scientific reports

OPEN

The evolution of broad seascape utility and ontogenetic life history variation in lutjanids

Aaron M. Davis[1], Marcus Sheaves[2,3], Ajay Venkataraman[2] & Ricardo Betancur-R.[4]

While ontogenetic habitat shifts are a widely appreciated phenomenon across fishes, the macroevolutionary implications of habitat shifts and subsequent ecological opportunity have mainly focused on adult organisms, largely overlooking juvenile life history diversification. The snappers and fusiliers (Lutjanidae) represent a successful tropical teleost radiation exhibiting complex ontogenetic shifts and use of diverse nursery and adult habitats across the marine–freshwater interface. Lutjanids collectively occupy a broad range of environments within the seascape mosaic, including freshwater rivers, estuaries, reefs, and deep offshore slopes. Using an extensive phylogenomic dataset of ~110 species, we test models of juvenile and adult habitat evolution across seascape gradients. Evolutionary model fitting and ancestral state reconstructions, conducted independently for juvenile nurseries and adult habitats, both support an ordered, stepwise pattern of habitat transitions, with low-salinity associations evolving only via intermediate coastal habitats. This 'stepping stone' model of marine–freshwater macroevolution saw adoption of low salinity habitats preceded by adaptation to intermediate brackish habitats, rather than random jumps between widely separated seascape components. While our results highlight that ontogenetic shifts have been central to lutjanid diversification, more consistent and transferable research frameworks are required to clarify the ecological and evolutionary implications of lutjanid life history diversity.

Keywords Macroevolution, Marine-freshwater interface, Nursery habitat, Ontogeny

Ontogenetic habitat shifts requiring an organism to spend different portions of its life in fundamentally different habitats are a common evolutionary occurrence across diverse clades of amphibians, fishes, insects, and crustaceans[1,2]. Niche shifts in aquatic species are especially common, particularly in the various forms of diadromy, and the large- and small-scale life cycle migrations seen in many freshwater fishes[3,4]. Associated life cycle, and longer-term evolutionary transitions between macrohabitats can similarly expose fish lineages to shifting, and often novel, abiotic and biotic contexts[5–7]. For example, marine/freshwater transitions may alter the selective landscape for traits associated with osmoregulation, spawning ecology, swimming efficiency, predator avoidance, and competition for resources[5,7,8]. Several studies have also described habitat-mediated diversification in conjunction with coral reef colonization in numerous marine fish[9,10]. Research assessing the macroevolutionary implications of macrohabitat shifts and subsequent ecological opportunity has, however, primarily focused on adult organisms[7,9]while larvae and juveniles have largely been overlooked[11,12]. Developing an expanded ontogenetic perspective on patterns of phenotypic diversification therefore represents an often neglected, yet critical, aspect of evolutionary biology.

Evolution of life-history characteristics relating to ontogenetic habitat shifts are particularly relevant to marine ray-finned fishes, such as the snappers and fusiliers of the family Lutjanidae. An ecologically and economically significant fisheries complex, the lutjanids comprise about 135 extant species of medium- to large-sized fishes[6,13]representing a successful radiation of largely reef-and nearshore-associated percomorphs in marine and brackish coastal waters across tropical and subtropical oceans. A recent phylogenomic study[6] dates the crown age of lutjanids to the middle Eocene (~46 Ma) and identify seven major clades: the monophyletic subfamilies Apsilinae, Etelinae, and Paradicichthyinae; Clade A (*Lutjanus adetii*, *L. sebae*, and *Pinjalo* spp.); Clade B (*Lutjanus bohar*, *L. gibbus*, *Macolor* spp., and fusiliers, formerly Caesionidae); *Hoplopagrus guentherii* (sometimes placed in Hoplopagrinae); and Clade C, which includes most Lutjanus diversity along with *Ocyurus*

[1]Centre for Tropical Water and Aquatic Ecosystem Research (TropWATER), Australian Tropical Sciences and Innovation Precinct (ATSIP), James Cook University, Building 145, Townsville, QLD 4810, Australia. [2]College of Science and Engineering, James Cook University, Townsville, Australia. [3]Marine Data Technology Hub, James Cook University, Townsville, Australia. [4]Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA 92093, USA. ✉email: aaron.davis@jcu.edu.au

and *Rhomboplites*. The study found that several genera and subfamilies (e.g., Lutjaninae, *Lutjanus*, *Paracaesio*, *Pristipomoides*, and *Pterocaesio*) are grossly polyphyletic, prompting calls for taxonomic revision.

There is a considerable variation of habitat preferences among adult lutjanids. Most species live in shallow waters less than 100 m deep (e.g., *Aprion*, *Lutjanus*, *Symphorichthys* and *Symphorus*), while others, such as *Paracaesio*, are found at intermediate depths (100–200 m), and the species of the genera *Etelis*, *Aphareus* and *Rhomboplites* inhabit depths of up to 500 m[14]. Although patterns are somewhat species-specific, many lutjanids apparently undertake pronounced ontogenetic shifts across a suite of habitats (seagrass/mangroves to patch reefs to barrier reefs), often migrating seaward from coastal nursery habitats with ontogeny, to coral reefs or inner to outer shelf habitats with increasing size/age[15–18]. Because of these life history traits and shifting mosaics of often widely separated habitats utilised over life history, lutjanids are often presented as exemplars in concepts of 'seascapes' and 'critical chains of habitats'[19,20].

Collective life history traits and ontogenetic habitat affiliations of lutjanids have been periodically reviewed[14,18,] although typically limited in geographic scope. Assessment of evolutionary patterns in life history traits (such as the occurrence, nature, and scale of ontogenetic habitat shifts) has been similarly limited by the lack of understanding of phylogenetic relationships within this diverse and taxonomically challenging group of fishes. An increasing body of research is providing detailed insights into the ontogenetic habitat shifts and life history traits of diverse lutjanids, including several previously poorly known and ecologically diverse taxa[21]. Recent development of detailed and well-supported phylogenomic evolutionary histories for the group provide capacity to analyse evolution of ecological, morphological and life history traits in a more phylogenetically informed context[6]. In this paper we explore the phylogenetic history of juvenile habitat associations in lutjanids (ancestral nursery habitat types, invasions of novel nursery habitats). Using state-of-the-art models of evolution, we formally test hypotheses regarding the evolution of transitions among marine, brackish and freshwater habitats in the life history of both adult and juvenile lutjanids. Because shifts across salinity gradients, from marine environments to freshwaters, require significant adaptations in ecophysiology, we expect evolutionary models and ancestral character state reconstructions to recover a pattern consistent with gradual shifts between different salinity regimes. We then review and synthesise the current state of knowledge regarding lutjanid life history, highlight key research gaps, and provide conceptual frameworks to assist in consolidating future research.

Methods

Lutjanid phylogeny

For phylogenetic mapping and downstream analyses, we utilised the time-calibrated phylogenetic trees developed by Rincon-Sandoval et al.[6]using genome-wide exon data in conjunction with legacy markers for 110 (~80%) species in the group, and aggregated paleontological and geological information. In addition to a main tree ("master tree") estimated from the full concatenated dataset, 27 additional trees were generated from largely non-overlapping genomic subsets using both concatenation and coalescent approaches to account for phylogenetic uncertainty in comparative analyses.

Definition of habitat affiliation

A habitat occupancy dataset for lutjanid juveniles and adults was compiled by aggregating information from a wide range of sources, including primary literature, FishBase[13]museum records, databases and by consulting experts (data sources are outlined in Table S1 and associated references in Supplementary material). Juvenile fish habitat-association studies have been plagued by inconsistent definitions and lack of transferability across the literature, with little recognition of often complex, larval pelagic settlement and post settlement behaviors and habitat affiliations[22–24]. Wherever possible we assigned juvenile habitat affiliations to the smallest post-settlement size classes available in the literature (i.e., < 100 mm total length), while cognizant of variable, and sometimes only qualitative definitions available for some species. Because of the disparate data sources utilised for this phylogenetic-scale study, and similarly variable definition of habitats and life history stages available across species, we utilise a nested habitat hierarchy (Table 1) to simplify our definition of habitat associations over lutjanid life history; Process Zone, macrohabitat, mesohabitat and microhabitat[20].

Process Zones[25] comprise a gradient of overlapping environments from freshwater to offshore marine habitats, a concept amenable to what is already known regarding lutjanid life history shifts (i.e., a widespread theme of ontogenetic shifts to deeper habitats across the coastal seascape). Macrohabitats are large homogeneous units of

Juvenile habitat Process Zones	Description and associated macrohabitat types
Freshwater	Lower reaches of rivers and streams, upstream of brackish interface (may still be subject to tidal influence), riverine and connected off-channel lagoons[20,21].
Upper estuary-transitional	Brackish interface, *Nypa* spp. Palm swamps, mangroves, saltpans[20,21,28].
Lower estuary-nearshore	Headlands, shallow seagrass, foreshores, beaches, tidepools, coastal lagoons, deep estuary channels, coastal-fringing and shallow patch reefs[16–18,29].
Inshore-coastal	Unconsolidated benthic, 'scallop grounds', trawl grounds, shoals[19,30].
Reef	Barrier reefs, atolls, reef flats, reef lagoons, rocky and coral reefs, patch reefs, reef slopes, fore-reef, back-reef, coral heads[31–34].
Offshore	Relatively low relief open habitats, ≥ 100 m depth on upper parts of the continental and insular slopes[35–37].

Table 1. Process Zones used to define Lutjanid juvenile habitat associations and example macrohabitat types from literature sources relevant to each zone.

the seascape characterised by particular biological (e.g. mangrove forests, seagrass beds, coral reefs) or hydro-geomorphological (e.g. open sandy or rubble areas, back-reefs, sub-tidal channel, pelagic waters) attributes that are identifiable at scales of tens to hundreds of metres (Fig. 1) within a Process Zone[20]. Mesohabitats represent subdivisions of macro-habitats into their functional component parts, such as a sand bar in a river, mangrove forest or salt marsh edges (metres to tens of metres) are the parts of the environment where a fish is located at a particular point in time, i.e. *the present moment space*. Microhabitats are small-scale areas (centimetres in size and smaller) within a larger mesohabitat, like silt, gravel beds, pebbles, small cracks, crevices, and coral and root spaces. Much of our phylogenetic and broad-scale conceptualisation of lutjanid life history focuses on the scale of Process Zones, while cognizant of the fact that lutjanids will utilise an array of scales of macro-, meso- and micro-habitat features within these Process Zones at different stages of life history (subsequently discussed in more detail). Habitat utilisation patterns of juvenile lutjanids were distilled into a simplified set of primary 'nursery' habitats based on the specific Process Zones where juveniles of different species predominantly settle (Table 1). Adult lutjanids are comparatively highly mobile, and often capable of utilising multiple process zones over daily or shorter time frames[20,26,27]. To avoid an unmanageable number of process zone utilisation patterns, adult habitat utilisation patterns were classified separately, instead emphasising different types of multi-Process Zone utilisation over the freshwater to offshore seascape mosaic (Table 2).

Ancestral juvenile habitats

We estimated the best fit of various evolutionary models, and reconstructed ancestral character states of juvenile and adult Process Zone utility across lutjanids using the best-fit model. The evolutionary history of nursery and adult habitat was reconstructed on a 'master tree' and a collection of 28 trees inferred with different methods and gene subsets[6] to account for phylogenetic uncertainty. We first assessed three commonly-used evolutionary transition rate models—equal-rates (ER; a single probability of transition from any Process Zone/habitat state to any other state), symmetrical (SYM; separate probabilities of transition between each habitat, but with no difference in the directionality of transitions) and all-rates-different (ARD; unique rate parameters for each habitat transition). Evolutionary transitions across high and low salinity environments (i.e., marine and freshwater) typically require major behavioral, physiological and morphological changes. Numerous

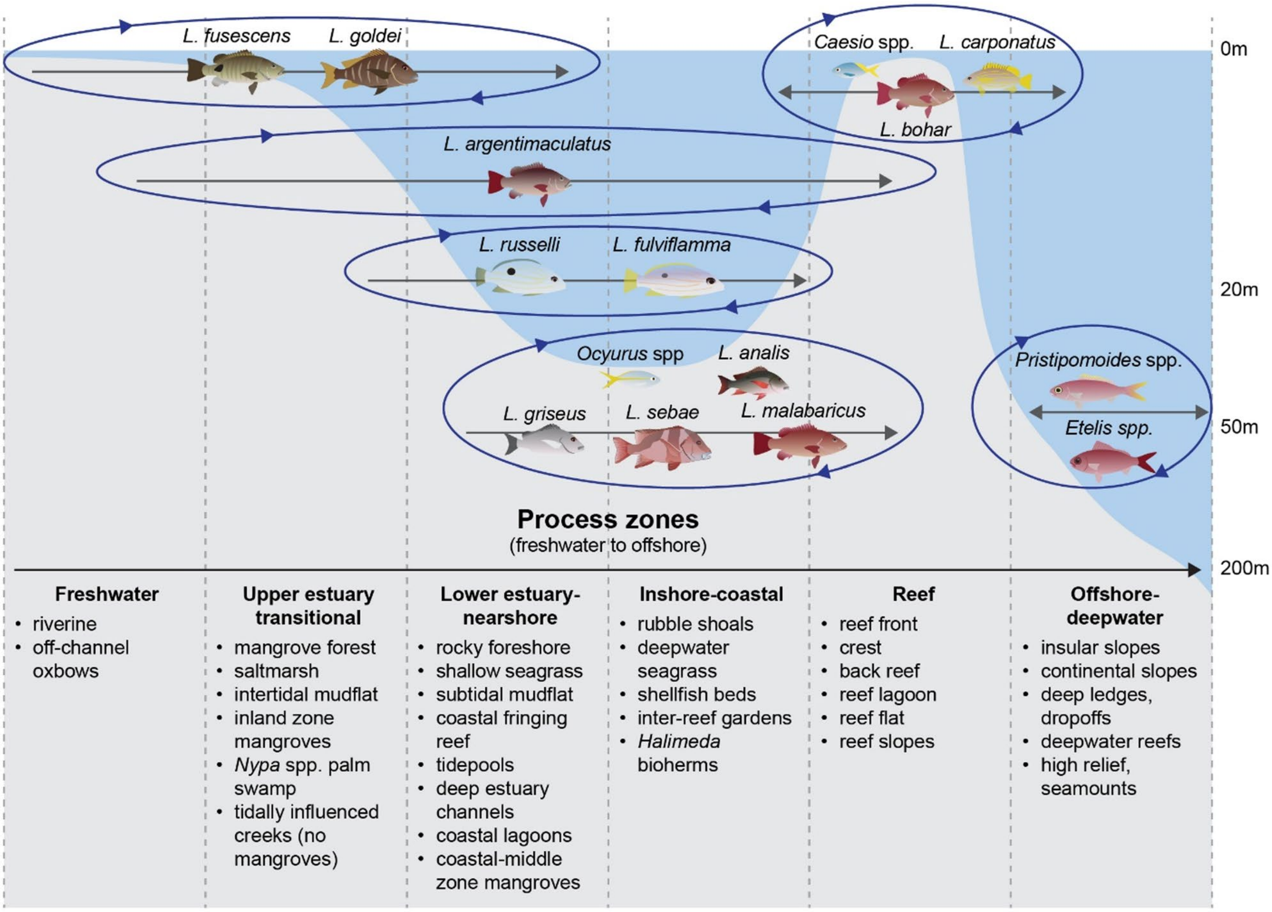

Fig. 1. Conceptual post-settlement life cycle migrations (nurseries to adult habitat) of multiple, representativelutjanid species across different Process Zones of the seascape macrohabitat mosaic, with indicative depth gradientsoutlined on right y-axis.

Adult Process Zone utility	Description and associated macrohabitat types
Freshwater-estuary	Adults predominantly use freshwater, transitional, and lower estuarine Process Zones[15–18, 20, 21]
Estuary-nearshore	Lower estuaries and nearshore habitats[19,20, 21].
Coastal-inshore	Adults utilise a variety of inshore (coastal) waters (incl. coral reefs, hard and softbottom shoals, trawl-grounds, inter-reefal areas of the continental shelf[19–21].
Reef	Adults primarily inhabit inshore (< 100 m depth) coral and rocky reefs and associated near-reef habitats[38–40].
Offshore-deepwater	Adults use deeper benthic and pelagic habitats of the outer continental shelf and continental slope including deepwater reefs, insular slopes and seamounts[36,37].

Table 2. Classification of adult utilisation of process Zones.

examples exist where clades require evolutionary intermediates between completely marine and completely freshwater lineages, but also of transitions directly from high to low salinity residency[41]. To assess whether stepwise evolutionary trajectories, with intermediate habitats may better explain the evolution of lutjanid life history diversity from deeper to shallower, low salinity habitats in the freshwater-estuary zone, we also assessed the fit of an ordered version of each ER, SYM and ARD model[42,43]. Here, a trait needs to follow an ordered evolutionary transition through sequential and intermediate Process Zones across the seascape, and the model explicitly prohibits transitions to non-adjacent states (i.e., juveniles: offshore ↔ reef ↔ inshore-coastal ↔ lower estuary-nearshore ↔ upper estuary-transitional ↔ freshwater; adults: offshore-deepwater ↔ reef ↔ coastal-inshore ↔ estuary-nearshore ↔ freshwater-estuary: see Tables 1 and 2). We also tested unidirectional, ordered 'deep to shallow' (i.e., juveniles: offshore → reef → inshore-coastal → lower estuary-nearshore → upper estuary-transitional → freshwater) and 'shallow to deep' (i.e., juveniles: freshwater → upper estuary-transitional → lower estuary-nearshore → inshore-coastal → reef → offshore) evolutionary trajectories for process zone diversification in juveniles and adults.

Model fits were evaluated using the "fitHRM" function in the corHMM package[44]with the number of rate classes set to 1. Because unidirectional models are not currently supported in corHMM, we used the "fitMk" function in phytools[43] to fit those specific models. Relative support for each model was assessed using Akaike Information Criterion (AIC) values and Akaike weights (AICw). In cases where juvenile habitat data were totally unknown (i.e., species with missing data), we provided a completely uninformative prior probability distribution for the tip state[43]. All trees were anchored using a broad representation of Haemulidae 'grunt' outgroups (a closely related clade with similar adult and juvenile habitat affiliations[15,45]) to provide better resolution of deeper root states (refer to Supplementary Table S1 online for complete species habitat coding data).

Results

Lutjanid juvenile habitats and ontogenetic habitat shifts

Considerable variability was evident in the nature and scale of nursery habitat utility, and subsequent ontogenetic habitat shifts, in the collective life history ecology of lutjanids (Fig. 1). Lutjanid juvenile nursery habitats spanned a broad diversity of environments, from freshwaters up to 1000 km upstream of the sea[28,46] to hundreds of metres depth on continental slopes[35,36]. Some lutjanids subsequent life history migration, particularly in 'Clade C *Lutjanus*', where ~ 85% of species life histories involved movement through multiple process zones across the freshwater to offshore marine continuum. In contrast, several others (> 90% of the Caesioniinae and multiple reef-associated *Lutjanus* 'Clade B' species) remained largely confined to a single 'Reef' Process Zone throughout life (although typically shifted through multiple micro-, meso- and macro-habitats within that one Process Zone with age). Ontogenetic shifts were variable across '*Lutjanus* Clade A' species, with several species remaining largely reef-associated through life history (*Pinjalo*, some *Lutjanus*), but several significant fisheries species (*L. erythopterus*, *L. malabaricus*) having nearshore juvenile phases prior to substantial offshore migration to inter-reef shoal areas to depths of at least 80 m as adults[14]. Collective literature suggests most species' juveniles settle to some form of complex, relatively shallow habitat (shallow reefs, seagrass, mangroves, intertidal-freshwater habitats)[14,16]. Some notable exceptions do apparently occur. The putative nursery habitats utilised by *Pristipomoides* and *Etelis* spp. appear very different from that described for other lutjanids. Juveniles are typically recorded inhabiting nearly flat, featureless offshore plains (depths of ~ 100 m) before shifting to high-relief features in deeper water, much like adults[35–37]. Some economically significant *Lutjanus* species also apparently settle to shallow inshore-coastal shelf habitats of relatively low vertical complexity (sand, shell, and mud) before moving gradually from inner to outer shelf hardbottom and reef habitats as they mature[30].

One notable study outcome is the marked knowledge gaps evident regarding early life histories, behaviour and subsequent migration in several major lutjanid clades. The nursery grounds for newly settled and young juveniles from several of the 'deepwater' lutjanid clades (*Paracaesio* spp.) are particularly poorly described, a surprising outcome for such commercially significant species. Underlining the challenges of research in deep-sea habitats, the limited available data on juvenile habitats is often collected largely opportunistically[35] and juvenile habitat associations for several taxa were based on limited datasets simply documenting juvenile presence in a particular habitat. Habitat preferences and distribution patterns for early life stages of many other species, particularly settling early juveniles remain similarly unknown, with individuals of these sizes (~ 30–100 mm TL) largely absent from collections or available survey data[47].

Ancestral habitat reconstructions and models of discrete habitat evolution for juveniles and adults

Of the tested evolutionary models, an ordered ARD model generated the highest AIC_W (0.77) on the 'master tree' for juvenile nursery affiliation (Table S2), with some support for a SYM model (0.23 AIC_W). This finding, consistent across the 'master tree' and 17 of the 28 'best trees' (Fig. 2a, b; Table S2), supports the interpretation that nursery habitat evolution follows a stepwise pattern through the seascape. Modelling results underscore, however, the importance of accounting for phylogenetic uncertainty in comparative analyses, with the SYM model predominating in several trees (Fig. 2b). Ancestral character state reconstruction conducted on discrete habitats using the best-fit model suggests that low salinity nurseries ('freshwater' and 'upper estuary-transitional') have evolved independently from 'lower estuary-nearshore' and 'inshore' ancestral nurseries multiple times across *Lutjanus* clade C, in African and Australasian species, rather than directly from 'Offshore' or 'Reef' nursery ancestors (Fig. 3). This implies that an intermediate step in the nearshore coastal zone is necessary to transition to low salinity nurseries. The considerable diversity of lutjanid nursery habitats (freshwater, upper estuary-transitional, lower estuary-nearshore, and inshore and offshore) seen across the clade likely all evolved from a reef nursery ancestor (posterior likelihood > 0.9), with several reversals back to utilisation of reef juvenile habitats also evident.

Reconstruction of adult Process Zone evolution and ancestry was more equivocal (Table S2), although with the strongest support for two variations of the ordered models (ordered ARD: 0.54 AIC_W; and ordered SYM: 0.46 AIC_W). Again, reflecting phylogenetic uncertainty, these models received nearly equal support across the set of 28 phylogenetic trees (Figs. 2d and 13/28 ordered ARD, 15/28 for ordered ER). While the two models differ with respect to the dynamics of underlying evolutionary rate transitions between habitat states, the analysis showed almost complete support for an ordered evolution of adult habitat utilization of Process Zones in the seascape. While use of shallower, lower salinity 'estuary nearshore' and 'fresh-coastal' affiliations only occurred 3–4 times in adult lutjanids, they typically evolved from 'coastal inshore' or 'reef' ancestors. Immediate transitions from offshore-deepwater habitats in adults, for example, to nearshore and freshwater habitats did not occur (Fig. 3),

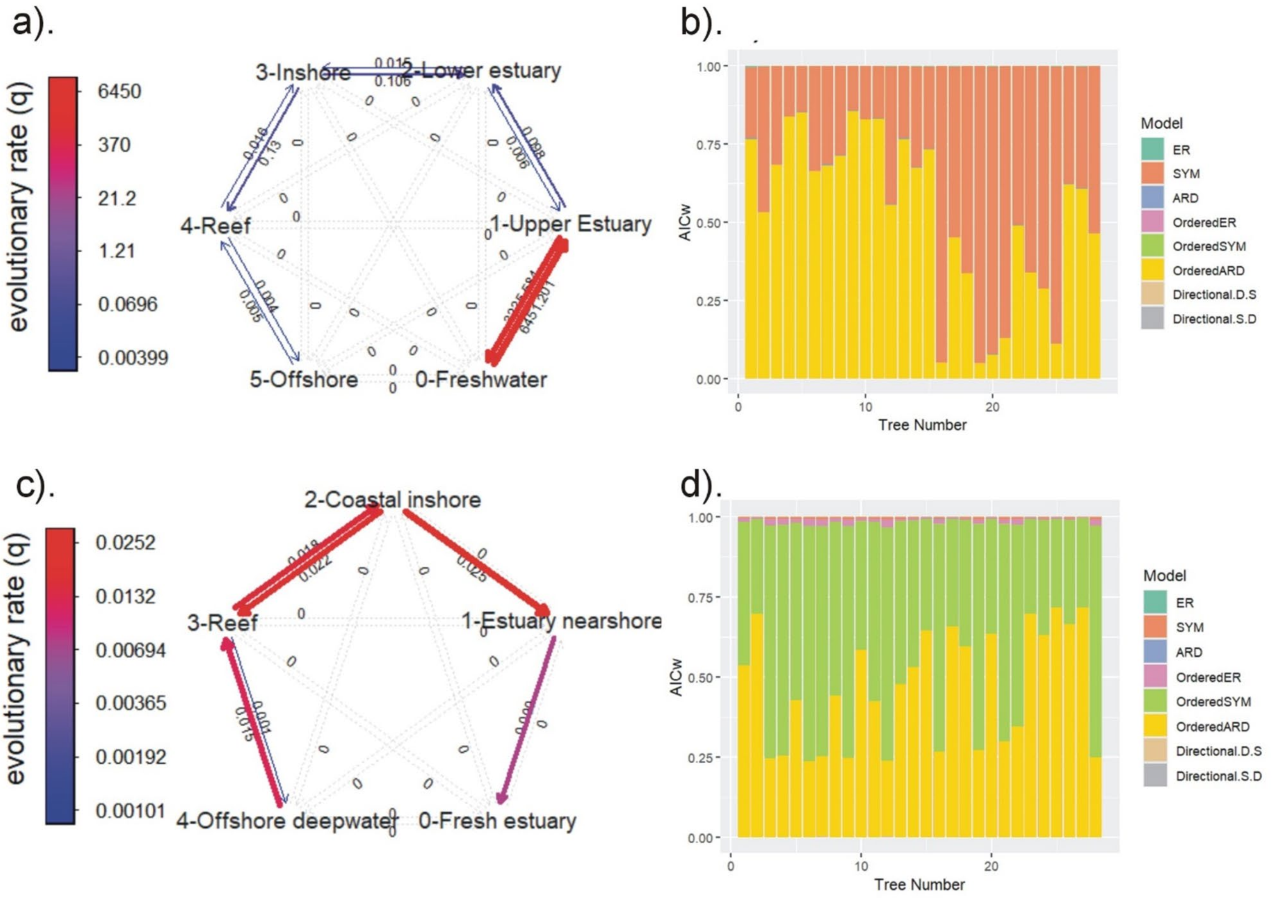

Fig. 2. **a** Fitted ordered model for juvenile nursery habitat affiliation based on the 'master tree'? (i.e., offshore (5) ➔ reef (4) ➔ inshore (3) ➔ lower estuary (2) ➔ upper estuary (1) ➔ freshwater (0); the heatbar denotes rate variations across states). **b** AIC_W for each evolutionary model based on each of the 28 'best' trees. **c** Fitted ordered model for adult habitat affiliation based on the 'master tree'? (i.e., offshore (4) ➔ reef (3) ➔ coastal inshore (2) ➔ estuary nearshore (1) ➔ fresh estuary (0)), and **d** AIC_W for each evolutionary model based on each of the 28 'best' trees.

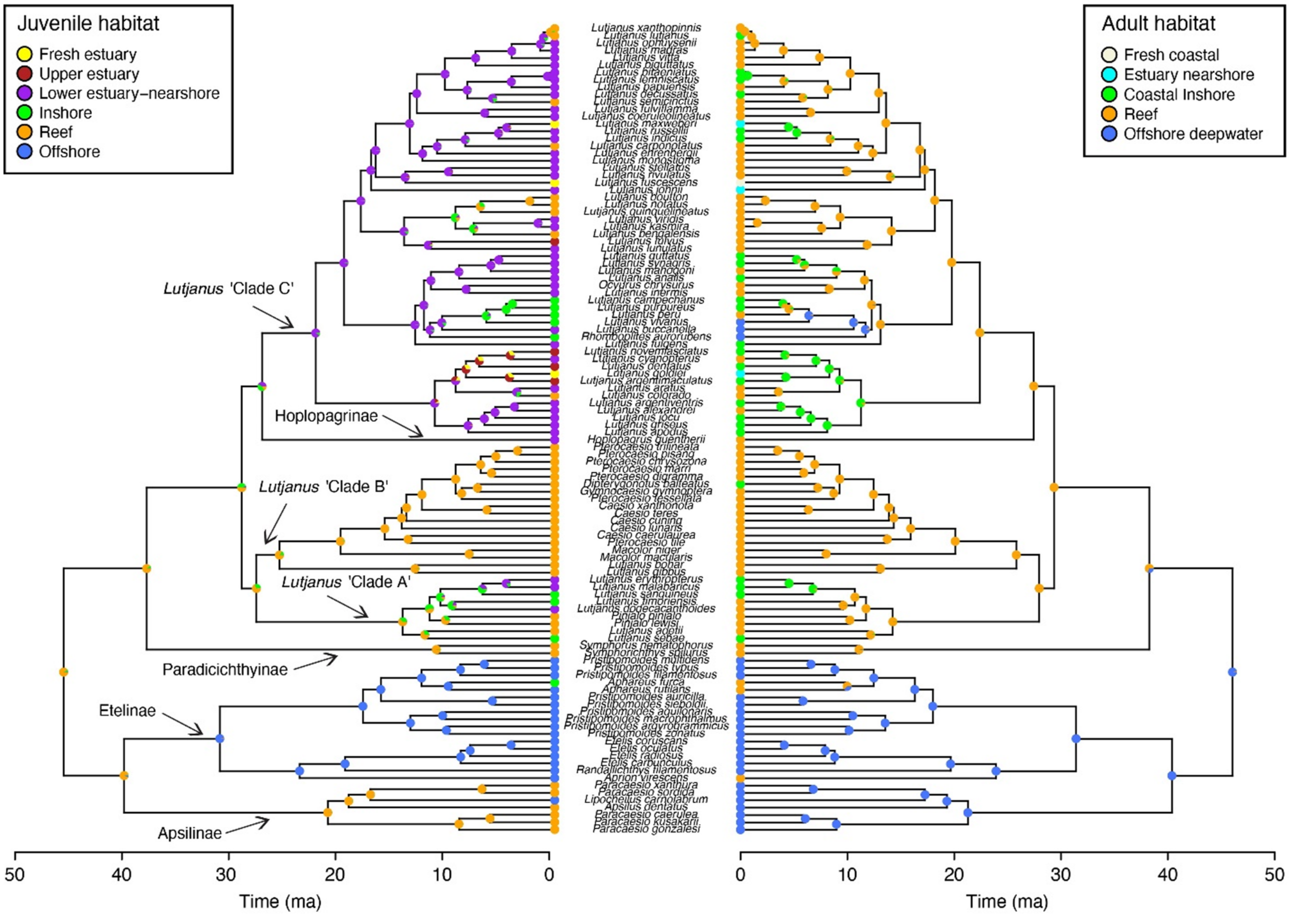

Fig. 3. Ancestral character state reconstructions based on the 'master tree' (RAxML) for juvenile (left; best-fit ordered all rates different or ARD model) and adult lutjanid habitat affiliations (right; ordered ARD model) and best-fit model derived from "fitHRM" function in the corHMM package[44]. Habitat coding based on Table 1, and major clades[6] indicated with arrows. The reconstructions were based on an expanded tree that included outgroup haemulids to obtain a better estimate of the lutjanid root states. However, the haemulid subclade was pruned for visualization purposes (for a complete tree, see Fig. S1).

and stepwise evolutionary transitions between habitats across the Process Zone continuum have a significantly better fit. Ancestral character reconstruction varied between the best-fit ordered ARD and ordered SYM models but suggested the current diversity of lutjanid adult habitat diversity likely evolved from ancestors associated with 'offshore-deepwater' or 'reef' habitat affiliations (Fig. S1). Regardless of the specific ontogenetic trajectories, juvenile and adult lutjanid habitats are typically divergent. Life history habitat shifts tend to be 'one-way', with instances of overlap in juvenile and adult habitat rare across most clades, although exceptions occur[36,48].

The plot also shows striking asymmetry between fresh coastal and nearshore estuary habitats (Fig. 2c and d), suggesting stronger habitat partitioning among adults (see synthesis below), a distinction that highlights the different ecological strategies and evolutionary pressures faced by juvenile and adult stages. Another key result of this analysis is that for both adults and juveniles, there is notable rate variation across different transitions. Rate shifts between lower salinity habitats for juveniles (states 0 to 1) and reefs to inshore and nearshore for adults (states 1 to 3), for example, typically have a higher incidence than between reefs and offshore/deepwater habitats in both stages (Fig. 2a, c).

Discussion

Macroevolutionary implications of Lutjanid habitat usage over life history

While changes in water column association have driven significant ecomorphological evolution across the lutjanid family[6,] this study highlights another major component of lutjanid ecological diversification involves life cycle migrations, particularly the nature of seascape utility across different species and clades. Study results suggest ordered, progressive shifts across the process zone continuum, in both juveniles and adults, drive this ecological diversity, particularly into lower salinity habitats. Considerable comparative research has focused on the evolutionary transitions between marine and freshwater life histories, and how migratory strategies such as diadromy may act as precursors or intermediates to macroevolutionary transitions between salinity regimes[41]. The role of low salinity nurseries as intermediate 'stepping stones' that facilitate marine-freshwater invasions, such as the largely freshwater existence of some *Lutjanus* species, has received relatively minimal research attention. How complete the transition to freshwater residency is in some lutjanids also remains unclear, with the possibility some species may now spawn in low salinity habitats (unlike the rest of the marine-spawning family)[20,21]. Interestingly, other Australasian families that have successfully invaded freshwaters, such as terapontids, also have many nearshore marine species, with juveniles that utilise freshwaters and other low salinity nurseries[7].

Much of this diversification has also apparently occurred within the constraints of a conserved perch-like (percomorph) body plan and minimal changes from a carnivorous diet. Ecological variability in lutjanids, particularly in some major clades (Lutjanid 'Clade C') involves substantial diversification in juvenile and sub-adult (and ostensibly adult) habitat associations around the freshwater-marine interface and how species utilise the coastal seascape through life history. Study results also raise questions about the macroevolutionary role of coral reefs in lutjanid diversification. Adoption or invasion of reef habitats has, for example, been consistently proposed as key drivers of lineage and ecomorphological diversification in many fishes and other taxa[9,10,49]. Habitat reconstructions raise the tantalising possibility that while a substantial component of the modern lutjanid fauna largely evolved in situ on reefs, the life history associations of adults and juveniles suggest reefs may have also promoted evolutionary 'spillover' into other habitats, exporting lineage and ecological diversification into adjacent process zones (particularly adoption of low salinity and coastal juvenile nursery and adult habitat associations).

While ontogenetic habitat shifts appear to be a widespread phenomenon across most lutjanids, the environmental scale of subsequent migration following pelagic larval settlement across different clades can vary dramatically. Size-related 'migration' following settlement can apparently be restricted to just the scale of individual reefs (from exclusive juvenile use of sheltered reef sites to exposed reef sites in adults), and occur in several different clades[32–34]. Long-range movements at the scales of tens to hundreds of kilometres, from freshwater-upper estuaries to offshore reefs, have also been documented in multiple species[28,50]. Until relatively recently, only indirect evidence (i.e., higher juvenile densities, size structure differences, presumably lower predation risk) existed regarding the actual contribution of higher juvenile biomass in these putative nursery habitats to adult lutjanid populations[51–53]. A growing body of literature employing multiple, emerging technologies is providing a much more integrated, longer-term, but also granular, definition of seascape use over the entire life history of many lutjanids[21]. The clear and often disproportionately large (per area of habitat) contribution of nearshore mangrove and seagrass habitats to adult *Lutjanus* offshore reef populations has now been repeatedly documented for many species across several different biogeographic regions[50,52–58]. Otolith microchemistry similarly reveals significant early juvenile recruitment into low salinity or freshwater areas in adult populations of several Australasian lutjanid species[21].

Previous studies (that included several lutjanids) have proposed several possible models for Post-settlement Life Cycle Migrations (PLCM) applicable to reef-dwelling adult fishes[18,59]. These include settlement and growth in nearshore habitats such as mangroves and seagrass beds, and a later stage migration to coral reefs (Long Distance PLCM); settlement in close proximity to the coral reef or on the reef itself, and subsequent migration involves a limited spatial scale (Short Distance PLCM); and a Stepwise PLCM pattern in which the smallest juveniles dwell in the mouth of the bay, larger individuals then move to habitats deeper into the bay, where they grow up to a (sub-) adult size at which they migrate to nearby coral reef habitats[18]. How applicable such definitions, based around geographic distance, are in adequately describing broader lutjanid habitat migrations seen in some contexts may be questionable. Some seascape configurations can see multiple process zones (freshwaters, transitional, estuary, nearshore, reef) located near each other, separated by just 100s of metres[21] but shifts can be profound in terms of environmental factors (salinity, depth, turbidity, temperature) over even these short distances. Similarly, it has been proposed that in some seascape contexts where coral reefs and seagrass nurseries exist in proximity, individuals that require both resources may simply expand their home range with maturity rather than shifting to deeper, offshore coral reefs[27]. We suggest instead ontogenetic shifts classified on the scale of Process Zones utilised over life history are a more appropriate conceptual framework for future evolutionary scale research questions on lutjanid life histories (Fig. 1). Some species, for example, can complete life history within a single Process Zones (settling and growing to adulthood entirely on offshore, oceanic reefs), whereas others will move across multiple Process Zones through life history.

The ecological drivers of Lutjanid life history variation

The specific mechanisms catalysing the almost ubiquitous ontogenetic habitat shifts seen across lutjanids have attracted considerable research attention. A range of ecological interactions have been posited, for example, dietary competition[18] maturation [23] and predation (regarded as particularly intense on reef habitats)[35,37,60]. Trade-offs likely exist between fitness advantages conferred for reef inhabitants (enhanced growth rates and high prey availability on reefs) and reduced survival rates for small fishes on reefs due to predation or competition. Nearshore habitats may function as predation refugia, but competition for prey and foraging efficiency may also play roles in catalysing ontogenetic niche shifts towards more profitable adult habitats in these systems[60–62]. A somewhat surprisingly overlooked catalyst for ontogenetic habitat shifts observed in lutjanids is the potential bioenergetic benefits of reduced osmoregulatory demands in lower salinity environments. Maintaining cellular ion and osmotic concentrations within relatively narrow limits (1/3 osmotic strength of seawater) is a requirement for normal function in most bony fishes[63–65]. Studies on the aquaculture potential of various *Lutjanus* species have documented frequent outcomes where survivorship or growth of developing juveniles is greater in salinity ranges intermediate between freshwater and seawater[66,67]. The increased metabolic costs in high salinities represent a significant energy cost for developing lutjanid juveniles that would need to be balanced by lower predation risk or greater food availability to result in similar juvenile production compared to lower salinity environments[67].

Few lutjanid species, however, appear confined to obligate use of a single nursery habitat, and some species are ‘nursery generalists’, being found in nearly all the habitats examined (seagrass, channels, hardbottom, patch reefs, etc.)[60]. Collective evidence suggests, however, species-specific habitat preferences occur in many species[15,22,58–60]but with capacity to utilise alternative nurseries when preferred habitats are absent[16,21,50,60,68]. There may also be significant flexibility in life-history movement patterns, and the possibility for multiple migratory contingents and skip spawners (otherwise mature individuals yet to make seascape scale movements) in lutjanid populations[21,27]. Sex-based differences in ontogenetic habitat shifts are also yet to be well-studied, with some species, at least, exhibiting some apparent degree of sexual differentiation in habitat utilisation in adult size classes[69]. Further study of lutjanid species broadly across their range could provide insights into the extent to which seascape and life cycle movement patterns are fixed throughout a species’ range, or if some species exhibit flexible life-history movement patterns depending on the seascape context[24,70].

The need for more consistent, transferable and structured research frameworks

Comparative studies at a broad phylogenetic scale, by necessity, often simplify ecological complexity. Future research into the ecological and evolutionary drivers of lutjanid life history evolution would undoubtedly benefit from more considered and consistent hierarchical framing of habitat use over life history[24]. One fish settlement dynamic apparent in lutjanids (as well as more broadly) is that initial fish settlement areas, i.e. primary nurseries, are often followed by subsequent movement by fishes to other habitats, i.e. secondary nurseries[71]. For several of the better-studied lutjanid species, such multiple ontogenetic habitat shifts are evident during the early juvenile period, and immediate post-settlement juveniles (< 5 cm) can inhabit very different habitats from later post-settlement juveniles (50–100 mm) and sub-adults[18,52,68]. Many lutjanid species, particularly those utilising nearshore, and particularly low salinity nurseries, have settling larvae (and early-stage juveniles) that navigate through the open ocean ‘wall of mouths’ formed by coastal predators[55,72]across multiple coastal environments, making deliberate upstream movement into low salinity nurseries, bypassing, or only temporarily using, several habitat types known to attract juveniles of other lutjanids.

Many previous juvenile nursery function studies also apply a landscape-scale perspective, in which seagrass beds and coral reefs, for example, are treated as independent, homogenous macrohabitat units. Settling and early-stage juveniles of many species appear to preferentially target very distinctive microhabitat-scale features within larger meso- and macrohabitats for settlement (pebble beds, mangrove prop roots, coral rubble with holes, small coral heads in open sand habitats close to reefs[19,31,73–75]. While data is scarce, movement studies of recently settled lutjanids suggest mean home ranges of just several square metres[17]. A more precise partitioning of these often-missed, transient, first-stage habitat periods would be very informative for future macroevolutionary (and other) studies evaluating the nursery and seascape function of particular habitats as they may form population bottlenecks for early post-settlement stages[21,76]. In contrast, large individuals of many lutjanids are increasingly recognised as making regular short-term (diel, monthly, seasonal) wide-ranging seascape movements, spanning tens of kilometres, often encompassing multiple macrohabitat patches, if not entire Process Zones in the seascape mosaic[21,26,27].

Seascape configuration (the geographic distribution of habitats) appears to play a particularly critical role in determining connectivity among habitats and contributions of specific nurseries to adult populations at a landscape scale[24,50,76,77]. The concept of ecological constraints (environmental, spatial, etc.) are also yet to be fully adapted and applied to nursery habitat definition and identification[78,79]. Local environmental factors such as tidal and salinity regimes, for example, appear to act as important drivers of specific habitat connectivity, and subsequent utility of certain potential nursery habitats by many lutjanids[24,68,78]. Presence of resident con- and hetero-specifics can also play a strong attracting role for settling lutjanid larvae, the strength of which depends on the type of microhabitat available and the body size of conspecifics[74,80]. The roles of the seascape matrix and specific movement corridors used by many lutjanids to migrate through life history also remain unknown, but likely have crucial conservation and management considerations[19,36]. Specific habitats such as *Halimeda* beds, inter-reefal habitat, and deepwater estuaries could be significant conduits for many species in facilitating direct interaction between nearshore nurseries and marine fauna[19,79]. Increases in body size and temporal activity behaviours see the hierarchical scaling of lutjanid habitat association shift from the scale of micro- to macrohabitat over life history. Figure 4 outlines a conceptual model for the habitat components, drivers and different research approaches relevant to better defining different ontogenetic elements of lutjanid habitat use across a seascape mosaic.

Conclusions

Synthesised data on lutjanids demonstrates that ontogenetic habitat shifts are a recurrent theme throughout lutjanid evolution, and these shifts are often complex and multi-stage for many species. Even with the broad-ranging movements as adults, stepped movements through the seascape, and a general trend for the centre of the home range for larger individuals to shift into deeper process zones remain common[21]. Lutjanids also collectively utilise a diverse spectrum of nursery habitats across the seascape mosaic, from freshwaters through to the benthos of continental slopes far offshore, and these transitions often require intermediate stages in coastal zones, illustrating the gradual nature of habitat evolution. The distinct partitioning of habitats between juvenile and adult stages also reflects the varying ecological strategies and pressures they face, with juveniles often inhabiting different environments from adults. Variability in juvenile habitat usage could play a significant and currently underappreciated role in the broader macroevolution of lutjanids, particularly in relation to utility of low salinity habitats. Complex interplays and trade-offs between predation, competition, and osmoregulatory demands likely drive the nature and scale of nursery habitat diversification across different clades.

For the ecological and macroevolutionary implications of these shifts to be fully unpacked will require a more consistent and transferable application of research frameworks, definitions, and integration of multiple research

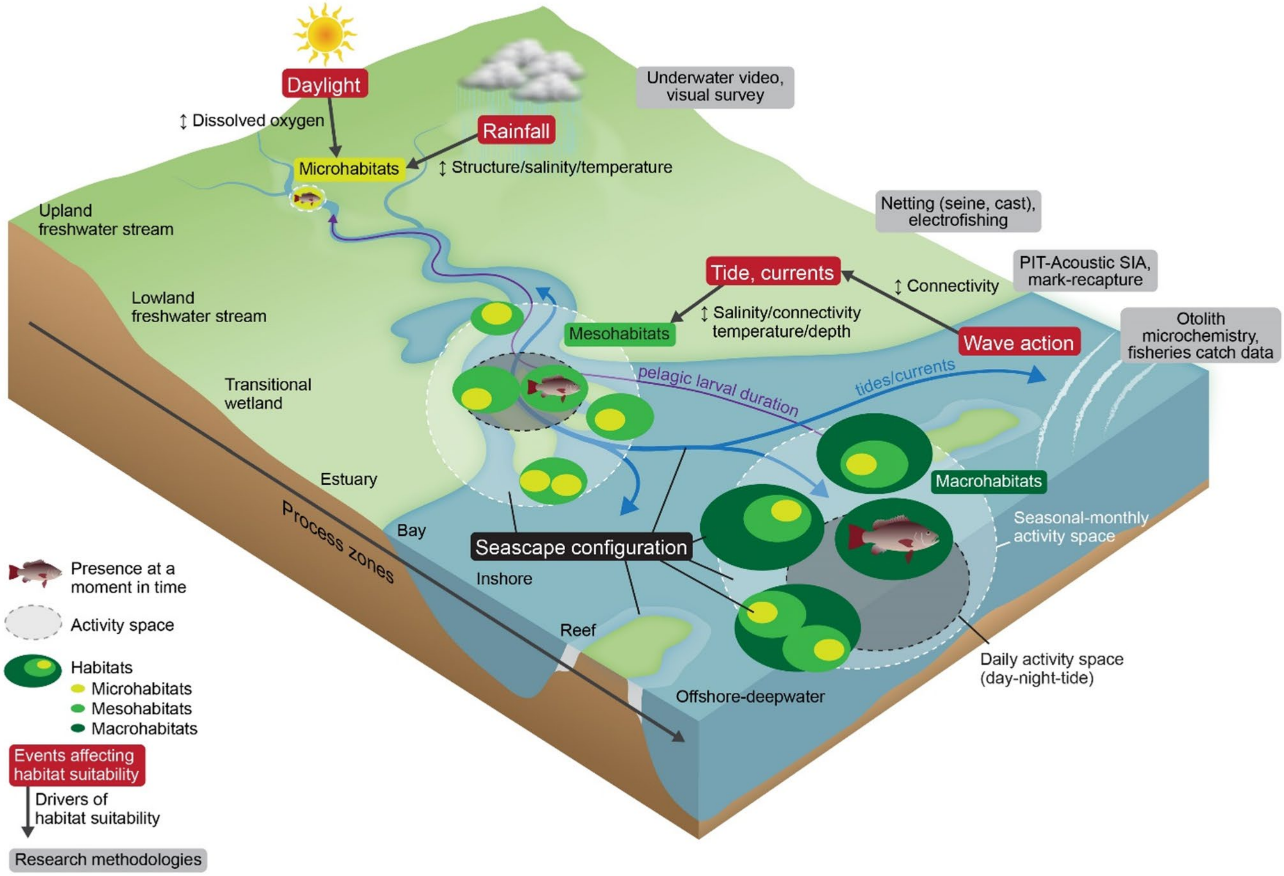

Fig. 4. Conceptual schematic of the spatial scaling (micro- to macro-habitats) and environmental-ecological factors influencing and constraining the utilisation of different habitat types over the life history of a lutjanid in a coastal seascape mosaic. The different research methodologies relevant to defining different habitat associations for different life history stages are outlined in grey boxes.

approaches and methodologies. Issues of appropriately spatially scaling the habitat context of lutjanid life history become particularly apparent across the literature. Post-settlement of juveniles, daily activity ranges increase with fish size, from just metres to tens if not hundreds of kilometres in some cases, spanning multiple Process Zones and macrohabitats, and moving from the scale of micro- to macrohabitat[27,50]. Lutjanids also exhibit considerable diversity in other notable aspects of life history strategy, such as longevity and body size traits[14,37] , which aredocumented in other clades as associating with migratory behaviours[3]. Failure to recognise these ontogenetic niche shifts as a potential source of ecological opportunity, could lead to incomplete frameworks describing the major drivers of ecomorphological diversity and the key mechanisms governing macroevolutionary processes within clades.

Data availability

All data generated or analysed (phylogenetic trees and species habitat coding) during this study are included in this manuscript, and its supplementary information files, or available from the corresponding author on request.

Received: 12 September 2024; Accepted: 3 June 2025

References

1. Werner, E. & Gilliam, J. The ontogenetic niche and species interactions in Size-Structured populations. *Ann. Rev. Ecol. Syst.* **15**, 393–425. https://doi.org/10.1146/annurev.es.15.110184.002141 (2003).
2. Burns, M. D. & Bloom, D. D. Migratory lineages rapidly evolve larger body sizes than non-migratory relatives in ray-finned fishes. *Proc. Royal Soc. B* 287. https://doi.org/10.1098/rspb.2019.2615 (2020).
3. Feutry, P. et al. Evolution of diadromy in fish: insights from a tropical genus (*Kuhlia* species). *Am. Nat.* **181**, 52–63 (2013).
4. Bloom, D. D. & Lovejoy, N. R. On the origins of marine-derived freshwater fishes in South America. *J. Biogeog.* **44**, 1927–1938 (2017).
5. Lee, C. E. & Bell, M. A. Causes and consequences of recent freshwater invasions by saltwater animals. *Trends Ecol. Evol.* **14**, 284–288 (1999).
6. Rincon-Sandoval, M. et al. Evolutionary determinism and convergence associated with water-column transitions in marine fishes. *Proc. Nat. Acad. Sci. USA*. **117**, 33396–33403. https://doi.org/10.1073/pnas.2006511117 (2022).

7. Davis, A. M., Pusey, B. J. & Betancur-R, R. Effects of adoption of freshwater residency on life-history ecology of terapontid grunters. *Freshw. Biol.* **65**, 1139–1152. https://doi.org/10.1111/fwb.13499 (2020).
8. Rincon-Sandoval, M. et al. Dramatic ecological diversification of sea catfishes is accompanied by genome-wide signatures of positive selection. *Nat. Comm.* In press. (2024).
9. Alfaro, M., Santini, F. & Brock, C. D. Do reefs drive diversification in marine teleosts? Evidence from the pufferfishes and their allies (order Tetraodontiformes). *Evolution* **61**, 2104–2126 (2007).
10. Price, S. A., Holzman, R., Near, T. J. & Wainwright, P. C. Coral reefs promote the evolution of morphological diversity and ecological novelty in labrid fishes. *Ecol. Lett.* **14**, 462–469 (2011).
11. Gray, J. A., Sherratt, E., Hutchinson, M. N. & Jones, M. E. H. Changes in ontogenetic patterns facilitate diversification in skull shape of Australian Agamid lizards. *BMC Evol. Biol.* **19** https://doi.org/10.1186/s12862-018-1335-6 (2015).
12. Dornburg et al. Considering decoupled phenotypic diversification between ontogenetic phases in macroevolution: An example using triggerfishes (Balistidae), *System. Biol.* 73, 434–454; (2024). https://doi.org/10.1093/sysbio/syae014 (2024).
13. Froese, R., & Pauly, D. Editors. 2023.FishBase. World wide web electronic publication. http://www.Fishbase.Org (2023).
14. Newman, S. J. & Williams, D. M. Variation in reef associated assemblages of the Lutjanidae and Lethrinidae at different distances offshore in the central great barrier reef. *Environ. Biol. Fish.* **46**, 123–138. https://doi.org/10.1007/BF00005214 (1996).
15. Lindeman, K. C., Diaz, G. A., Serafy, J. E. & Ault, J. S. A Spatial framework for assessing cross-shelf habitat use among newly settled grunts and snappers. *Proc. Gulf Carib Fish. Inst.* **50**, 385–416 (1998).
16. Nagelkerken, I., Dorenbosch, M., Verberk, W. C. E. P., Cocheret de la Moriniére, E. & van der Velde, G. Importance of shallow-water biotopes of a Caribbean Bay for juvenile coral reef fishes: patterns in biotope association, community structure and Spatial distribution. *Mar. Ecol. Prog Ser.* **202**, 175–192 (2000).
17. Watson, M., Munro, J. & Gell, F. R. Settlement, movement and early juvenile mortality of the Yellowtail snapper *Ocyurus chrysurus*. *Mar. Ecol. Prog Ser.* **237**, 247–256 (2002).
18. de la Cocheret, E., Pollux, B. J. A., Nagelkerken, I. & van der Velde, G. Postsettlement life cycle migration patterns and habitat preference of coral reef fish that use seagrass and Mangrove habitats as nurseries. *Estuar. Coast Shelf Sci.* **55**, 309–321 (2002).
19. Cappo, M. & Kelley, R. Connectivity in the Great Barrier Reef World Heritage Area - An Overview of Pathways and Processes in *Oceanographic Processes of Coral Reefs: Physical and Biological Links in the Great Barrier Reef* (ed. Wolanski, E.) 161–187CRC Press, (2001).
20. Sheaves, M., Barnett, A., Bradley, M., Abrantes, K. G. & Bryans, M. *Life History Specific Habitat Utilisation of Tropical Fisheries Species* (James Cook University, Townsville, 2016).
21. Baker, R. et al. Contrasting seascape use by a coastal fish assemblage: a Multi-methods approach. *Estuar. Coast.* **42**, 292–307. https://doi.org/10.1007/s12237-018-0455-y (2019).
22. Adams, A. et al. Nursery function of tropical back-reef systems. *Mar. Ecol. Progr Ser.* **318**, 287–301. https://doi.org/10.3354/meps318287 (2006).
23. Sheaves, M. Large Lutjanid and serranid fishes in tropical estuaries: are they adults or juveniles? *Mar. Ecol. Prog Ser.* **129**, 31–40 (1995).
24. Bradley, M., Nagelkerken, I., Baker, R. & Sheaves, M. Context dependence: a conceptual approach for Understanding the habitat relationships of coastal marine fauna. *Bioscience* **70**, 986–1004 (2020).
25. Thorp, J. H., Thoms, M. C. & Delong, M. D. The riverine ecosystem synthesis: biocomplexity in river networks across space and time. *River Res. Applic.* **22**, 123–147 (2006).
26. Luo, J. G., Serafy, J. E., Sponaugle, S., Teare, P. B. & Kieckbusch, D. Movement of Gray snapper *Lutjanus griseus* among subtropical seagrass, mangrove, and coral reef habitats. *Mar. Ecol. Progr Ser.* **380**, 255–269 (2009).
27. Hitt, S., Pittman, S. J. & Nemeth, R. S. Diel movements of fishes linked to benthic seascape structure in a Caribbean coral reef ecosystem. *Mar. Ecol. Progr Ser.* **427**, 275–291 (2011).
28. Russell, D. J. & McDougall, A. J. Movement and juvenile recruitment of Mangrove jack, *Lutjanus argentimaculatus* (Forsskal), in Northern Australia. *Mar. Freshw. Res.* **56**, 465–475 (2005).
29. Moura, R. L. & Lindeman, K. C. A new species of snapper (Perciformes: Lutjanidae) from brazil, with comments on distribution of *Lutjanus griseus* and *L. apodus zootaxa*, **1422**, 31–43 (2007).
30. Szedlmayer, S. T. & Lee, J. D. Diet shifts of juvenile red snapper (*Lutjanus campechanus*) with changes in habitat and fish size. *Fish. Bull.* **102**, 366–375 (2004).
31. Sweatman, H. P. A. Tropical snapper (Lutjanldae) that is piscivorous at settlement. *Copeia* 1133–1139 (1993). (1993).
32. Wright, A., Dalzell, P. J. & Richards, A. H. Some aspects of the biology of the red bass, *Lutjanus bohar* (Forsskal), from the Tigak islands. Papua new Guinea. *J. Fish. Biol.* **28**, 588–544 (1986).
33. Quéré, G. & Leis, J. Settlement behaviour of larvae of the Stripey snapper, *Lutjanus carponotatus* (Teleostei: Lutjanidae). *Environ. Biol. Fishes*. **88**, 227–238. https://doi.org/10.1007/s10641-010-9633-x (2010).
34. Valenzuela, J., Bellwood, D., Morais, R. & & Ontogenetic habitat shifts in Fusiliers (Lutjanidae): evidence from *Caesio cuning* at Lizard island, great barrier reef. *Coral Reefs*. **40** https://doi.org/10.1007/s00338-021-02180-0 (2021).
35. Moffitt, R. & Parrish, F. Habitat and life history of juvenile Hawaiian Pink snapper, *Pristipomoides filamentosus*. *Pac. Sci.* **50**, 371–381 (1996).
36. Kelley, C. D. & Moriwake, V. N. Appendix 3: Essential Fish Habitat descriptions, Part 1: bottomfish in *Final fishery management plan for coral reef ecosystems of the western Pacific region, volume III, Essential Fish Habitat for Management Unit Species* (ed. WPRFMC) 597 (2012).
37. Newman, S. J. et al. Review of the life history characteristics, ecology and fisheries for deep-water tropical demersal fish in the indo-pacific region. *Rev. Fish. Biol. Fish.* **26**, 537–562. https://doi.org/10.1007/s11160-016-9442-1 (2016).
38. Lindeman, K. & DeMaria, D. Juveniles of the caribbean's largest coral reef snapper do not use reefs. *Coral Reefs*. **24**, 359–359. https://doi.org/10.1007/s00338-005-0015-3 (2005).
39. Shibuno, T., Nakamura, Y., Horinouchi, M. & Sano, M. Habitat use patterns of fishes across the mangrove-seagrass-coral reef seascape at Ishigaki island, Southern Japan. *Ichthyol. Res.* **55**, 218–237. https://doi.org/10.1007/s10228-007-0022-1 (2008).
40. Vignon, M. Ontogenetic trajectories of otolith shape during shift in habitat use: interaction between otolith growth and environment. *J. Exp. Mar. Biol. Ecol.* **420**, 26–32. https://doi.org/10.1016/j.jembe.2012.03.021 (2012).
41. Corush, J. B. Evolutionary patterns of diadromy in fishes: more than a transitional state between marine and freshwater. *BMC Evol. Biol.* **19**, 168. https://doi.org/10.1186/s12862-019-1492-2 (2019).
42. Revell, L. & phytools An R package for phylogenetic comparative biology (and other things). *Meth Ecol. Evol.* **3**, 217–223. https://doi.org/10.1111/j.2041-210X.2011.00169.x (2012).
43. Revell, L. Phytools 2.0: an updated R ecosystem for phylogenetic comparative methods (and other things). *BioRxiv* **2023.03.08.531791** https://doi.org/10.1101/2023.03.08.531791 (2023).
44. Beaulieu, J., O'Meara, B., Oliver, J. & Boyko, J. corhmm: Hidden Markov models of character evolution. [URL]. R package version 2.8 (2022).
45. Tavera, J., Acero, P. A. & Wainwright, P. C. Multilocus phylogeny, divergence times, and a major role for the benthic-to-pelagic axis in the diversification of grunts (Haemulidae). *Mol. Phylogenet Evol.* **121**, 212–223. https://doi.org/10.1016/j.ympev.2017.12.032 (2018).
46. Sheaves, M. et al. The conservation status of Niugini black bass: a world-renowned sport fish with an uncertain future. *Fish. Manag Ecol.* **23**, 243–252 (2016).

47. Leis, J. M. & Lee, K. Larval development in the Lutjanid subfamily Etelinae (Pisces): the genera *Aphareus, aprion, Etelis* and *Pristipomoides*. *Bullet Mar. Sci.* **55**, 46–125 (1994).
48. Ikehara, W. FAO Rome,. Bottomfish management and monitoring in the main Hawaiian Islands in *Deep Sea 2003: Conference on the Governance and Management of Deep-sea Fisheries. Part 2: Conference Poster Papers and Workshop Papers, Queenstown, New Zealand, 1–5 December 2003, Dunedin, New Zealand, 27–29 November 2003, FAO Fisheries Proceedings 3/2* (ed. Shotton, R.) 289–300 (2006).
49. Kiessling, W., Simpson, C. & Foote, M. Reefs as cradles of evolution and sources of biodiversity in the phanerozoic. *Science* **327**, 196–198 (2010).
50. McMahon, K. W., Berumen, M. L. & Thorrold, S. R. Linking habitat mosaics and connectivity in a coral reef seascape. *Proc. Nat. Acad. Sci. USA*. **109**, 15372–15376 (2012).
51. Verweij, M. C., Nagelkerken, I., Hol, K. E. M., van den Beld, A. H. J. B. & van der Velde, G. Space use of *Lutjanus apodus* including movement between a putative nursery and a coral reef. *Bull. Mar. Sci.* **81**, 127–138 (2007).
52. Mateo, I. et al. Role of mangroves as nurseries for French grunt *Haemulon flavolineatum* and schoolmaster *Lutjanus apodus* assessed by otolith elemental fingerprints. *Mar. Ecol. Prog Ser.* **402**, 197–212 (2010).
53. Kimirei, I. A., Nagelkerken, I., Mgaya, Y. D. & Huijbers, C. M. The Mangrove nursery paradigm revisited: otolith stable isotopes support nursery-to-reef movements by Indo-Pacific fishes. *PLoS ONE*. **8**, e66320. https://doi.org/10.1371/journal.pone.0066320 (2013).
54. Nakamura, Y. et al. Evidence of ontogenetic migration from mangroves to coral reefs by black-tail snapper *Lutjanus fulvus*: stable isotope approach. *Mar. Ecol. Prog Ser.* **355**, 257–266 (2008).
55. Huijbers, C. M., Nagelkerken, I., Debrot, A. O. & Jongejans, E. Geographic coupling of juvenile and adult habitat shapes Spatial population dynamics of a coral reef fish. *Ecology* **94**, 1859–1870 (2013).
56. Berkström, C., Jörgensen, T. L. & Hellström, M. Ecological connectivity and niche differentiation between two closely related fish species in the mangrove – seagrass – coral reef continuum. *Mar. Ecol. Prog Ser.* **477**, 201–215 (2013). https://www.jstor.org/stable/24891498
57. Gerard, T., Malca, E., Muhling, B. A., Mateo, I. & Lamkin, J. T. Isotopic signatures in the otoliths of reef-associated fishes of Southern florida: linkages between nursery grounds and coral reefs. *Reg. Stud. Mar. Sci.* **2**, 95–104 (2015).
58. Bastos, R. F. et al. Ontogeny drives allochthonous trophic support of snappers: seascape connectivity along the mangrove-seagrass-coral reef continuum of a tropical marine protected area. *Estuar. Coast Shelf Sci.* **264**, 107591. https://doi.org/10.1016/J.ECSS.2021.107591 (2022).
59. Díaz-Ruiz, S., Aguirre-León, A., Pérez-Solís, O. & Macuitl-Montes, C. Seasonal patterns of distribution and abundance of snappers in the Mexican Caribbean. In *Biology, Fisheries and Culture of Tropical Groupers and Snappers* (eds. Arreguín-Sánchez, F., Munro, J.L., Balgos, M.C. & Pauly, D.). *ICLARM Conf. Proc.* 48, 449 (1996).
60. Eggleston, D. B., Dahlgren, C. P. & Johnson, E. G. Fish density, diversity, and size-structure within multiple back reef habitats of key West National wildlife refuge. *Bull. Mar. Sci.* **75**, 175–204 (2004).
61. Bartels, C. T. & Ferguson, K. L. Preliminary observations of abundance and distribution of settlement—stage snappers in shallow, nearshore seagrass beds in the middle Florida keys. *Proc. Gulf Carib Fish. Inst.* **67**, 235–247 (2006).
62. Chittaro, P. M., Usseglio, P. & Sale, P. F. Variation in fish density, assemblage composition and relative rates of predation among mangrove, seagrass and coral reef habitats. *Environ. Biol. Fish.* **72**, 175–187. https://doi.org/10.1007/s10641-004-9077-2 (2005).
63. Edwards, S. & Marshall, W. Principles and patterns of osmoregulation and euryhalinity in fishes. *Fish. Physiol.* **32**, 1–44. https://doi.org/10.1016/B978-0-12-396951-4.00001-3 (2013).
64. Ishikawa, A. et al. A key metabolic gene for recurrent freshwater colonization and radiation in fishes. *Science* **364**, 886–889. https://doi.org/10.1126/science.aau5656 (2019).
65. Velotta, J. P., McCormick, S. D., Whitehead, A., Durso, C. S. & Schultz, E. T. Repeated genetic targets of natural selection underlying adaptation of fishes to changing salinity. *Integr. Comparat Biol.* **62**, 357–375. https://doi.org/10.1093/icb/icac072 (2024).
66. Estudillo, C. B., Duray, M. N., Marasigan, E. T. & Emata, A. C. Salinity tolerance of larvae of the Mangrove red snapper *Lutjanus argentimaculatus* during ontogeny. *Aquaculture* **190**, 155–167 (2000).
67. Wuenschel, M. J., Jugovich, A. R. & Hare, J. A. Metabolic response of juvenile Gray snapper (*Lutjanus griseus*) to temperature and salinity: physiological cost of different environments. *J. Exp. Mar. Biol. Ecol.* **321**, 145–154 (2005).
68. Dorenbosch, M. et al. Homing and daytime tidal movements of juvenile snappers (Lutjanidae) between shallow-water nursery habitats in zanzibar, Western Indian ocean. *Environ. Biol. Fish.* **70**, 203–209. https://doi.org/10.1023/B:EBFI.0000033336.10737.f5 (2004).
69. Starck, W. A. The biology of the grey snapper, *Lutjanus griseus* (Linnaeus), in the Florida Keys in *Investigations on the gray snapper, Lutjanus griseus. Studies in Tropical Oceanography 10* (eds. Starck, W. A & Schroeder, R.E.). Rosenstiel School of Marine and Atmospheric Sciences, University of Miami Press, Florida, 150p. (1971).
70. Kimirei, I. A., Nagelkerken, I., Griffioen, B., Wagner, C. & Mgaya, Y. D. Ontogenetic habitat use by mangrove/seagrass-associated coral reef fishes shows flexibility in time and space. *Estuar. Coast Shelf Sci.* **92**, 47–58 (2011).
71. Able, K. W., Simenstad, C. A., Strydom, N. A., Bradley, M. & Sheaves, M. in *Habitat Use and Connectivity in Fish and Fisheries in Estuaries: A Global Perspective*. 188–254 (eds Whitfield, A. K., Able, K. W., Blaber, S. J. M. & Elliott, M.) (Wiley Blackwell, 2022).
72. Igulu, M. M. et al. Orientation from open water to settlement habitats by coral reef fish: behavioral flexibility in the use of multiple reliable cues. *Mar. Ecol. Prog Ser.* **493**, 243–257 (2013). https://www.jstor.org/stable/24892817
73. Nanami, A. & Yamada, H. Seasonality, lunar periodicity of settlement and microhabitat association of juvenile humpback red snapper Lutjanus gibbus (Lutjanidae) in an Okinawan coral reef. *Mar. Biol.* **156**, 407–414. https://doi.org/10.1007/s00227-008-1093-x (2008).
74. Igulu, M. M. et al. The potential role of visual cues for microhabitat selection during the early life phase of a coral reef fish (*Lutjanus fulviflamma*). *J. Exp. Mar. Biol. Ecol.* **401**, 118–125. https://doi.org/10.1016/j.jembe.2011.01.022 (2011).
75. Nanami, A. Co-occurrence of seagrass vegetation and coral colonies supports unique fish assemblages: a microhabitat-scale perspective. *PeerJ* e14466. https://doi.org/10.7717/peerj.14466 (2022).
76. Nagelkerken, I., Sheaves, M., Baker, R. & Connolly, R. M. The seascape nursery: a novel Spatial approach to identify and manage nurseries for coastal marine fauna. *Fish. Fish.* **16**, 362–371. https://doi.org/10.1111/faf.12057 (2015).
77. Paillon, C., Wantiez, L., Kulbicki, M., Labonne, M. & Vigliola, L. Extent of Mangrove nursery habitats determines the geographic distribution of a coral reef fish in a South-Pacific Archipelago. *PLoS ONE*. **9**, e105158. https://doi.org/10.1371/journal.pone.0105158 (2014).
78. Mattone, C., Bradley, M., Barnett, A., Konovalov, D. & Sheaves, M. Environmental conditions constrain nursery habitat value in Australian sub-tropical estuaries. *Mar. Environ. Res.* **175**, 105568. https://doi.org/10.1016/j.marenvres.2022.105568 (2022).
79. Bradley, M., Baker, R. & Sheaves, M. Hidden components in tropical seascapes: deep-estuary habitats support unique fish assemblages. *Estuar. Coast.* **40**, 1195–1206 (2017).
80. Lee, C. L. & Lin, H. J. Ontogenetic habitat utilization patterns of juvenile reef fish in low-predation habitats. *Mar. Biol.* **162**, 1799–1811. https://doi.org/10.1007/s00227-015-2712-y (2015).

Acknowledgements

Kate Hodge (Hodge Environmental) is acknowledged for support in producing conceptual models. Christopher Kelley (University of Hawaii) and Andrea Schmidt (Cooperative Institute for Marine and Atmospheric Research, Pacific Islands Fisheries Science Center) are acknowledged for valuable assistance with deepwater snapper habitat associations. Two anonymous reviewers are thanked for comments and suggestions that greatly strengthened an earlier version of the manuscript. This research was supported by the National Science Foundation grant NSF DEB-2225130 awarded to R.B.R.

Author contributions

A.M.D. and R.B.R. conceived the study. A.M.D., M.S. and A.V. performed the data compilation. A.M.D. performed the data analysis. A.M.D., R.B.R., A.V. and M.S. discussed the results and drafted the manuscript. All authors provided comments on the manuscript. Two anonymous reviewers are thanked for comments that strengthened the manuscript.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1038/s41598-025-05879-0.

Correspondence and requests for materials should be addressed to A.M.D.

Reprints and permissions information is available at www.nature.com/reprints.