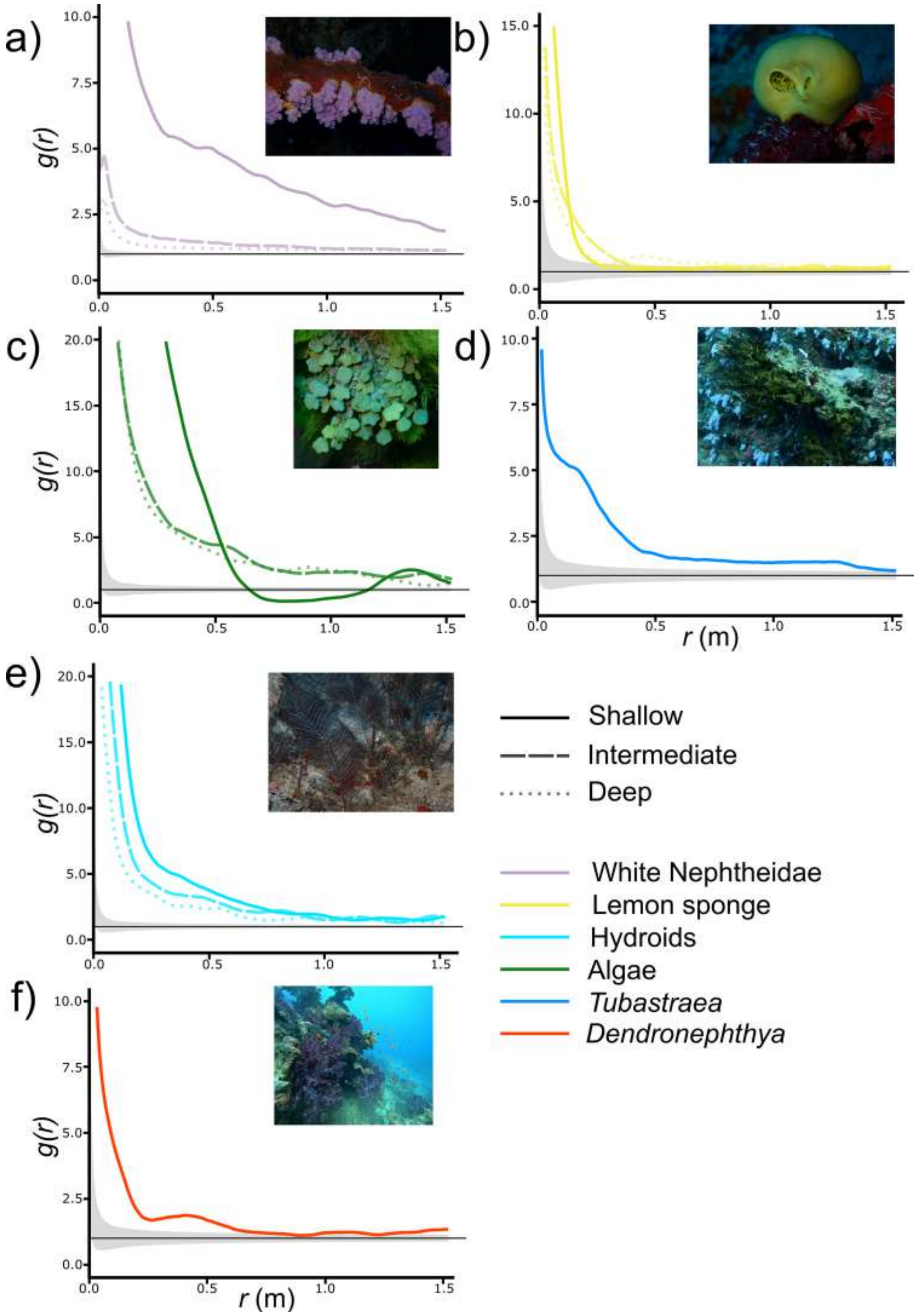

Fig. 3 PCF plots of univariate analyses at each depth bin for **a** white Nephtheidae, **b** lemon sponges, **c** algae, **d** *Tubastraea* **e** hydroids, and **f** *Dendronephthya* on the Great White Wall. Solid lines indicate PCF for the shallow depth bin, dashed lines for the intermediate depth bin, and dotted lines in the deep depth bin

than any other morphospecies (Table 1, Fig. 4a). All morphospecies decreased in the mean number of individuals per cluster (μ) with increasing depth, with white Nephtheidae and algae showing the most marked change, whereas for hydroid and lemon sponges, number of organisms per cluster was relatively constant with depth (Table 1, Fig. 5b). Likewise, all morphospecies (except for lemon sponges) showed a decrease in cluster radius (σ) with increasing depth: algae showed the most notable decline; white Nephtheidae and the hydroids showed a gentle decrease with depth (Table 1, Fig. 4). Lemon sponges increased in cluster radius from shallow to intermediate depth bins, and then slightly decreased in the deep depth bin (Table 1, Fig. 4). For the *Denndronephthya*, which were only found in abundance in the shallow part of the wall, density of parent points was larger than any other morphospecies, but clusters were relatively small in diameter, and with fewer individuals (Table 1). *Tubastraea* had relatively low parent point density, with larger cluster

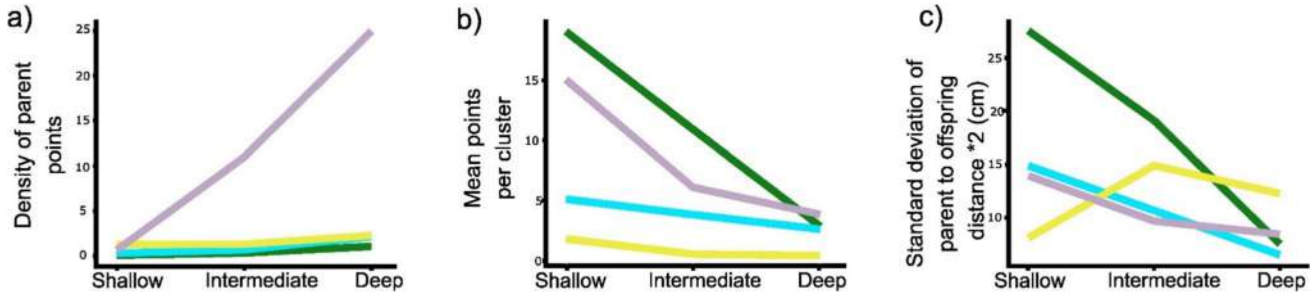

Fig. 4 Cluster parameters across shallow, intermediate, and deep depth bins for the four morphospecies found in each depth bin. **a** density of parent points (κ), **b** mean points per cluster (μ), and **c** double standard deviation of parent of offspring distance (cluster radius, or σ*2). Colours indicate morphospecies: lilac = white Nephtheidae, yellow = lemon sponges, green = algae, and blue = hydroids

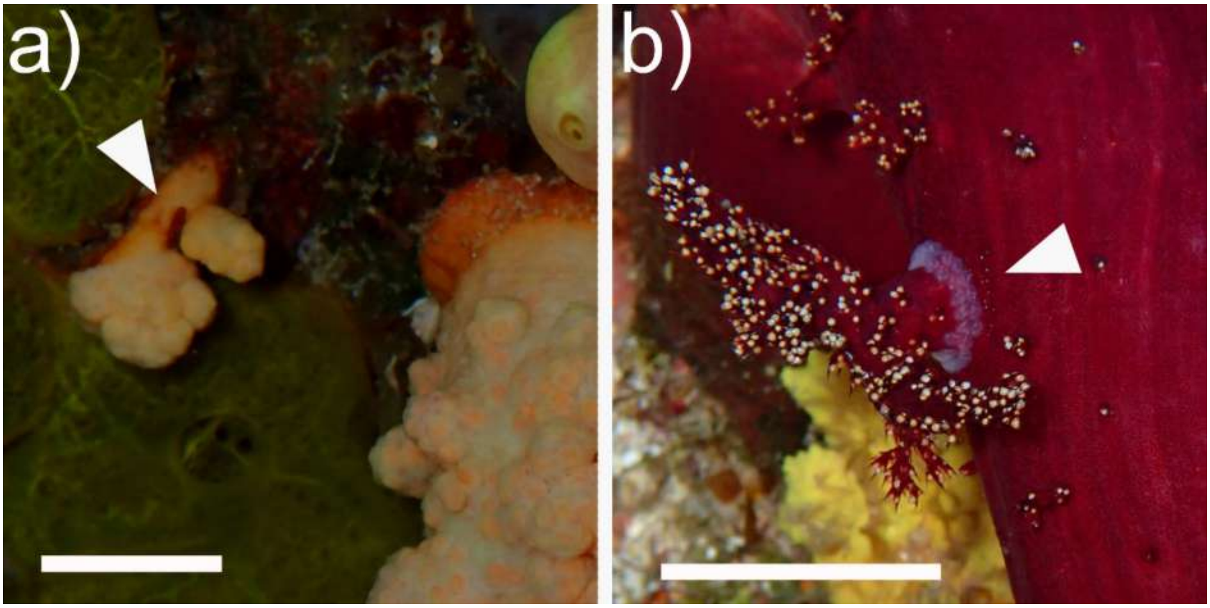

Fig. 5 Nephtheidae reproductive methods that could aid colonisation. **a** likely fission observed at the base of Nephtheidae (possible *Scleronephthya*) at the Yellow Tunnel locality (north of GWW in the Somosomo Strait). **b** Likely formation of a fragment on a *Dendronephthya* specimen on the GWW. Stolon and sexual reproduction have also been observed as reproductive strategies in these soft corals (Fabricius and Alderslade 2001; Larkin et al. 2023) Scale bars are ~ 3 cm

radii than any other morphospecies in the shallow depth bin and with each cluster containing relatively few individuals (Table 1).

Discussion

Both the white Nephtheidae and hydroid populations were well fit by TC and ITC models at all depths, reflecting the shared importance of reproductive processes and the local environment for these morphospecies. These best-fit models likely reflect the influence of combined reproductive and feeding dynamics, and are similar for each morphospecies due to shared ecological traits of filter-feeding colonial cnidaria. The Great White Wall (GWW) is positioned on the edge of a barrier reef in the southern part of the strait, with no nearby reef precluding water flow to the south, allowing nutrient-rich water the flow over the wall. It is likely that the abundance of filter feeders on the GWW therefore capitalises on this abundance of food, particularly at ~ 30 m, which is also reflected in the optimal niche observed in planktivorous coral reef fishes (Richardson et al. 2023). Lemon sponge spatial patterns were also fit well by reproductive models with habitat associations (ITC) at each depth bin. However, the lemon sponge patterns appeared to be well modelled by environmental heterogeneity in the shallow depth bin, and only have good fit to reproductive (TC) models at smaller spatial scales in the intermediate and deep depth bins, indicating that habitat preferences were much more important where food was scarcer in the shallows. Lemon sponges had very small cluster radii in the shallow depth bin, which increased in the intermediate depth bin where resources were likely more plentiful, and then slightly decreased (as with all morphospecies) between intermediate and deep bins. Decreases in cluster radii ubiquitous across all morphospecies could be caused by competition for space as specimen densities increased with depth. Algae were best fit by reproductive (TC) models at all depth bins, but a good fit to reproductive models with habitat associations (ITC) was only found at intermediate and deep bins, indicating no response to environmental heterogeneity in the shallow depth bin. The algae also had the largest cluster radii and the greatest number of individuals per cluster in the shallow depth bin, but these cluster metrices declined at a greater rate with depth than for all other morphospecies. Our results for algae likely reflect more plentiful light in the shallow depth bin, whereas wall topography and water depth created an impediment to light access at greater depths, resulting in a better fit to reproductive models with habitat associations (ITC), and a reduction in cluster size and number of individuals per cluster. *Tubastraea* and *Dendronephthya* spatial patterns were best modelled by reproductive processes (TC), but these morphospecies were only plentiful in the shallow bin. We observed that *Tubastraea* had the largest body sizes, and was found in intermediate and deep depth bins, but a much lower densities. This change in size dynamics could be reflective of competition for space precluding larger morphospecies with slower growth rates at greater depths where overall density is higher.

The white Nephtheidae were the dominant filter feeders over the hydroid and sponge populations on the GWW. In other locations where soft corals show local dominance, reproductive lability (Bastidas et al. 2004), fast growth rates (Benayahu and Loya 1977), and higher competitive ability over zooxanthellate hard corals (e.g., resistance to anthropogenic pressures, ability to overgrow scleractinian corals) (Sammarco 1985) have been suggested as mechanisms of dominance. On the GWW, few zooxanthellate hard corals are present, though this likely reflects a lack of suitable habitat due to lack of light from depth and shading caused by other organisms on the GWW, rather than poor competitive ability, as hard corals tend to have significantly lower cover on vertical wall reefs (Kikuzawa et al. 2020; Perkol-Finkel and Benayahu 2004). We observed fission and budding reproductive modes from photographs of Nephtheidae near and on the GWW (Fig. 5). Stoloniferous reproduction has also been observed in Nephtheidae elsewhere (Fabricius and Alderslade 2001; Larkin et al. 2023) and colloquial reports of sexual reproduction matching with lunar cycles on the GWW (similar to brooding observed in other Nephtheidae elsewhere (Hwang and Song 2007; Larkin et al. 2023)) also offer a method of sexual reproduction in this morphospecies. Nephtheidae have been considered a “weedy”, early succession species—so dominance of Nephtheidae over other filter feeders could also be due to trade-offs between guerilla and phalanx strategies during asexual colonisation (Winkler et al. 1999). The GWW is prone to very high current speeds, so later successional, slow-growing taxa (e.g., *Sarcophyton* soft corals (Fabricius 1995), skeletonised hard corals) could struggle to grow and dominate—these taxa are present on GWW, but at low abundances. It could be that the soft coral community on the GWW is kept in a suspended state of “early succession” due to periodic intermediate disturbance (e.g., by storms) precluding later succession taxa. The patterns here resemble other octocoral communities that have relatively stable communities structures dominated by gorgonians, although in these instances this is due to alternative ecological processes, namely portfolio effects and slow growth rates (Edmunds and Lasker 2022; Lasker et al. 2020). The capacity for Nephtheidae to grow quickly and reproduce using a variety of strategies, regular rapid and plentiful nutrient influx, and a potentially high disturbance regime are likely the combined contributors to the local dominance of white Nephtheidae on the GWW. These factors could also explain the disproportional increase in cluster density of white Nephtheidae compared to other morphospecies with depth (Fig. 4a).

Despite the dominance displayed by the white Nephtheidae on the GWW, as seen in other soft coral taxa elsewhere (Bastidas et al. 2004), substantial populations of other filter feeders (hydroids, lemon sponges, *Dendronephthya*) were still able to coexist. One possible explanation for coexistence of filter feeders is that Nephtheidae soft corals have a temporal feeding niche—they actively filter feed at times of high current, but otherwise retract their polyps and so can undergo dramatic, current-induced reductions in size (Hellström and Benzie 2011). This hypothesised strategy would permit other filter-feeding taxa to feed continuously or perhaps maximise their feeding unsynchronised from the tidal rhythms that influence current regimes, with maximal energy intake at times of low current when the dominant white Nephtheidae are not feeding. Similar patterns of temporally restricting feeding are seen in coral reef systems generated by synchronicity between tide times and landscape of fear effects driving herbivore grazing strategies (Atwood et al. 2018). Partitioning of time as an ecological resource is not a novel suggestion (Kronfeld-Schor and Dayan 2003), and has been observed over various temporal scales (tidal, dial, seasonal, annual), leading to coexistence via niche partitioning, but to our knowledge this partitioning of time has not before been suggested as a mechanism of coexistence for marine animal forests. This feeding strategy may therefore be a mechanism for increasing invertebrate biodiversity on some soft coral-dominated reefs.

Conclusion

In this study, we found that dominance of white Nephtheidae soft corals was shaped through a combination of suitable habitat—inferred to be related to food availability—and dispersal limitation. However, other invertebrate filter feeders—hydroids, azooxanthellate hard corals, and lemon sponges—were able to coexist alongside populations of algae. We found that clustering patterns driven by reproductive and habitat association processes were the most dominant ecological drivers of the populations of the most common morphospecies, and that these clusters typically became more numerous, but smaller and with fewer individuals, with depth. We speculate that the coexistence of functionally similar species may be due to a temporal niche partitioning of feeding, with Nephtheidae feeding coinciding with periods of high current on the GWW. This partitioning may be a mechanism to promote benthic diversity on some soft coral-dominated reefs.

Acknowledgements We thank the Yavusa Mabuco for access to their traditional fishing ground to conduct this research. NPS and KMD thank F. Bugeja, J. Lycett, EK. Gobert, M. Bugeja, A. Ruffinengo, and C. McKinven for provision of training. We thank M. Walser for logistical support.

Author contributions This work was conceptualised by NPS, AM, and EGM. Data collection was carried out by NPS, KMD, JW, VB, CGK, and EGM, and the data were processed by NPS, KMD, AB, and EGM. Spatial analyses were conducted by NPS and EGM. The original draft was written by NPS, AM, and EGM, and all authors contributed to the review and editing of the final manuscript.

Funding The work was funded by a School of Biological Sciences Balfour Studentship and St. Catharine's College Travel Grant, University of Cambridge to NPS, a NERC Natural Environment Research Council (NERC) DTP and the University of Cambridge Earth Sciences Fieldwork Fund to KMD, a Leverhulme Trust Research Award to AAB, and Natural Environment Research Council (NERC) Independent Research Fellowship NE/S014756/1, awarded to EGM.

Data availability Data are available at: https://figshare.com/s/f5d0a7f5879e7f31e2b7

Code availability Code used in this work is available at: https://github.com/nis38/GWW_pop_ecol

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose. The authors have no conflicts of interest to declare that are relevant to the content of this article. All authors certify that they have no affiliations with or involvement in any organisation or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript. The authors have no financial or proprietary interests in any material discussed in this article.

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