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Seascape effects on the nursery function of macroalgal habitats

Molly Moustaka [a,b,c,*], William D. Robbins [c,d], Shaun K. Wilson [b,e], Corey Wakefield [f], Michael VW. Cuttler [b,g], Michael J. O'Leary [b,h], Richard D. Evans [b,c]

[a] School of Biological Sciences, The University of Western Australia, Perth, WA, 6009, Australia
[b] The Oceans Institute, The University of Western Australia, Perth, WA, 6009, Australia
[c] Marine Science Program, Biodiversity and Conservation Science, Department of Biodiversity, Conservation and Attractions, Kensington, WA, 6151, Australia
[d] Wildlife Marine, Perth, WA, 6019, Australia
[e] Australian Institute of Marine Science, Indian Ocean Marine Research Centre, Perth, WA, 6009, Australia
[f] Western Australian Fisheries and Marine Research Laboratories, Department of Primary Industries and Regional Development, Government of Western Australia, North Beach, WA, 6020, Australia
[g] Oceans Graduate School, The University of Western Australia, Perth, WA, 6009, Australia
[h] Centre for Energy Geoscience, School of Earth Sciences, The University of Western Australia, Perth, WA, 6009, Australia

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ABSTRACT

Understanding how seascape configuration influences nursery function is important for spatial management and conservation of essential habitats. Here, we examine how local habitat, seascape, and environmental factors influence demographic metrics of juvenile *Lethrinus punctulatus* and assess spatial variation in macroalgae nursery function. We quantified abundance, biomass, and productivity of juvenile *L. punctulatus* over three years and estimated size-at-age and condition from collected fish. Abundance, biomass, productivity, and size-at-age exhibited significant spatial variation, although each pattern was best explained by different factors. *Lethrinus punctulatus* were most abundant in macroalgae-rich seascapes, whereas biomass and productivity peaked where macroalgal cover and water temperatures were high. Conversely, fish exhibited the greatest average daily growth at sites near coral reefs. Processes contributing to spatial variation in size-at-age occur prior to fish reaching ~5 cm in length and may be due to differences in resource availability, size at settlement, or size-selective mortality. Our findings suggest habitat and resource availability constrain *L. punctulatus* abundance and productivity, while size-at-age is influenced by size-selective mortality and prey quality. Thus, while seascape configuration can affect nursery function, the degree of influence will depend on the processes involved, emphasising the value of considering multiple metrics when identifying nurseries.

1. Introduction

Many fish species exhibit distinct habitat preferences as juveniles and adults (Fulton et al., 2020; Sambrook et al., 2019). These preferences are typically driven by the divergent habitat conditions that maximise growth and minimise predation rates (Dahlgren and Eggleston, 2000; Grol et al., 2011). Immediately following settlement into benthic habitats, juvenile fish face intense predation and competition, leading to higher natural mortality rates during this early life history stage (Almany and Webster, 2006). During this period, mortality rates and competition success of individuals are often size and/or density-dependent, with relatively faster growing fishes passing through vulnerable size classes more rapidly (Hoey and McCormick, 2004; Sogard, 1997). Consequently, many juvenile fishes tend to favour shallow, structurally complex coastal habitats (e.g., seagrass meadows, mangroves and macroalgae beds) that offer both refuge from predators and plentiful food to enhance growth and survival (Adams et al., 2006; Grol et al., 2011; Lefcheck et al., 2019; Shulman, 1985). The availability of such 'nursery' habitats may then have a positive influence on future population sizes (Caley et al., 1996; Doherty et al., 2004; McCormick, 1998). As coastal seascapes are subject to a variety of competing demands (e.g., fishing, development, and conservation), identifying and conserving critical nursery habitats is important for sustainable management of the fish stocks (Barbier et al., 2011; Beck et al., 2001).

Functional nursery habitats are characterised by high density, growth, and survival of juvenile fish, along with successful migration to

* Corresponding author. School of Biological Sciences, The University of Western Australia, Perth, WA, 6009, Australia.
E-mail address: molly.moustaka@dbca.wa.gov.au (M. Moustaka).

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adult habitats (Beck et al., 2001). Over time, the nursery concept has evolved to encompass not only the focal habitat in which a juvenile fish primarily resides, but also the interconnected network of adjacent habitats and migration corridors used for daily and ontogenetic migrations (the 'Seascape Nursery' *sensu* Nagelkerken et al., 2015). Seascape configuration can influence juvenile fish growth rates and body condition by enhancing access to trophic resources (e.g., prey and detrital subsides; Rypel and Layman 2008; Yeager et al., 2012; Olson et al., 2019). Moreover, seascape configuration may moderate predation pressure on juvenile fish by providing access to additional refugia (Dorenbosch et al., 2004; Hitt et al., 2011), or restricting predator movement (Hammerschlag et al., 2010; Rooker et al., 2018). Despite increasing recognition of potential seascape effects on nursery function, empirical studies are limited and have primarily focused on seagrass meadows (e.g., Yeager et al., 2012; Williams et al., 2016; Olson et al., 2019). Consequently, the extent to which seascape effects on nursery function can be generalised across other habitat types (e.g., macroalgae), and how these effects are moderated by environmental conditions, remains unclear.

Habitat choice by juvenile fish often involves trade-offs between food availability and predation risk (Dahlgren and Eggleston, 2000; Grol et al., 2011). Moreover, the growth and mortality rates of juvenile fish often depend on the density of conspecifics (Gust et al., 2002; Johnson, 2008; Watson et al., 2022). Consequently, some habitats may maximise certain indicators of nursery function (e.g., density) but not others (e.g., growth rates; Grol et al., 2008; Kimirei et al., 2013). While abundance indices are commonly used to infer nursery value (e.g., Drew and Eggleston, 2008; Nagelkerken et al., 2000; Wilson et al., 2010), they can overlook how habitat quality influences individual growth and survival rates, and cannot capture sublethal effects of poor habitat quality (Hinz et al., 2019). Accordingly, evaluations of nursery function based solely on juvenile abundance may lead to inaccurate assessments of the relative value of habitats. For example, Yeager et al. (2012) found that higher seagrass cover in the surrounding seascape positively influenced the abundance and secondary productivity of juvenile white grunts (*Haemulon plumierii*) on artificial patch reefs. However, differences in juvenile densities lead to comparable per-capita resource availability among reefs, resulting in similar growth and condition of individuals. Approaches that integrate multiple measures of nursery function may therefore offer a more accurate depiction of habitat quality (Grol et al., 2008; Hinz et al., 2019; Yeager et al., 2012)

Many fish species, including some important to fisheries, preferentially occupy macroalgal habitats as juveniles (Fulton et al., 2020; Wilson et al., 2022). While variation in the abundance of juvenile fish has been linked to differences in macroalgal canopy cover, density, and height (Aburto-Oropeza et al., 2007; Wilson et al., 2017), seascape effects on nursery function of macroalgal habitats remain largely unexplored (Fulton et al., 2020). Identifying the confluence of local habitat, seascape, and environmental conditions that underpin macroalgal nursery habitats is important for understanding how juvenile fish population dynamics may respond to changing conditions across a range of spatial scales. This is particularly relevant in areas where coastal development may impact local habitats and disrupt important connections within the seascape, or where large-scale disturbances cause extensive changes to habitat composition (Berkström et al., 2013; Haddad et al., 2015). To that end, this study 1) quantified multiple metrics of nursery function (abundance, biomass, productivity, size-at-age, and body condition) for juvenile *Lethrinus punctulatus* (bluespotted emperor), 2) examined whether these metrics varied significantly and consistently among sites, and 3) explored how these measures were influenced by local habitat composition, seascape configuration, and environmental conditions. In doing so, we provide novel insights into the factors underpinning macroalgal nursery function for an important fishery species.

2. Methods

2.1. Site description

The Dampier Archipelago, located in the coastal waters of northwestern Australia, contains expansive shallow macroalgal habitats that consistently harbour high abundances of juvenile *L. punctulatus* (Table A2; Candland 2016; Taylor 2016). The 42 islands comprising the Archipelago are fringed by variable mosaics of coral, macroalgae, mangrove, seagrass, sand, and rubble habitats (Moustaka et al., 2024), providing an ideal opportunity to investigate seascape effects on the nursery value of macroalgal habitats. The region experiences a large tidal range (maximum spring tide 5.1 m), which contributes to the presence of a strong cross-shelf turbidity gradient (Pearce et al., 2003). Thirteen shallow (<7 m depth) bays were selected as study sites based on the presence of macroalgae habitat and spatial spread across the Archipelago (Fig. 1; Moustaka et al., 2024). The macroalgae assemblages in these bays are dominated by canopy-forming *Sargassum* spp. which undergoes seasonal cycles of growth and senescence (Fulton et al., 2014).

2.2. Study species

Lethrinus punctulatus occurs across some 2500 km of coastline in northwestern Australia (Newman et al., 2021). It is a commercially and recreationally valuable species, supporting the highest catches of any demersal species in the Pilbara region of Western Australia (Newman et al., 2021). *Lethrinus punctulatus* serves as an indicator species whose population is periodically assessed using an age-based integrated model, and its status is considered to represent other exploited teleosts with similar life history characteristics within the fishery (Newman et al., 2023). Juvenile *L. punctulatus* are thought to exclusively occupy shallow macroalgal habitats before migrating offshore into deeper waters as adults (Taylor, 2016). Although it is yet to be formally confirmed, *L. punctulatus* is considered to be a distinct species, with preliminary morphological and CO1 genetic sequencing data distinguishing it from other *Lethrinus* species (Glenn Moore, Curator of Fishes, Western Australian Museum, personal communication). *Lethrinus punctulatus* are gonochoristic broadcast spawners with a protracted spawning period (i.e., ca. 10 months) and exhibit biannual recruitment associated with peaks in reproduction during spring and late summer (C Wakefield unpublished results). Our study predominantly sampled fish produced in the former of these two peak reproductive periods.

2.3. Fish surveys

The abundance of juvenile *L. punctulatus* was quantified at each site every January from 2021 to 2023, using underwater visual census (UVC). At each site, divers recorded the number and size (total length) of all *L. punctulatus* observed across three 30 m × 1 m end-to-end transects, separated by at least 5 m. Surveys were conducted in coral, macroalgae, and mangrove habitats (where present) at each site to confirm the habitat associations of juvenile *L. punctulatus*. As juvenile *L. punctulatus* were seldom observed in mangroves and were entirely absent from coral reefs (Table A2), only data from macroalgal habitats are presented here. Surveys recorded all young-of-the-year *L. punctulatus* (<17 cm; C Wakefield unpublished results); however, only fish <14 cm (hereafter referred to as juveniles) were included in analyses (n excluded = 5). This was done to facilitate comparisons with data from fish collected for size-at-age and condition assessments, which were all <14 cm and estimated to be < 6 months post-settlement (Table A3). Divers calibrated their visual size estimates daily, before commencing fish surveys, by estimating and then measuring small pieces of rubble and coral (Harvey et al., 2004; Wilson et al., 2016). Discrepancies between estimated and measured sizes were found to be < 7% (0.35 mm) and were insignificant (paired *t*-test, $t_{220} = -0.72$, $p = 0.47$).

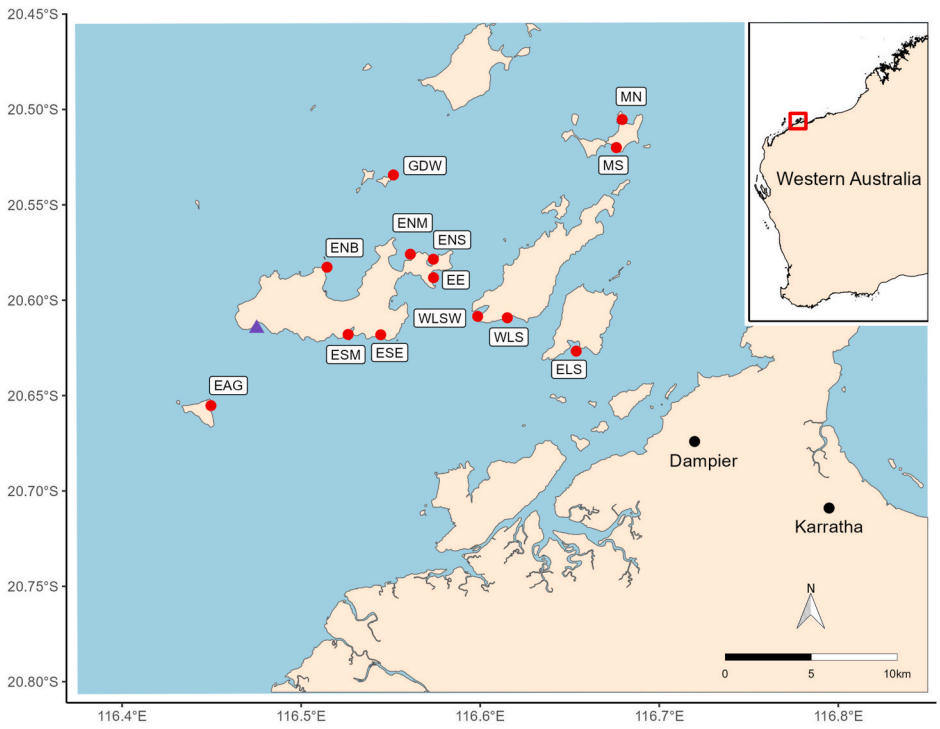

Fig. 1. Location of thirteen shallow (<7 m depth) macroalgae beds (red dots) in the Dampier Archipelago, Western Australia where annual underwater visual census was carried out between 2021 and 2023, and juvenile *Lethrinus punctulatus* were collected in 2021. Three letter codes are abbreviated site names. Purple triangle indicates the location of the temperature logger at site ESW.

Diver-operated underwater stereo-video (stereo-DOV) surveys were used to quantify densities of potential predators of juvenile *L. punctulatus* at each site (for details of stereo-DOV construction and calibration see Moustaka et al., 2024). Stereo-DOV surveys (three 30 m × 5 m transects) were conducted during an initial pass, while UVC surveys for juvenile fish were completedon the return pass along the same transect. UVC was chosen as the survey method because most juvenile fish are too small or cryptic to be accurately surveyed using video techniques (Brock 1954; Wilson et al., 2018a). While the stereo-DOV pass may have influenced estimates of juvenile *L. punctulatus* abundance, juveniles are typically more site attached than adults and therefore are less likely to relocate in response to divers (Wilson et al., 2017). Furthermore, the sampling effect was consistent among sites and is unlikely to confound results. Stereo-DOV transects were swum at a speed of ~0.3 m/s (20 m/min) and height of ~0.5 m above the substrate, with cameras tilted on a slight downward angle (Goetze et al., 2019). The resulting video footage was analysed using EventMeasure™ software with all fish identified to the lowest possible taxonomic level (SeaGIS Pty Ltd, 2020a). Taxa identified as potential predators included all species of Belonidae, Carangidae, Carcharhinidae, Latidae, Lutjanidae, Pseudochromidae, Scorpaenidae, Scombridae, Serranidae, Sphyraenidae, and Synodontidae (Connell, 1998; Wilson et al., 2017). The abundance of predatory fish (excluding juveniles) was subsequently summed across all families to obtain the total abundance of predators per transect.

2.4. Fish collections, sample preparation, and daily increment analysis

In February 2021, juvenile *L. punctulatus* were collected from shallow macroalgae beds using baited traps and small spearguns with pronged heads (n = 1–25 per site; Table A3). As the width of trap mesh meant they were size-selective, few recent recruits (<6 cm) were collected. Post-capture, fish were immediately euthanised and frozen until processed. In the laboratory, fish were defrosted, and the fork length (mm) and weight (mg) recorded. Fork length was used rather than total length as the caudal fin tips of some samples were damaged during transport and processing. Sagittal otoliths were then extracted, cleaned, and air dried. The length, height, and thickness (μm) of each otolith were measured using callipers, and the weight (mg) of each otolith recorded. One otolith from each fish was prepared for aging. Either the left or right otolith was embedded in resin (Kirkside K36 Epoxy Resin) and sectioned transversely through the primordium and perpendicular to the sulcus acusticus using a low-speed Buehler Isomet saw with a diamond-tipped blade to yield a ~230 μm thick section (Boddington et al., 2021; Wakefield et al., 2017). Each section was wet polished by hand using 30 μm, followed by 5 μm, diamond impregnated paper to a thickness of ~150 μm. Sections were then dipped in a 2% hydrochloric acid solution for ~20 s (Gauldie et al., 1990), rinsed in water, and mounted on a glass slide with casting resin and a coverslip (Newman et al., 2015).

Daily otolith rings provide a reliable record of age and growth rates for juvenile fish (Campana and Neilson, 1985; Jones, 1986). Annual growth rings have been validated for *L. punctulatus* (Stephenson and Hall, 2003) and daily rings have been validated for congeneric species (Nakamura et al., 2010), as well as a variety of other reef fish (Bergenius et al., 2002; Vigliola et al., 2000; Wilson et al., 2009). Images of otolith sections were taken using a compound microscope under transmitted light at 100× and 200× magnification using Nikon NIS-Elements software (Fig. A1). Each section was independently examined without knowledge of fish length by two readers (MM and WDR), who each recorded the number of daily increments (represented by a pair of alternating transparent and opaque bands) present and the location of the settlement mark. The settlement mark was typically characterised by a sharp decrease in increment width (Wilson and McCormick, 1999). The position of any ambiguous settlement marks was mutually determined. If ring counts differed by > 5 % between readers, the section was re-read by both readers at least one week later. If the second counts still differed by > 5% the section was discarded (n = 2). As we were interested in factors influencing fish growth after settlement into benthic habitats, the mean of the two post-settlement counts (rounded to the nearest whole integer) was accepted as the post-settlement age in days for retained otoliths (henceforth referred to as age). Back-calculated

settlement dates confirmed that all collected fish had settled in the six months preceding collection.

2.5. Covariate data

Data was compiled for a suite of local habitat, seascape, environmental, and biotic covariates that may influence the nursery function of macroalgal habitats for *L. punctulatus*. A summary of all predictor variables, associated data collection methods, ecological justifications, and any data transformations applied are provided in Table A4.

Local habitat composition (percent cover of macroalgae and consolidated substrate) was quantified using benthic imagery. Digital images were taken every 0.5 m along the fish survey transects at a height of 0.5 m above the benthos ($n = 60$ per transect). Benthic images were analysed using TransectMeasure™ software by randomly overlaying fifteen points on each image and classifying the substrate (unconsolidated or consolidated) and dominant biota (if present) using a simplified version of the hierarchical CATAMI classification scheme (Althaus et al., 2015; SeaGIS Pty Ltd, 2020b). The resulting data was then expressed as percent cover of each transect. Macroalgal canopy condition was also assessed along fish and benthic transects using *in situ* surveys. Divers recorded the average *Sargassum* spp. canopy height and holdfast density in six 0.25 × 0.25 m quadrats per transect at each site. Estimates of habitat structural complexity were extracted from stereo-DOV footage (collection methods described in Section 2.3). Benthic complexity was scored by a single analyst using a scale from low (0) to high (5) complexity (Polunin and Roberts, 1993) at five locations (~6 m apart) on each of the stereo-DOV videos (Collins et al., 2017).

Seascape metrics were derived from benthic habitat maps and shapefiles of mangrove extent taken from Moustaka et al. (2024). Connectivity between the focal macroalgal patch or transect and other macroalgal patches, coral reefs, and sand/pavement habitats within a 500 m buffer (bounded by land and the 7 m depth contour) was quantified using a connectivity index (CI). CI was calculated as a function of the total patch area of a given habitat type, weighted by their distance from the focal transect or collection site (Berkström et al., 2013; Hanski, 1998; Moilanen and Nieminen, 2002). As mangroves in the Dampier Archipelago are intertidal, connectivity to mangrove habitat was quantified using a modified CI that also incorporated temporal availability (CAI). CAI was calculated as function of seaward mangrove perimeter length, minimum navigable distance between the mangrove fringe and the survey site, and the proportion of a given tidal cycle during which the seaward fringe of the mangrove would be inundated (for further details see Moustaka et al., 2024). The length of the seaward perimeter of mangrove forests was used in place of areal extent as the majority of fish only utilise the fringe of intertidal mangrove habitat (Dunbar et al., 2017; Sheaves et al., 2016). The intertidal extent of each site (expressed as a proportion of the 500 m buffer) was quantified using Sentinel-2 Normalised Difference Water Index (NDWI = (B03 - B08)/(B03 + B08); McFeeters, 1996) rasters that coincided with the most extreme low and hightide events according to historical tide gauge data (Moustaka et al., 2024).

Environmental metrics included depth, as well as average (over the six months preceding sampling) water temperature, turbidity, significant wave height, and water velocity. Water depth (relative to mean sea level) was extracted from bathymetry derived from a compilation of the highest resolution datasets available for the region (see Moustaka et al., 2024 for full details). Water temperature data was collected using *in situ* HOBO temperature loggers. As temperature loggers were not deployed at all sites (or failed in some instances), where logger data was not available for a given site data from the closest site was used (see Table A1 for details). To confirm that neighbouring sites exhibited similar temperature profiles, all available temperature logger data (March 2020 to August 2023) was modelled against sea surface temperature (SST) data obtained from the NOAA ERDDAP server (dataset ID: jplMURSST41; Chin et al., 2017). This model ($R^2 = 0.95$) was then used to predict *in situ* temperatures at all sites to enable spatial comparisons of temperature profiles. While using temperature logger data from neighbouring sites may not fully capture fine-scale spatial variations in water temperature, it was deemed preferable using satellite-derived sea surface temperature data because the latter often fails to adequately detect ecologically significant among-site variability in shallow waters (Smale and Wernberg, 2009; Smit et al., 2013). Average turbidity was calculated using satellite derived KD490 data (the diffuse attenuation coefficient at 490 nm; KD2 algorithm) obtained from the NOAA ERDDAP server (dataset ID: nesdisVHNSQkd490Daily). Where sites fell within KD490 pixels that contained mostly land, data was taken from the adjacent cell. Significant wave height and water velocity were derived from a two-way coupled, wave-flow model was developed using the Delft3D Flexible Mesh (D3D-FM) modelling suite. This numerical model configuration and settings have been previously validated for the Dampier Archipelago region (Moustaka et al., 2024; Tebbett et al., 2023) and therefore only the details of the simulations used in the present study are provided here. Following validation, numerical hindcasts were conducted for the six-month period preceding each fish survey. Wave height and velocity results were extracted for the model nodes closest to the sample locations and then time-averaged to provide mean quantities that represent the average wave height or velocity over the six-month period preceding fish surveys.

Finally, biotic variables comprised the average density of conspecifics (based on UVC surveys) per transect as an indicator of potential intraspecific competition (growth models only), and the total abundance of predators per transect (recorded on stereo-DOVs, see section 2.3).

2.6. Data analyses

2.6.1. Fish abundance, biomass, and productivity

UVC data were used to explore spatial patterns in juvenile *L. punctulatus* abundance, biomass, and productivity. Standing biomass (g 30 m^{-2}) of *L. punctulatus* recorded in each UVC transect was calculated using length-weight relationships following Eq. (1):

$$W = aL^b \quad \text{Eq. 1}$$

Where W is the mass of the fish (g), L is the total length of the fish (cm) and a (0.00002014) and b (3.0056) are species-specific length-weight parameters obtained from Wakefield et al. (2024).

While biomass of fish provides a static measure of material and energy storage, net productivity (in this instance the amount of fish biomass produced, accounting for mortality, g 30 m^{-2} $year^{-1}$) reflects the dynamic flow of energy and materials (Bellwood et al., 2019). Net productivity is a dynamic ecosystem rate that is a function of abundance, size-structure, growth rates, and mortality, and can be decoupled from static measures such as abundance and biomass (Morais et al., 2020; Valentine-Rose et al., 2007). Indeed, productivity is a sensitive indicator of habitat quality on fish (Valentine-Rose et al., 2007) and combining both static and dynamic measures can yield a more complete picture of ecosystem functioning (Bellwood et al., 2019).

The productivity of *L. punctulatus* observed during UVC transects was calculated following the methods described in (Morais and Bellwood, 2020) using the rfishprod package (version 0.0.3) in R. Briefly, visual censuses were converted into daily estimates of fish biomass production (Morais and Bellwood, 2018, 2020). Rfishprod uses a trait based approach incorporating details of diet, position on the reef, maximum known length for each species and mean SST for the study location to estimate K_{max} (the growth coefficient at the maximum theoretical size; Morais and Bellwood, 2018). Mean satellite-derived SST over the study period (i.e., 3 years beginning on the date the first UVC surveys were conducted to correspond with the period over which productivity was estimated – see below) was obtained from the NOAA ERDDAP server (dataset ID: jplMURSST41; Chin et al., 2017) for the Dampier Archipelago. Each fish is first placed within its respective growth curve (von

Bertalanffy, 1949) and its daily growth in length is estimated using the von Bertalanffy growth function (VBGF; Eq. (2)):

$$L_{t+1} = L_{max}(1 - \exp(-K_{max} \times t)) \quad \text{Eq. 2}$$

Where L is the total length of the fish (cm) and t is the estimated age of the fish in days simulated as being derived from otolith increment analysis using rfishprod (Morais and Bellwood, 2020). Increases in length were converted to increases in somatic mass using species-specific length-weight relationships as described above. Daily productivity estimates were simulated over one year so that the growth of a fish on a given day resulted in an increase in length that affected the productivity estimate of the following day (Hamilton et al., 2022).

The probability of natural mortality was then estimated for each individual based on an ontogenetic size-based mortality risk function (Morais and Bellwood, 2020). We did not include an estimate of fishing mortality (F) as all individuals were below the minimum legal length (28 cm; http://rules.fish.wa.gov.au/Species/Index/171). The instantaneous rate of mortality (M) was calculated for each fish based on its length estimate, K_{max}, and the maximum known size of the species following Lorenzen et al. (2022). Survival of individual fish was simulated over one year by calculating the cumulative survival rate (i.e., multiplying the survival probability at time t by the survival probability the preceding day t_{-1}). Once a fish 'died' it no longer contributed to productivity estimates for the remainder of the simulation. Thus, the resulting productivity metric reflects the total somatic growth of fish expected to survive over a one-year time frame. Due to the stochastic probabilistic nature of natural mortality in fishes, the removal of individuals was iterated 1000 times. After each iteration, the estimated somatic growth per day, per surviving individual was summed over the year to obtain an estimate of net productivity at each site (Hamilton et al., 2022). The mean value of all iterations was used as the final estimate of annual net productivity at each site.

To explore how variation in average daily growth of fish among sites influenced estimates of productivity ('adjusted productivity'), a second set of productivity estimates were calculated using adjusted K_{max} values (Benkwitt et al., 2020). Adjusted K_{max} values were obtained by multiplying the K_{max} of each site (as estimated using the rfishprod package as described above) by the proportional difference in site-level average daily growth (i.e., length/post-settlement age) compared to the site with the lowest average daily growth (ENB). A linear growth rate was used to model fish growth, rather than an exponential model such as the von Bertalanffy growth function, because the latter tend to produce inconsistent estimates for juvenile fish due to the rapid early growth exhibited by many species (Allman and Grimes, 2002; Faunce and Serafy, 2008).

As the data were non-normal and contained random effects, generalised linear mixed models (GLMMs) were used to explore differences in the abundance, biomass, and annual net productivity of *L. punctulatus* among sites (Bolker et al., 2009). All models included a fixed effect of site and a random effect of year and were based on a Tweedie distribution with a log-link function. Significance for all analyses was $p < 0.05$ and analyses were conducted in R using the glmmTMB package (Brooks et al., 2017; R Core Team, 2022). Model fit and assumptions were assessed via simulation based-model checking using the DHARMa package (version 0.4.6; Hartig, 2020).

2.6.2. Fish growth and condition

Size-at-age and relative condition factor were quantified for collected fish as indicators of habitat quality. Fork lengths of collected fish were firstly converted to total length using a length-length conversion equation for juvenile *L. punctulatus* (<23 cm fork length; $L_{Total} = 1.1784\ L_{Fork} - 9.2507$; $n = 3133$; $R^2 = 0.998$; C Wakefield unpublished results) for consistency with data from UVC surveys.

Availability and quality of resources within a site can affect both the length and weight of fish, which subsequently influences their survival rates (Sogard, 1997; Johnson, 2008). Length and weight of collected fish were therefore used to calculate the relative condition factor (K_n; Cren 1951). A $K_n > 1$ indicates that a fish is heavier than would be expected given its length, while $K_n < 1$ indicates lower weight for length and poorer condition. K_n was calculated by first determining the relationship between fish length and weight in this system using Eq. (3):

$$W_e = aL^n \quad \text{Eq. 3}$$

Where W_e is the calculated weight (g) of the fish, L is the measured length (cm) of the fish, and a (the intercept; 0.0000354) and n (the exponent; 3.0067) are constants derived from log-log linear regression of measured fish lengths against measured weights (Froese, 2006). K_n can then be calculated per Eq. (4):

$$K_n = \frac{W}{W_e} \quad \text{Eq. 4}$$

Where W is the weight (g) of a fish, and W_e is the weight of the fish estimated from the population length-weight relationship based on all the fish collected in this study.

Three analysis of variance (ANOVA) tests were used to examine growth variations of juvenile *L. punctulatus*. Two of the ANOVAs included fish length as the response variable, site as a fixed effect, and post-settlement age as a continuous covariate. The first model tested for differences in growth rates (i.e., regression slopes, as indicated by the site × age interaction). As slopes did not differ among sites (Table A5), a second model was fitted without the interaction to test for differences in mean size-at-age (i.e., regression elevation). The final ANOVA tested for differences in average daily growth (i.e., length/post-settlement age) among sites. Where a significant effect of site was detected, Bonferroni post-hoc tests were used to evaluate among-site differences. Differences in fish condition among sites were evaluated using a non-parametric Kruskal-Wallis test due to non-normality of residuals. Three sites (ESE, MS, and MN) were excluded from growth and condition analyses due to low sample sizes. Additionally, one outlier sample (a very recently settled fish [post-settlement age = 5 days]) from EE was excluded from the growth ANOVAs and two samples from ELS were excluded from the condition ANOVA as accurate weight measurements could not be obtained (Table A3). Analyses were conducted in R using the using the stats package (version 4.2.2) and model fit and assumptions were assessed as above (Hartig, 2020; R Core Team, 2022).

2.6.3. Effects of covariates on response variables

Variation in the availability and quality of resources can influence the abundance and growth rates of fish, thereby influencing secondary productivity (Hamilton et al., 2022; Taylor et al., 2020). Therefore, a full-subsets approach (FSS) and generalised additive mixed models (GAMMs) were used to explore potential factors influencing measures of nursery function (Table A4). Condition was excluded as a response variable as no significant spatial variation was evident (Table A5).

GAMMs were chosen for their flexibility in modelling complex data as they do not require assumptions about the parametric relationship between the response and predictor variables (Wood, 2011). Models for abundance, biomass, and productivity were conducted using transect-level data and were limited to two explanatory variables to avoid overfitting and difficulty interpreting results. Growth models were conducted using average daily growth as the response variable and predictor variables averaged to site level. Growth models were limited to a single explanatory variable due to the low number of observations (i.e., predictor variables are at the level of site). Models containing variables with pairwise correlations > 0.28 (Fig. A2) were excluded to avoid issues such as inaccurate model parametrisation, exclusion of significant predictor variables, and reduced power (Graham, 2003). Year and site were included as random variables in abundance and productivity models to account for overdispersion and potential spatial autocorrelation (Harrison, 2014; Wood, 2017). The distributions of predictor variables were inspected and transformed or removed prior to analysis if

necessary (Table A4). Response variables were not transformed as the use of an appropriate error distribution (in this case a Tweedie distribution) accounted for the non-normal distribution of response data. Variable importance was calculated by summing the model weight of all models containing each variable (Burnham and Anderson, 2002). Models within two units of the lowest AICc (Akaike information criterion corrected for small sample size) were considered as candidate models (Akaike, 1998). Analyses were conducted in R using the mgcv (version 1.9-0) and FSSgam (version 1.11) packages (Fisher et al., 2018; R Core Team, 2022; Wood, 2011).

3. Results

3.1. Fish abundance, biomass, and productivity

A total of 177 transects spanning 13 sites and three years revealed significant spatial variation in juvenile *L. punctulatus* abundance, biomass, and productivity (Fig. 2; Table A7). Three sites (EAG, ENB, and ENS) exhibited the highest abundance and productivity of *L. punctulatus*, while ENM exhibited similar levels of biomass, but significantly lower abundances and productivity ($p < 0.05$; Fig. 2; Table A7). Productivity was positively correlated with biomass and, to a lesser extent, with abundance (pairwise correlations = 0.98 and 0.88, respectively; Fig. A3). In contrast, abundance and biomass were more weakly correlated (pairwise correlation = 0.79), likely due to spatial and temporal variation in the size-frequency of juvenile *L. punctulatus* observed on UVC transects (Fig. A3; Fig. A4).

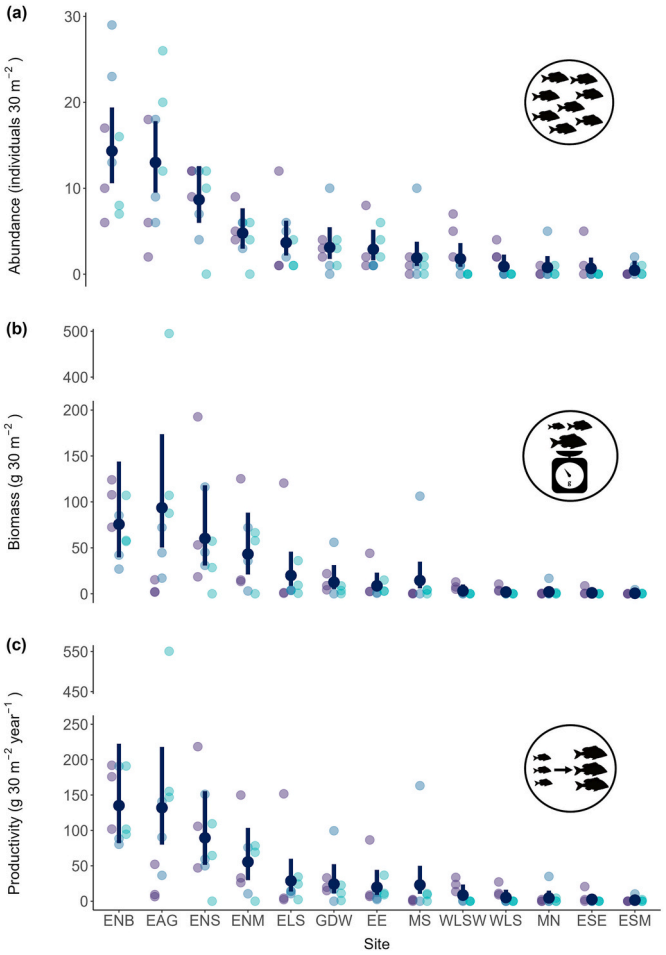

Fig. 2. a) Abundance, b) biomass, and c) simulated annual productivity of juvenile (<14 cm and <6 months post-settlement) *Lethrinus punctulatus* observed during underwater visual census at thirteen sites in the Dampier Archipelago, Western Australia. The points and ranges indicate the mean predicted fit and 95% confidence intervals from the generalised linear models (random effect of year and fixed effect of site), while dots indicate raw transect values (purple: 2021; blue: 2022; turquoise: 2023). Note the break in the y-axes of plots b) and c).

Adjusted productivity estimates (i.e., those generated using K_{max} values adjusted for differences in average daily growth of fish among sites) resulted in slightly higher estimates of productivity for most sites, compared to estimates derived from the unadjusted K_{max} values (Fig. 3). This led to a moderate shift in the rank-order of sites; however, EAG, ENB, ENS, and ENM remained significantly more productive than other sites (Table A7).

3.2. Fish growth and condition

Size-at-age and average daily growth of juvenile *L. punctulatus* differed significantly ($p < 0.001$) among the 10 sites where sufficient sample sizes (≥ 5 fish) were collected to evaluate spatial differences, while growth rates (i.e., regression slopes) did not ($p = 0.26$; Fig. 4; Table A3; Table A5). Size-at-age and average daily growth were greatest for fish collected from ELS, ENM, ENS, and WLSW and were lowest for fish from ENB and GDW (Fig. 4b; Table A8). Average daily growth of fish differed by as much as 48% among sites, with site-level averages ranging from 0.09 (±0.002 SE; standard error) cm day^{-1} at ENB to 0.13 cm day^{-1} (±0.003) at ENS (Fig. 4b; Table A3). However, as size-at-age slopes did not differ, differences in growth must have occurred prior to settlement and/or in the first ~50 days post-settlement, before fish reached 5 cm in length. Conversely, the condition of juvenile *L. punctulatus* was highly variable but did not exhibit significant variation among sites ($p = 0.31$; Fig. 4c; Table A5). When considering the data from 2021 (the year that both UVC and collections occurred), average abundance, biomass, and productivity of juvenile *L. punctulatus* were negatively correlated with average daily growth (pairwise correlation coefficients = −0.21, −0.14, and −0.20, respectively; Fig. A3), although these relationships were weak. Average condition was similarly weakly correlated with average abundance and daily growth (pairwise correlation coefficients = 0.18 and −0.31, respectively), while relationships with average biomass and productivity were slightly stronger (pairwise correlation coefficients = 0.51 and 0.47, respectively; Fig. A3).

3.3. Predictors of spatial variation in abundance, productivity, and growth

Seascape configuration influenced both the abundance and the average daily growth of juvenile *L. punctulatus*, while juvenile biomass and net productivity were best predicted by local habitat composition and environmental conditions (Fig. 5; Table 1). Juvenile *L. punctulatus* were more abundant at sites where the surrounding seascape was predominantly composed of macroalgae (i.e., high connectivity to macroalgae; CI macroalgae; Fig. 5; Table 1). Abundance was also weakly negatively correlated with the abundance of predators observed on stereo-DOVs (Fig. 5). Biomass and net productivity of juvenile *L. punctulatus* were also related to habitat availability, increasing with higher levels of macroalgae cover, as well as warmer average water temperatures (Fig. 5; Table 1). The positive effect of increasing macroalgae cover on biomass and net productivity appeared to asymptote when cover reached ~55% and slowed down at temperatures above 25.2 °C (Fig. 5). The relationships between biomass, productivity, and water temperature appeared to be a function of both spatial and temporal variation, as average biomass and productivity were greatest in 2021 (the warmest of the three survey years; Fig. 2) and tended to be higher at the warmest sites within a given year. Connectivity to coral habitat was the strongest predictor of average daily growth of *L. punctulatus*, with fish exhibiting faster average growth in macroalgae meadows with greater connectivity to coral reefs (Fig. 5; Table 1).

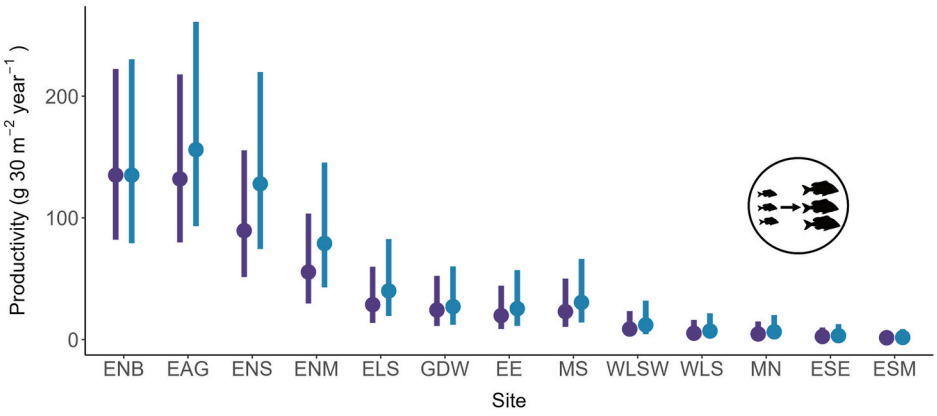

Fig. 3. Comparison of estimated annual productivity of juvenile (<14 cm and <6 months post-settlement) *Lethrinus punctulatus* under two scenarios: assuming no difference in average growth rates among sites (i.e., using the unadjusted K_{max} values; purple) versus adjusting K_{max} values according to the average daily growth of collected fish at each site (blue; see section 2.6.1). Points and ranges indicate the mean predicted fit and 95% confidence intervals from the generalised linear models.

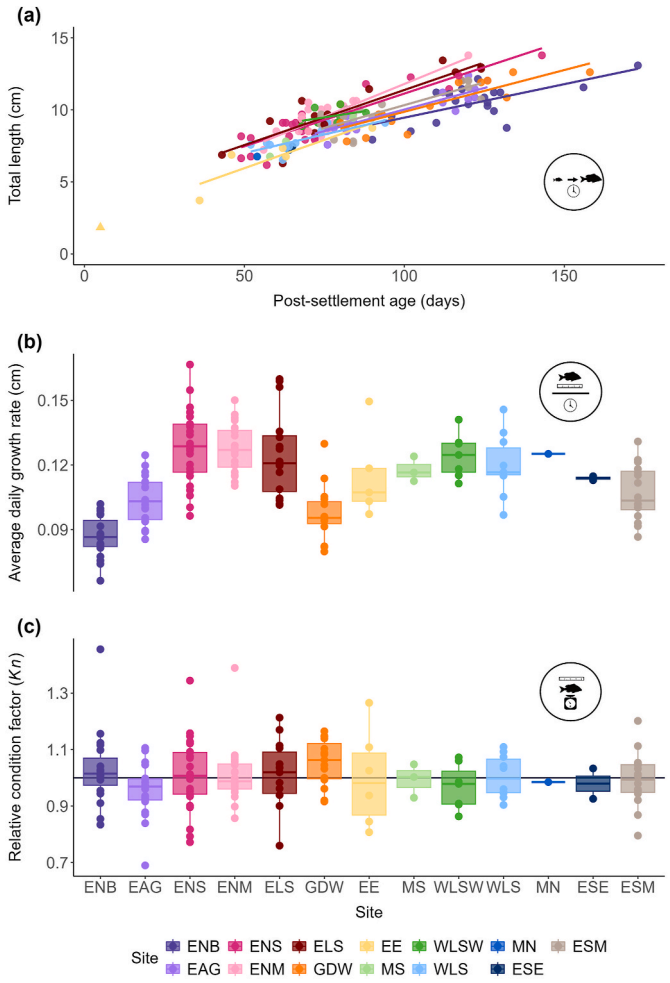

Fig. 4. a) Linear relationships fitted to size-at-age (days post-settlement) data from each site where ≥5 fish were collected (10 sites), b) average daily growth (i.e., length/post-settlement age), and c) relative condition factor (K_n) of juvenile *Lethrinus punctulatus* collected from 13 sites in the Dampier Archipelago, Western Australia. $K_n > 1$ indicates that a fish had higher body weight than predicted for its length (i.e., relatively better condition).

4. Discussion

Abundance, biomass, productivity, size-at-age, and average daily growth of juvenile *L. punctulatus* clearly differed among macroalgal sites; however, spatial patterns were inconsistent among nursery metrics, as were the factors that best explained this variation. Juvenile fish were most abundant in macroalgae patches that were highly connected to other macroalgae patches, while average daily growth peaked at sites with high connectivity to coral reefs. Biomass and net productivity of juvenile *L. punctulatus* also exhibited significant spatial variation, which was best explained by positive relationships with local macroalgal cover and water temperature. Conversely, neither the condition nor growth rates of collected juvenile fish varied significantly among sites across the observed age range. Although several indicators of nursery function were correlated (abundance, biomass, and productivity), others were decoupled (measures of growth and condition). Consequently, no single site was associated with maximum values across all nursery indicators, concurring with previous studies in seagrass meadows (Williams et al., 2016; Yeager et al., 2012). This finding highlights the importance of considering multiple indicators to accurately identify nursery habitats. Collectively, our findings demonstrate that seascape-scale processes have the greatest impact on the abundance and average daily growth of juvenile *L. punctulatus,* while biomass and net productivity are more closely linked to local habitat quality and resource availability.

Spatial variation in juvenile *L. punctulatus* abundance was influenced by a combination of seascape-scale habitat availability (CI macroalgae) and predation pressure. While local habitat quality (i.e., macroalgae cover, height, and density) strongly influences juvenile lethrinid abundance (Wilson et al., 2014), our findings suggest that habitat availability at broader scales also plays an important role. Juvenile *L. punctulatus* are almost exclusively observed in macroalgal habitats (Table A2; Candland 2016; Taylor 2016). As such, greater areal extent of macroalgae in the surrounding seascape likely provides increased shelter and foraging grounds, supporting higher densities of juvenile fish. Predator abundance also negatively impacted juvenile *L. punctulatus* abundance. However, this relationship was weak, possibly due to the influence of highly mobile and/or nocturnal predators that were not captured in our surveys (Green et al., 2015; Helfman, 1986). Alternatively, macroalgal structure may moderate predation pressure, such that spatial variation in canopy structure and interspecific differences in predator behaviour somewhat obscured the negative effects of predation (Horinouchi, 2007; Wilson et al., 2014). It is also possible that spatial variation in juvenile *L. punctulatus* abundance is partially driven by differences in recruit supply. However, Wilson et al. (2017) found that the abundance of lethrinid recruits was a poor predictor of local density of conspecific juveniles, suggesting that variation in larval supply is quickly moderated

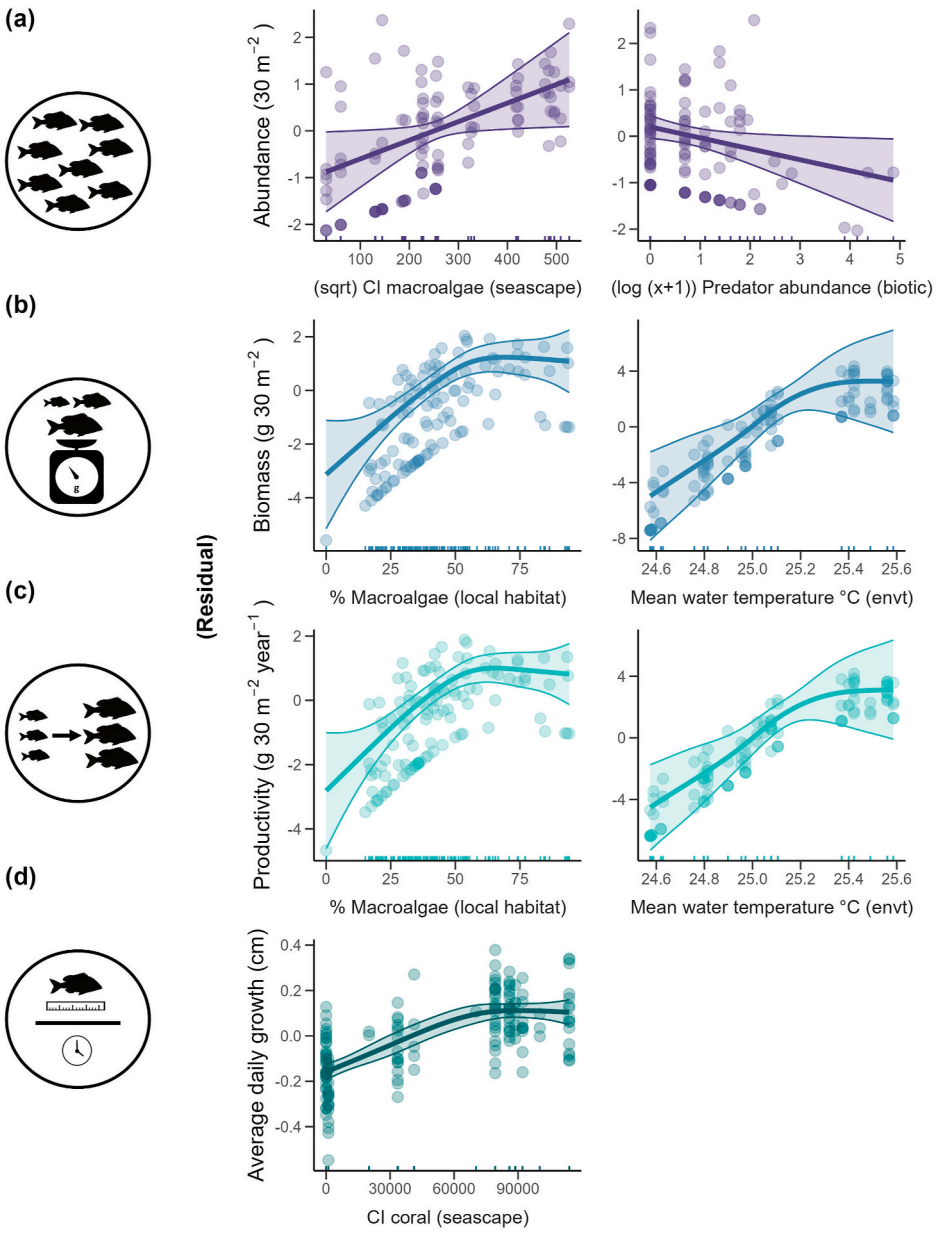

Fig. 5. Best generalised additive mixed model partial effects plots describing the residual a) total abundance (purple; $R^2 = 0.52$), b) biomass (blue; $R^2 = 0.27$), c) simulated net annual productivity (turquoise; $R^2 = 0.38$), and d) average daily growth (green; $R^2 = 0.47$) of juvenile *Lethrinus punctulatus* in the Dampier Archipelago, Western Australia (Table 1). Bracketed text on x-axes labels denotes predictor variable category. *CI* connectivity index, *envt* environmental.

Table 1
Generalised additive mixed models for predicting the total abundance, biomass, simulated net annual productivity, and average daily growth of juvenile *Lethrinus punctulatus* in the Dampier Archipelago, Western Australia. Table A6 contains the five models with the lowest AICc (Akaike information criterion corrected for small sample sizes) for each response variable. *ΔAICc* delta AIC, *wAICc* AICc weight, *edf* estimated degrees of freedom, *CI* connectivity index.

Response variable	R^2	ΔAICc	wAICc	edf	Best model
Abundance	0.52	0	0.81	15.65	CI macroalgae 500 m + Predator abundance
Biomass	0.27	0	0.96	18.27	% Macroalgae + Water temperature
Productivity	0.38	0	0.99	18.41	% Macroalgae + Water temperature
Average daily growth	0.47	0	0.92	3.53	CI coral

by post-settlement processes (e.g., predation and habitat selection; Webster 2002). A similar interaction between seascape structure and predation has been shown to influence post-settlement processes for juvenile red drum (*Sciaenops ocellatus*), whereby fish settled indiscriminately across seagrass meadows with varying levels of fragmentation, but then rapidly migrated to more contiguous meadows or were removed by predators (Williams et al., 2016). Highly connected macroalgal seascapes appear to similarly moderate post-settlement processes for *L. punctulatus*. Modification or fragmentation of these macroalgal habitats may therefore reduce their value for juvenile fish, with potential consequences for adult population replenishment.

Seascape configuration also appeared to influence the early growth of juvenile *L. punctulatus*, with the fastest average daily growth recorded at sites with high connectivity to coral reefs. While there was significant spatial variation in size-at-age and average daily growth of *L. punctulatus*, growth rates were consistent among sites across the observed age range. This discrepancy implies that the processes

contributing to variation in size-at-age occur prior to fish reaching ~5 cm in length. These processes may include differences in the size of juvenile fish at settlement and/or differences in early rates of growth and survival within the first ~50 days post-settlement. In the shallow bays of the Dampier Archipelago, coral reefs are typically situated in deeper water, seaward of macroalgal habitats. Consequently, coral reef communities likely receive a larger amount of nutritionally-valuable planktonic material compared to proximal macroalgal habitats (i.e., the 'wall of mouths'; Hamner et al., 1988; Atkinson and Falter 2020). Despite their strong association with macroalgal habitats, juvenile *L. punctulatus* derive a considerable proportion of their energetic resources (average proportional contribution 34 ± 9%; Moustaka et al., 2024) from microalgal sources (i.e., phytoplankton or microphytobenthos). As prey quality can influence the growth rates of juvenile fish (Nunn et al., 2012), increased proximity to coral reefs may be linked to greater availability of high-quality planktonic resources, supporting faster growth of recently recruited *L. punctulatus*. This observation aligns with previous research showing that juvenile lethrinids, lutjanids, and haemulids exhibit faster growth rates on coral reefs, compared to seagrass and mangrove habitats, due to greater availability of their preferred prey (Grol et al., 2008; Kimirei et al., 2013). Sites with high connectivity to coral reefs may also experience greater predation rates, resulting in more intense size-selective mortality. This phenomenon occurs when slower-growing fish are selectively removed from the population, creating the impression of faster growth rates (Holmes and McCormick, 2006; Searcy et al., 2007). Size-selective mortality of juvenile fish tends to be strongest in the initial post-settlement period (Gagliano and McCormick, 2007; Sogard, 1997), and is more intense where predator densities (Holmes and McCormick, 2006) or juvenile cohort sizes (Vigliola et al., 2007) are larger. However, experimental manipulations (e.g., predator exclusion cages) are necessary to explicitly test and confirm the mechanisms underlying spatial variation in the densities and size-at-age of juvenile *L. punctulatus*.

The abundance of *L. punctulatus* was best predicted by habitat availability at the seascape scale, whereas increasing local macroalgae cover and water temperatures had the greatest impact on biomass and net productivity. Although abundance, biomass, and productivity were highly correlated, variation in size-structure of *L. punctulatus* assemblages among sites weakened this relationship (Fig. A4). Consequently, while abundance of *L. punctulatus* was best predicted by habitat availability at the seascape scale, biomass and productivity were most strongly influenced by local macroalgal cover and warmer water temperatures. Water temperature can influence fish productivity (and thus biomass) directly via physiological mechanisms or indirectly by influencing prey productivity or macroalgal habitat structure (Fulton et al., 2014; Lindmark et al., 2022; Wilson et al. 2018b). *In situ* water temperature did not emerge as an important predictor of *L. punctulatus* growth rates in this study, nor was it strongly correlated with macroalgal cover or canopy structure (pairwise correlations = −0.1, −0.22, and −0.27 for cover, height, and holdfast density, respectively; Fig. A2). Instead, increased presence of larger fish (and thus higher productivity) in response to high macroalgal cover and warmer water temperatures is likely a function of increased prey availability, and possibly greater availability of shelter allowing for more efficient foraging. Both biomass of canopy-forming macroalgae and warmer water temperatures have been linked to increased abundance, biomass, and productivity of macroalgal-associated epifaunal invertebrates (Chen et al., 2020, 2021). Many lethrinid species are generalist carnivores, whose diet predominantly consists of crustaceans and small fish (Farmer and Wilson, 2011). As such, epifaunal invertebrates within the macroalgal meadows represent a potentially important dietary resource. The notion that local resource availability influences productivity of juvenile *L. punctulatus* is supported by the positive correlations between average condition of fish with both productivity and biomass, suggesting that more productive sites contained fish that were not only larger but also in better condition. It has been posited that prey production is a limiting factor for juvenile fish (Day et al., 2020; Le Pape and Bonhommeau, 2015) and similar positive relationships between benthic cover, prey availability, and juvenile fish productivity have been observed in seagrass meadows (Yeager et al., 2012). The absence of a concurrent relationship between either macroalgal cover or water temperature and *L. punctulatus* growth rates supports the notion that size-selective predation and/or differences in prey quality underly the observed spatial variation in growth rates. Overall, our findings indicate that abundance (and possibly early growth) of juvenile *L. punctulatus* is driven by seascape-scale processes (i.e., areal habitat extent), while the size-structure of *L. punctulatus* assemblages, and thus biomass and productivity, are better aligned with local habitat quality and resource availability.

Abundance is commonly used to infer the value of habitats for juvenile fish (e.g., Nagelkerken et al., 2000; Drew and Eggleston 2008). However, both fisheries yields and ecosystem functioning depend on the continuous production of new biomass, which can be decoupled from static measures such as abundance and biomass (Morais et al., 2023; Morais and Bellwood, 2020; Seguin et al., 2022). Consequently, the use of productivity metrics has become increasingly common in ecological studies (e.g., Rogers et al., 2014; Hamilton et al., 2022; Tebbett et al., 2023). Yet few studies have explored how productivity estimates may be impacted by local variation in growth rates (i.e., K_{max}) due to differences in resource availability (but see Benkwitt et al., 2020). We found that while incorporating spatial heterogeneity in average daily growth of fish impacted mean predictions of net annual productivity by up to 31%, the rank order of sites remained largely unchanged. Accordingly, spatial variation in estimated secondary production was predominantly a function of variation in fish abundance and size-structure. Both overall mortality rates and the intensity of size-dependent mortality diminish rapidly after settlement (Almany and Webster, 2006; Sogard, 1997). Consequently, it appears that spatial variation in growth rates is already reflected in the abundance and size structure of juvenile *L. punctulatus* assemblages by ~50 days post-settlement. As this method of estimating secondary production integrates data on abundance, size-structure, and size-dependent mortality rates (Morais and Bellwood, 2020), it may offer a more comprehensive indication of nursery function than considering abundance alone (Yeager et al., 2012).

The conditions that maximised nursery function of macroalgal habitats for juvenile *L. punctulatus* differ depending on the specific indicator being examined. Sites with the highest densities and productivity of fish differed from those with the largest size-at-age and greatest average daily growth, emphasising the importance of considering multiple indicators to accurately identify nursery habitats (Grol et al., 2008; Kimirei et al., 2013). However, this phenomenon presents a dilemma for managers: should conservation efforts focus on habitats that maximise one particular aspect of nursery function, or should they prioritise habitats with the highest overall value across multiple indicators? A crucial aspect of nursery function that was not considered in this study is the successful migration of juvenile fish to the adult population (Beck et al., 2001). It therefore remains to be seen whether higher abundance, biomass, productivity, and growth rates translate to greater contributions to the adult population. Moreover, although the abundance of juvenile lethrinids fluctuates considerably across years in response to macroalgal habitat condition (Wilson et al., 2017), it is uncertain whether this variation is subsequently reflected in the offshore adult population. *Lethrinus punctulatus* undertake extensive cross-shelf ontogenetic migrations from shallow coastal macroalgal habitats to deeper waters offshore (Taylor, 2016). The scale of this migration poses challenges to quantifying the relative contribution of potential nurseries to the adult stock (Thorrold et al., 2002). However, high-resolution geochemical tagging techniques, such as compound-specific stable isotope analysis of otoliths, may resolve this knowledge gap (McMahon et al., 2012, 2016).

This study demonstrated the combined effects of seascape configuration, local habitat quality, environmental conditions, and predator abundance on the nursery function of macroalgal habitats for

L. punctulatus in the Dampier Archipelago, Western Australia. We found that seascape configuration influenced both the abundance and average daily growth of juvenile fish, adding to the emerging body of evidence demonstrating seascape effects on nursery function of coastal habitats (Olson et al., 2019; Williams et al., 2016; Yeager et al., 2012). Our results also revealed that while juvenile fish densities were best predicted by seascape-scale habitat quantity, the size-structure of assemblages was most strongly influenced by local habitat quality. These results emphasise the importance of considering factors that operate at multiple spatial scales when examining drivers of macroalgal habitat quality for juvenile fish. Taken together, our findings suggest that a connected network of high cover macroalgae patches, close to coral reefs may best support continued population replenishment for this important fishery species. However, further research is required to understand the processes underlying the positive correlation between proximity to coral reefs and the average daily growth of juvenile *L. punctulatus*. Clearly, the structure and location of macroalgal meadows within the seascape can have profound effects on the abundance, size, and potentially the early post-settlement growth of juvenile fish, thereby influencing productivity. Nevertheless, it remains to be seen whether seascape effects on the nursery function of macroalgal habitats can be generalised to other macroalgal-affiliated species and environmental contexts (Bradley et al., 2019; Fulton et al., 2020). Moreover, the degree of linkage between macroalgal habitats and adult fish stocks warrants further investigation.

CRediT authorship contribution statement

Molly Moustaka: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **William D. Robbins:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis. **Shaun K. Wilson:** Writing – review & editing, Supervision, Formal analysis, Conceptualization. **Corey Wakefield:** Writing – review & editing, Methodology, Conceptualization. **Michael VW. Cuttler:** Writing – review & editing, Software, Formal analysis. **Michael J. O'Leary:** Writing – review & editing, Methodology, Formal analysis. **Richard D. Evans:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data supporting this research have been archived in the University of Western Australia data repository (DOI: 10.26182/1gvm-na62).

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This research was conducted in accordance with the Department of Biodiversity, Conservation and Attractions animal ethics permit #2020–16A and Department of Primary Industries and Regional Development exemption #3671.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2024.106767.

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