Nearshore seascape connectivity enhances seagrass meadow nursery function

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Abstract. Diverse habitats composing coastal seascapes occur in close proximity, connected by the flux of materials and fauna across habitat boundaries. Understanding how seascape connectivity alters important ecosystem functions for fish, however, is not well established. For a seagrass-dominant seascape, we predicted that configuration and composition of adjacent habitats would alter habitat access for fauna and trophic subsidies, enhancing nursery function for juvenile fish. In an extensive *Zostera marina* seagrass meadow, we established sites adjacent to (1) highly complex and productive kelp forests (*Nereocystis luetkeana*), (2) unvegetated sand habitats, and (3) in the seagrass meadow interior. Using SCUBA, we conducted underwater observations of young-of the-year (YOY) rockfish (*Sebastes* spp.) recruitment across sites. Using generalized linear mixed effects models, we assessed the role of seascape adjacency relative to seagrass provisions (habitat complexity and prey) on YOY recruitment. YOY rockfish collections were used to trace sources of allochthonous vs. autochthonous primary production in the seagrass food web, via a $\delta^{13}C$ and $\delta^{15}N$ isotopic mixing model, and prey consumption using stomach contents. Overall, seagrass nursery function was strongly influenced by adjacent habitats and associated subsidies. Allochthonous *N. luetkeana* was the greatest source of energy assimilated by YOY rockfish within seagrass sites. In seagrass sites adjacent to *N. luetkeana* kelp forests, YOYs consumed higher quality prey, which corresponded with better body condition relative to sites adjacent to sand. Moreover, kelp forest adjacency enhanced YOY rockfish recruitment within the seagrass meadow, suggesting that habitat complexity is a key seascape feature influencing the nursery function of nearshore habitats. In general, to promote seascape connectivity, the conservation and restoration of nursery habitats should prioritize the inclusion of habitat mosaics of high structural complexity and productivity. We illustrate and emphasize the importance of using a seascape-level approach that considers linkages among habitats for the management of important nearshore ecosystem functions.

Key words: eelgrass; food web; habitat complexity; habitat configuration; kelp forests; predator–prey interactions; rockfish; spatial subsidies; stable isotopes; Zostera marina.

INTRODUCTION

Ecosystems are naturally linked by fluxes across habitat boundaries, influencing the structure and function of communities (Loreau et al. 2003). However, accelerating habitat loss and fragmentation from anthropogenic activities are altering landscape and seascape connectivity worldwide (Haddad et al. 2015). Accordingly, declines in habitat-dependent biota and key ecosystem functions are widespread (Ellison et al. 2005, Hughes et al. 2009). Yet, in the oceans, little is known about how seascape connectivity affects nearshore ecosystem functions, such as nursery effects, and how such functions will respond to the progression of habitat loss (Boström et al. 2011), or have the potential to mitigate this loss (Olds et al. 2015).

"Seascapes" are a spatially defined marine area consisting of multiple habitat patches. Seascapes are connected by proximity to neighboring habitats and the movement of fauna, material, and nutrients, herein "seascape connectivity" (Grober-Dunsmore et al. 2009, Sheaves 2009). Seascape connectivity may alter the role of habitats in supporting marine communities when linkages among habitats are established and/or lost (Ries et al. 2004, Ellison et al. 2005, Hughes et al. 2009, Thompson et al. 2017). Within seascapes, specific

habitat attributes ("seascape features") can mediate the flow and access of materials among habitats, resulting in varying effects on biological communities. These interactive seascape features can be grouped into broad categories: (1) the spatial arrangement of habitats and (2) the composition of habitat (Olds et al. 2015, Staveley et al. 2017, Van Wynsberge et al. 2017).

The spatial arrangement of habitats can alter movement patterns of fauna in the seascape via edge effects, corridors, and patch sizes, by providing optimal areas for shelter, foraging, or migration (McMahon et al. 2012, Berkström et al. 2013). Edges, distinct boundaries between two habitats, can facilitate access to spatially distinct subsidies, such as nutrients and prey, or access to habitat (Fagan et al. 1999, Ries et al. 2004, Rand et al. 2006). In addition, the composition (i.e., type) of habitats can further alter connectivity depending on their structural complexity. Habitats with high structural complexity (e.g., mangroves, biogenic reefs) offer contrasting shelter, productivity, and provision of subsidies compared to unvegetated habitats with low structural complexity (e.g., unvegetated sand). Mediated by these seascape features and transported by hydrodynamics forces or mobile fauna, resources from donor habitats can dramatically affect consumer–resource dynamics that enhance community diversity and/or densities in recipient habitats (i.e., "spatial subsidies"; Polis et al. 1997, Fagan et al. 1999, Massol et al. 2011); important components of nursery function (Fig. 1).

Located within nearshore habitat mosaics spanning coastlines globally, seagrass meadows are an important nursery habitat for many marine fishes and invertebrates (Beck et al. 2001, Nagelkerken et al. 2002, Dorenbosch et al. 2005). Seagrass meadows provide complexity in the water column, increase faunal refugia, support epiphytic algal production, and in turn, sustain invertebrate grazers available for consumers (Orth et al. 1984, Kennedy et al. 2018). Seagrass meadows, therefore, tend to have higher juvenile densities, survival, and growth, potentially resulting in increased movements to adult habitats relative to unvegetated habitats (Heck et al. 2003, McDevitt-Irwin et al. 2016). Seagrass meadow nurseries have primarily been studied at a single-habitat scale, but it is increasingly acknowledged that they are highly connected to their surrounding habitats (McMahon et al. 2012, Olds et al. 2012, Hyndes et al. 2014). Recent evidence suggests that fluxes of nutrients and materials (Davis et al. 2014, Ricart et al. 2015), as well as fauna (Staveley et al. 2017, Perry et al. 2018) to seagrass meadows are spatially mediated by adjacent habitats. As seagrass and other nearshore habitats decline worldwide (Orth et al. 2006, Waycott et al. 2009), understanding how seagrass nursery function is affected by seascape connectivity can fill a critical knowledge gap for coastal conservation and management that often occurs at seascape-level scales (Boström et al. 2006, Nagelkerken et al. 2013).

In marine environments, the cross-boundary exchange of resources between ecosystems (Dale and
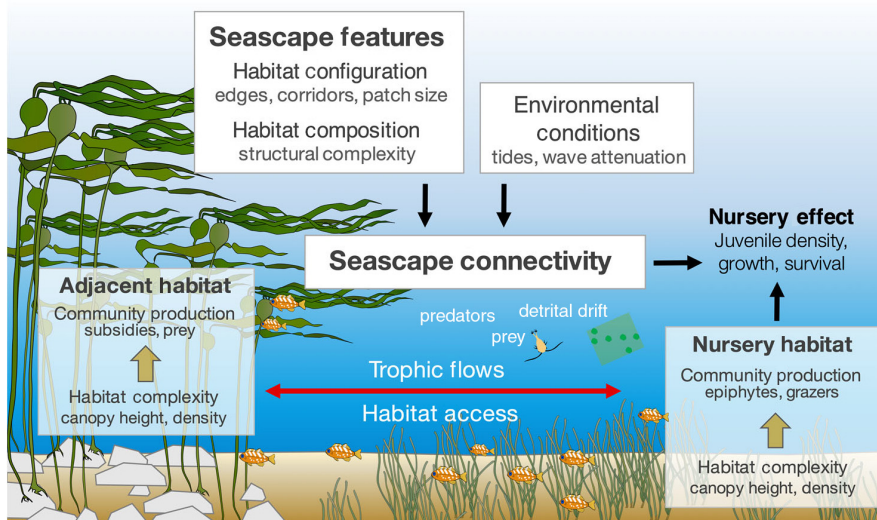

Fig. 1. A conceptual diagram of seascape connectivity influencing nearshore nursery habitats. Seascape features, such as (1) habitat configuration and (2) habitat composition, together with environmental processes, can mediate trophic flows and proximity between nearshore habitats (i.e., seascape connectivity). Nursery habitats and their adjacent habitat neighbors vary in their structural complexity, which influences their overall community productivity (e.g., basal production, prey diversity, epiphyte biomass), as well vary in spatial configuration to one another. As a result, key seascape features may facilitate connections between habitats, via allochthonous subsidies (prey and detritus) or habitat access, and in turn, influence juvenile densities, growth, and survival in nursery habitats.

Prego 2002, Naiman et al. 2002), and between tropical seascape habitats (Berkström et al. 2013, Davis et al. 2014) is well documented. Yet, empirical studies on connectivity between high complexity temperate coastal habitats are limited (McDevitt-Irwin et al. 2016). Kelp forests and seagrass habitats can form coastal habitat mosaics along northern temperate coastlines, where kelp forests may support seagrass nurseries in a number of ways (Fig. 1). Adding vertical structure and biomass to the water column, kelp forests increase habitat complexity available for organisms (Graham 2004, Trebilco et al. 2015), as well as export nutrients and detritus into the marine environment (Krumhansl and Scheibling 2012, Hyndes et al. 2014). This allochthonous production can become important food sources to recipient consumers in seagrass meadows (Doropoulos et al. 2009, Hyndes et al. 2012), and has been observed to promote secondary production in other marine systems (Kelly et al. 2012).

In the northeast Pacific, temperate seagrass meadows are nurseries for rockfishes (*Sebastes* spp.): a biologically, culturally, and commercially important group of fishes in decline due to overfishing (Love et al. 2002, Yamanaka and Logan 2010, Eckert et al. 2017). After a pelagic larval stage, some rockfish species recruit to shallow nearshore habitats, such as seagrass meadows and kelp forests, before transitioning to deeper adult habitats (Love et al. 1991). Post-recruitment processes that can be mediated by habitat complexity, such as reduced mortality or increased growth, are critical during these juvenile stages (Johnson 2007, Juanes 2007) and may regulate population success (Haggarty et al. 2017, Tupper and Juanes 2017). Thus, increased habitat access and subsidies from seascape connections may affect juvenile rockfishes by increasing their growth or survival (Kamimura and Shoji 2013).

Determining how connectivity between seagrass meadows and kelp forests influences the nursery function for declining rockfish populations is important to nearshore habitat management. In response, this study investigated how adjacent habitats in a seagrass–kelp-forest–sand seascape influenced components of seagrass meadow nursery function. We observed young-of-the-year (YOY) rockfish recruitment and feeding ecology within a large temperate *Zostera marina* meadow at seagrass sites adjacent to kelp forests (*Nereocystis luetkeana*), unvegetated sand habitats, and in the meadow interior (Fig. 2). We hypothesized that adjacent *N. luetkeana* kelp forests would enhance seagrass meadow nursery function through two mechanisms: (1) increased allochthonous subsidies (primary production and prey) to YOY rockfish diets and (2) greater YOY rockfish recruitment to the meadow edge where habitat complexity is maximized from both seagrass and kelp forest three-dimensional structure (Connell and Jones 1991). Conversely, we predicted that nursery function would decrease at sites adjacent to unvegetated sand due to a lack of allochthonous inputs and habitat complexity.

METHODS

Study area and design

We conducted this study in a subtidal *Z. marina* meadow in Choked Passage on British Columbia's (Canada) central coast (Fig. 2a, b). The shoreline complexity of the central coast allows for a diverse matrix of nearshore marine habitats within this seascape (Hessing-Lewis et al. 2018). Similar to other northern-latitude coastlines, mixed patches of seagrass, kelp forest habitats (*N. luetkeana* and/or *Macrocystis pyrifera*), and sand habitats are common elements of this region. The expansive (367,300 m^2) and near-contiguous seagrass meadow is situated between a large outer coast island (Calvert Island) and exposed rocky islets to the west. Canopy-forming *N. luetkeana* kelp beds propagate from the adjacent rocky reefs, while unvegetated sand flats border Calvert Island's shoreline and deeper waters (Fig. 2c). The *Z. marina* meadow is, on average, 3.5 m deep and is subject to high-current tidal exchanges.

We used SCUBA surveys to identify seascape features around the *Z. marina* meadow, based on the arrangement (herein, "edge"), and composition of adjacent habitat: high complexity (*N. luetkeana* kelp forest) or low complexity (unvegetated sand). Once mapped, we partitioned the perimeter into 50-m sections, categorized the sections by adjacent habitat type, and assigned them a unique number, which was used for random site selection. We randomly selected seagrass edge sections (*n* = 4 per edge type) as study sites (Fig. 2c, white circles and squares, kelp edge and sand edge, respectively). The interior of the seagrass meadow (>200 m from edges) was also mapped, and randomized coordinates and compass directions were used to establish seagrass interior sites (*n* = 4, Fig. 2c, triangles). As rockfish have high site-fidelity during early life stages (Hoelzer 1988, Nelson 2001), we assumed biological site independence by maintaining a minimum distance of 100 m between meadow sites during site-selection. For additional habitat comparisons of recruitment, sites were also established within the *N. luetkeana* kelp forests (*n* = 4) and sand habitats (*n* = 4), directly adjacent to the seagrass edge sites (Fig. 2c, gray symbols).

Food web field collections and analyses

To quantify seascape subsidies in the seagrass meadow, we collected key constituents of the seagrass food web: YOY rockfish, invertebrate prey, and primary producers.

YOY Rockfish—In late August to early September 2015, we used a modified otter trawl (10-mm mesh) to capture
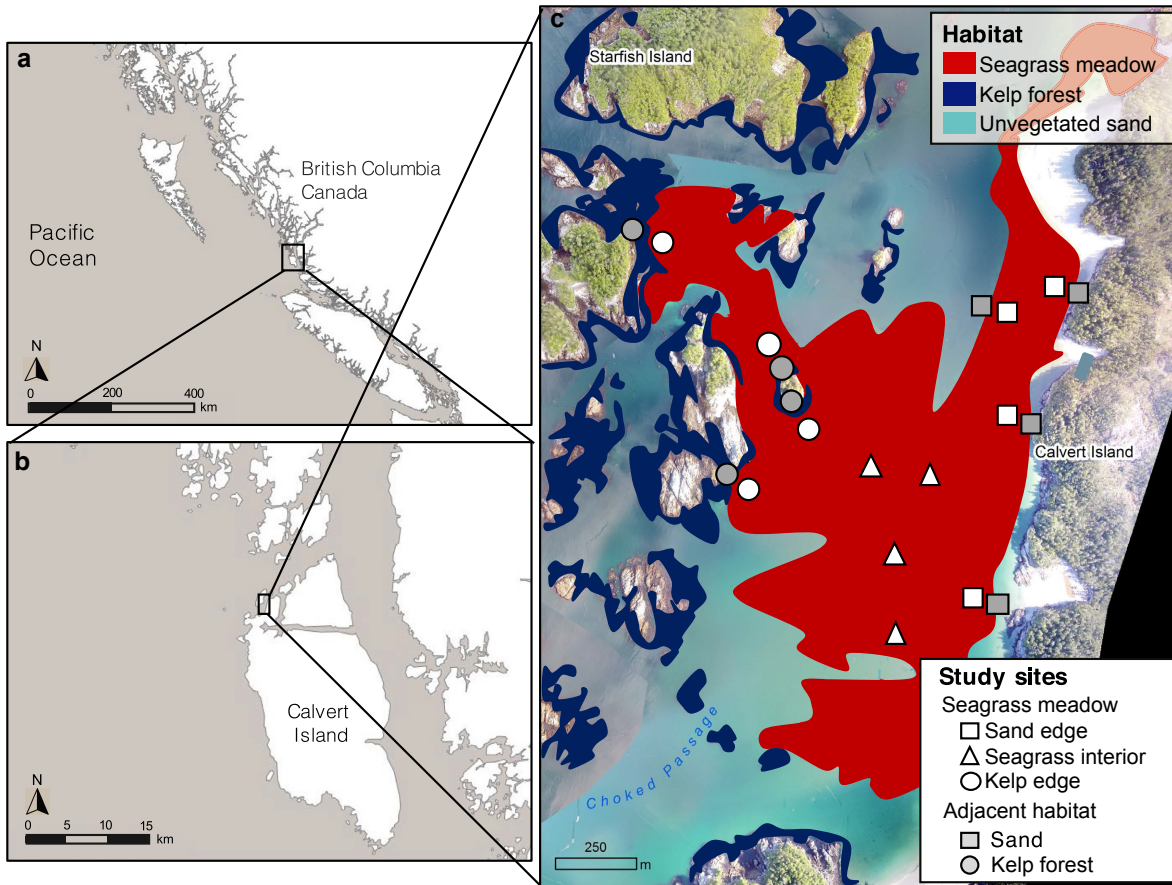
FIG. 2. (a, b) Map of the study area located northwest of Calvert Island, British Columbia, Canada and (c) the focal nearshore seascape in Choked Passage. The seagrass meadow (red) is ~367,000 m², bordered by *Nereocystis luetkeana* kelp forests (dark blue) and unvegetated sand (light blue). Study sites in the seagrass meadow (white) include seagrass interior (triangles), *N. luetkeana* kelp edge (circles, high complexity adjacent habitat), and sand edge sites (squares, low complexity adjacent habitat). Sites were also established within the adjacent habitats: *N. luetkeana* kelp forest (gray circles) and unvegetated sand sites (gray squares).

recently recruited YOY rockfish at seagrass sites. The trawl was towed from a small boat at slow speed for 5 min through the seagrass canopy. The majority of rockfish captured were identified as part of the copper rockfish (*Sebastes caurinus*)–quillback rockfish (*Sebastes maliger*) juvenile complex. YOY copper-quillbacks were immediately sacrificed by blunt force, and measured for total length (mm) and mass (g). Stomachs were dissected and stored in ethanol for dietary analysis. The remaining whole bodies were frozen for isotope analysis.

Stomach content analysis—Prey items retrieved from the stomachs were identified to the lowest taxonomic level possible using a dissecting microscope and grouped by similar taxonomy (Appendix S1: Table S1). Prey was counted and weighed to the nearest milligram per prey group. A conservative count of 1 was assigned to a group if digestion affected the intactness of prey. If a group was too light to register a mass, a conservative 0.001 mg was assigned. Proportional representation of a prey item, based on the total sum of prey across each

site type (e.g., sand edge, seagrass interior, and kelp edge), was estimated using percent numeric (% N), gravimetric (% G), and frequency of occurrence (% O). An index of relative importance (% IRI) facilitated comparisons (Liao et al. 2001, Hart et al. 2002), and was used in the calculations of prey diversity (Shannon index; H') and Pielou's evenness (J), defined as the similarity of prey items in consumer diet (Appendix S1: Section S1).

Primary producers—Dominant primary producers were haphazardly collected from all sites by SCUBA to estimate source contributions to the food web in an isotopic mixing model. Seagrass-associated sources (i.e., autochthonous) collected were *Z. marina*, and its locally dominant epiphytic algae, *Smithora naiadum*. Allochthonous sources were *N. luetkeana* blades collected from individual plants in the adjacent kelp forest sites. Other common macroalgae, *Cymathaere triplicata* and *Alaria marginata* (herein "understory kelps"), were collected because of their presence in small patches or as drift in

or near the seagrass meadow. Particulate organic matter (POM) was collected using plankton tows at 0 and 5 m depths over the seagrass meadow and 2 km outside of the seagrass bed, to represent oceanic conditions. Samples were stored frozen until laboratory processing. YOY rockfish and primary producers were collected within the same month to minimize confounding temporal changes in their isotopic signatures.

Isotope preparation and analysis—Primary producers were defrosted and cleaned of contaminating materials using visual inspection and gentle scraping. The longest *Z. marina* blade per shoot and the total epiphyte biomass per shoot were used for isotopic analysis. For *N. luetkeana*, *C. triplicata*, and *A. marginata*, a subsample of tissue from the outermost section of the blade was used for analysis. Due to the small body sizes of the YOY rockfishes, the whole body (except the gut) was used for isotopic analysis. All samples were rinsed in two baths of deionized water. The samples were dried at 60°C for 48 h and packed in tin capsules for isotopic measurement using a Delta IV Isotope Ratio Mass Spectrometer at the University of Victoria. $\delta^{15}N$ and $\delta^{13}C$ signatures were calculated using the ratio of heavy to light isotope relative to a laboratory standard and were measured in per mil (‰):

$$\delta^{15}N/\delta^{13}C = [(R_{sample}/R_{standard}) - 1] \times 10^3$$

where $R = {}^{15}N{:}^{14}N$ or ${}^{13}C{:}^{12}C$, respectively. Carbon to nitrogen (C:N) ratios were calculated using the mass ratio between the %C and %N in the samples. Because lipids contain mostly carbon, and little nitrogen, it is assumed that an increase in C:N value positively correlates with body condition. For juvenile rockfish, lipids may be a more accurate indicator of nutritional condition than inferences by length and mass regressions (Norton et al. 2001). Analysis of variance (ANOVA) and Tukey's HSD were used to test for differences in rockfish body condition (C:N ratio) among seagrass sites.

Mixing model—Using stable isotopes, we applied a Bayesian mixing model to estimate the relative contributions of autochthonous vs. allochthonous basal energy to YOY rockfish collected in seagrass sites: sand edge ($n = 25$), seagrass interior ($n = 30$), and kelp edge ($n = 33$; Appendix S2: Table S1). To trace energy movement from primary producer to consumer, trophic enrichment (TE) of consumer signatures needed to be accounted for. TE is the process in which the heavy isotope is preferentially assimilated into consumer tissue via metabolic processes, which results in an enrichment bias in consumer isotopic signatures (Deniro and Epstein 1981, Minagawa and Wada 1984). Discrimination factors (change per mil, Δ ‰) are used to estimate TE in consumer–prey interactions. By deducting TE from consumer isotope signatures based on prey interactions, it is possible to trace backwards to the isotopic signatures of primary producers from which energy was derived (Reid et al. 2008, Phillips et al. 2014).

To do this, we constructed a seagrass trophic model to estimate predatory–prey interactions in this seagrass food web (Appendix S2: Section S1, Fig. S1) based on long-term monitoring of the Choked Passage seagrass food web (Hessing-Lewis et al. 2018) and established trophic relationships in temperate seagrass food webs (Appendix S1, S2; Hughes et al. 2013). The seagrass trophic model outlines the consumption of primary sources (e.g., seagrass, macroalgae) by invertebrate grazers, which in turn, are consumed by YOY rockfish. Discrimination factors were assigned to each trophic interaction using averaged values from McCutchan et al. (2003), based on our isotope sample processing methods and consumer characteristics. Total TE was summed across all trophic levels and deducted from YOY rockfish signatures (Appendix S2: Fig. S2), after the latter were normalized for lipids as per Post et al. (2007). Mixing models are highly sensitive to discrimination factors (Bond and Diamond 2011), thus we incorporated estimates of uncertainty in TE (Appendix S2: Fig. S1) and assessed TE-corrected consumer signatures to be within an acceptable range of primary producer signatures (Appendix S2: Fig. S2; Phillips et al. 2014).

We used the R package MixSIAR (Version 3.1.10; Moore and Semmens 2008) to estimate the relative proportions of *Z. marina* ($n = 25$), *S. naiadum* ($n = 17$), *N. luetkeana* ($n = 5$), understory kelp ($n = 10$), and POM ($n = 8$) contributing to YOY rockfish. *C. triplicata* and *A. marginata* were grouped as understory kelps according to isotopic similarity, relative palatability, and biological characteristics (Phillips et al. 2014). An uninformative prior was used to give an equal probability of consumption among primary producers and site type was analyzed as a fixed effect. To retrieve the posterior density estimates of source contribution, model iterations were run 10^5 times, with the first half of the estimations discarded.

Observational surveys

To assess rockfish recruitment across the seascape, we used SCUBA diving and snorkel surveys to record rockfish densities associated with seagrass meadow habitat complexity, prey biomass, and predators.

Rockfish recruitment—YOY copper-quillback rockfish densities were quantified during three observation periods to establish seasonal recruitment dynamics: early (May–June), middle (early July), and late (July–August) summer. In nearshore habitats, rockfishes typically exhibit ontogenetic habitat shifts from an initial preference for the water column to later movement to benthic habitats (Carr 1991). To survey the full water column, both snorkel (high water column) and SCUBA (low water column) were used to record fish abundances and sizes on a

40×4 m permanent transect at each site. All fish species were recorded on surveys and fish sizes were estimated using an underwater ruler. Rockfish 3–6 cm in length were classified as YOY recruits (Love et al. 1991). Observed current was recorded on a six-point categorical scale from none to very strong. In each observation period, sites were surveyed by SCUBA (three or four surveys) and snorkel (three or four surveys); site surveys were separated by several days. Each survey included an instant repeat transect pass by a different recorder to capture observer effects. Seagrass edge sites were surveyed 2 m into the meadow from the perimeter. Fish surveys were also conducted in *N. luetkeana* kelp forest and sand sites. A total of 791 surveys were conducted, hierarchically nested by observation period, site visit, visual method, and observer.

Seagrass habitat complexity and prey provision—During observation periods, metrics of seagrass habitat complexity and prey availability were collected at seagrass meadow sites. Using SCUBA, shoot density (count per 25×25 cm quadrat) and canopy height (maximum blade length) were measured every 5 m along the transect ($n = 9$ quadrats per transect). Divers collected seagrass shoots every 10 m along the transect ($n = 5$ shoots per transect) for shoot, epifauna, and epiphyte biomass. Shoots were covered with a collection bag and detached from the rhizome to ensure seagrass invertebrates (herein, "mesograzers") were captured in association with the shoot sample. Shoots were scraped of epiphytes and weighed (g). Length was measured from the first internode to blade tip. Scraped material was combined with free-floating material from the sample bag and passed through a 500-μm sieve prior to enumeration. Epifaunal mesograzers (>500 μm) were identified, counted, and weighed (mg). Epiphytic algae >500 μm (e.g., *S. naiadum*, *Ulva* sp., and *Punctaria* sp.) were also sorted and weighed (mg). Biomass samples (shoots, mesograzers, epiphytes) were dried at 60°C for 48 h to obtain dry mass.

Factors influencing YOY recruitment—We used generalized linear mixed-effects models (GLMMs) to determine the relative roles of seagrass habitat complexity, seagrass prey, and adjacent habitat type on YOY rockfish densities. To aggregate key properties of seagrass habitat complexity (biomass, density, and canopy height), a principal component analysis (PCA) was performed to obtain a singular seagrass habitat complexity metric (Appendix S3: Table S1). We used gammarid amphipod biomass to represent seagrass meadow prey provision because they were prevalent in both the YOY stomach contents and seagrass shoot collections. Black rockfish (*S. maliger*, >10 cm), copper rockfish (>10 cm), and kelp greenling (*Hexagrammos decagrammus*) densities were used to represent predators (Hobson et al. 2001). To account for collinearity between seagrass habitat complexity and other faunal densities (rockfish prey and

predators), we used the residual values of gammarid biomass and residual predator density from sequential linear regressions with seagrass habitat complexity (slope $b = 0.19$, $P < 0.001$, $b = 0.12$, $P < 0.001$; respectively) as predictors in the GLMMS (Graham 2003). An a priori model set was used to assess the strength of evidence for seagrass habitat complexity, seagrass prey, predators, and adjacent habitat type in predicting YOY recruitment (Appendix S3: Table S2). Candidate models varied in fixed effects, but included the same random effects: depth (chart datum), current, and diver nested within ordinal date, the latter to account for repeated surveys on the same day and over time. Continuous variables were standardized as per Gelman (2008). Model fits were compared using Akaike's information criterion corrected for small sample size (AIC_c) values, where the lowest relative AIC_c (ΔAIC_c) and highest relative weight (W_i) indicated the best model (Burnham and Anderson 2004).

RESULTS

Relative contribution of basal sources to YOY copper-quillback rockfish

Allochthonous production was the dominant source of energy assimilated by YOY copper-quillback rockfish at all seagrass meadow sites, regardless of adjacent habitat (Fig. 3a–c; Appendix S2: Table S2). In particular, *N. luetkeana* macroalgae was the main source fueling YOY rockfish, contributing an average of 46% ± 7% (mean ± SD) of assimilated energy across all seagrass sites ($2.4\times$ greater than POM, the next highest contributor). The epiphyte *S. naiadum* was the largest contributor of autochthonous energy in YOY rockfish (18% ± 6%). Contributions by *Z. marina* and understory kelp were low across sites.

The relative contribution of basal sources to YOY rockfish varied among sites (Fig. 3a–c). For YOY rockfish at sand edge sites, *N. luetkeana* macroalgae contributions were highest (53% ± 14%), while autochthonous sources (e.g., *S. naiadum* and *Z. marina*) were minimal (Fig. 3a). In contrast, source contributions to YOY rockfish at kelp edge sites were more even (Fig. 3c). Autochthonous contributions were highest at these kelp edge sites, such that *S. naiadum* was the second highest contributor (27% ± 11%), after *N. luetkeana* (42% ± 12%). Similarly, *S. naiadum* was notable in the seagrass interior sites, albeit low overall (18% ± 10%, Fig. 3b).

YOY rockfish diets and body condition

YOY copper-quillback rockfish diets demonstrated differences in prey composition across seagrass meadow sites (Fig. 4; Appendix S1: Fig. S1). At kelp edge sites, pelagically associated calanoid copepods were the dominant prey item in diets (47%), followed by harpacticoids

(16%). Conversely, YOY rockfish diets at sand edge sites primarily consisted of harpacticoid copepods (55%) and gammarid amphipods (28%). At seagrass interior sites, YOY rockfish exhibited intermediate diets of the edge sites (Fig. 4a), as well as being the most diverse and even ($H' = 1.65$, $J = 0.85$, respectively). However, the stomach sample size at the seagrass interior was low ($n = 4$, due to sample loss) relative to edge sites ($n > 20$) and may be a less reliable representation of prey composition at these sites. The body condition of YOY rockfish also varied across the seagrass meadow, where YOY copper-quillback rockfish had higher body conditions at kelp edge and seagrass interior sites (Fig. 4b).

Patterns and drivers of rockfish recruitment in the seagrass seascape

YOY copper-quillback rockfish recruitment increased throughout the study period in Choked Passage, peaking in August, the last observation period (Fig. 5a). The highest recruitment in the seagrass meadow occurred consistently at the kelp edge sites, which was 6.3× and 2.2× greater than sand edge sites and seagrass interior sites, respectively. Overall, densities of YOY copper-quillback rockfish were greatest in adjacent *N. luetkeana* kelp forest sites, and consistently lowest in adjacent sand sites. Similarly, predators were most abundant in *N. luetkeana* kelp forest sites, followed by
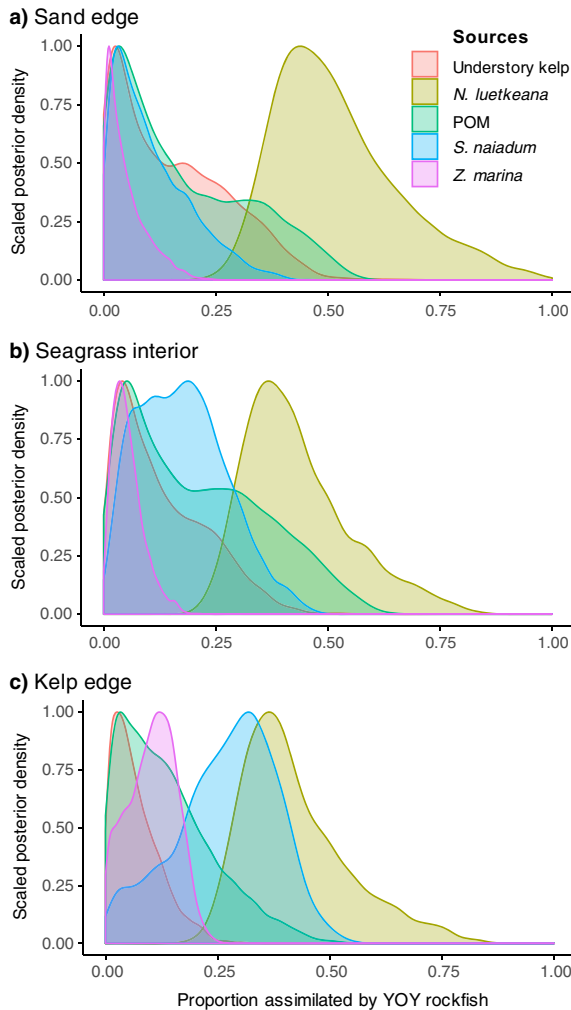

FIG. 3. Posterior distributions from the isotopic mixing model showing the relative proportional contribution of sources assimilated by YOY copper-quillback rockfish at sites in the seagrass meadow: (a) sand edge ($n = 25$ rockfish, $n = 3$ sites pooled), (b) seagrass interior ($n = 29$, $n = 4$ sites pooled), and (c) kelp edge sites ($n = 32$, $n = 3$ sites pooled). Sources in the model included understory kelps (*Cymathere triplicata* and *Alaria marginata*, red), *Nereocystis luetkeana* (light green), particulate organic matter (POM, dark green), *Zostera marina* (purple), and the epiphytic macroalgae *Smithora naiadum* (blue).
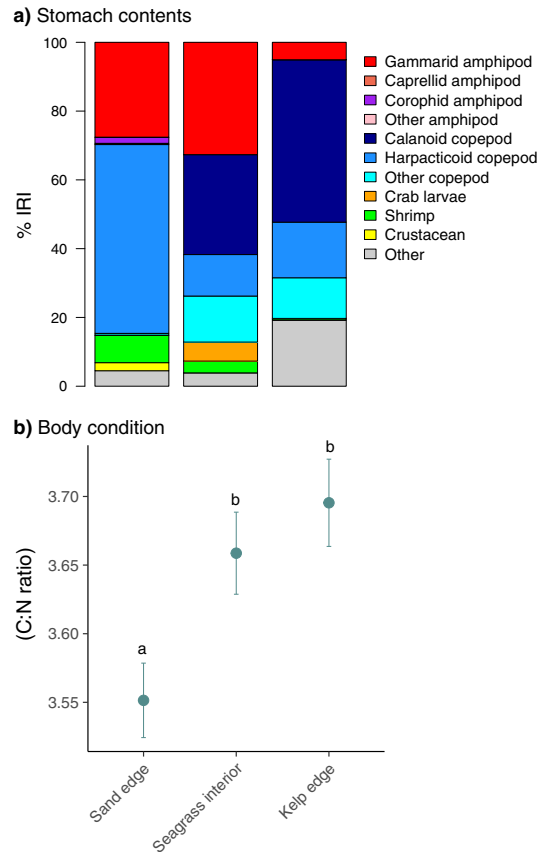

FIG. 4. (a) Prey consumed by YOY copper-quillback rockfish (index of relative importance, IRI) at sand edge ($n = 29$ rockfish), seagrass interior ($n = 4$), and kelp edge ($n = 19$) sites. (b) YOY copper-quillback rockfish body condition (mean C:N ratio ± SE) at sand edge ($n = 25$), seagrass interior ($n = 29$), and kelp edge ($n = 32$) sites. Means with the same letter are not significantly different from each other. See Appendix S1: Fig. S1 for numeric, gravimetric, and frequency of occurrence comparisons of prey.

kelp edge sites, where mean densities were significantly greater relative to seagrass interior and sand edge sites (Fig. 5b).

Multiple factors related to seascape connectivity influenced YOY copper-quillback rockfish densities in the seagrass meadow (Fig. 6; Appendix S3: Table S3). In the model with the highest support ($W_i = 1$, $\Delta AIC_c = 0$), seagrass habitat complexity and seagrass prey had positive effects on YOY copper-quillback rockfish recruitment in the meadow. Seascape features (i.e., edge and adjacent habitat type) had varying effects: (1) kelp edge sites had a large, positive effect on YOY densities, (2) sand edge sites had no evidence of an effect, and (3) interactions between seagrass habitat complexity and adjacent habitats influenced recruitment, such that adjacent habitats dampened

the positive effects of seagrass habitat complexity. In addition, predators had a small negative effect on seagrass recruitment densities. Similar to YOY recruits, predators also had a positive association with seagrass complexity ($b = 0.12$, $P < 0.001$).

DISCUSSION

Seascape connectivity is prevalent in the nearshore, affecting the community structure of seagrass meadows (Staveley et al. 2017, Perry et al. 2018). Yet, mechanistic links to nursery function are lacking. We found multiple lines of evidence that connectivity to highly productive and structurally complex *N. luetkeana* forests enhanced *Z. marina* meadow nursery function for YOY rockfishes. First, *N. luetkeana* production fueled YOY copper-quillback rockfish in the seagrass meadow via allochthonous nutrient subsidies. Secondly, rockfish prey composition shifted between seagrass edge sites adjacent to kelp forests vs. unvegetated sand, with corresponding differences in body condition of YOY rockfish recruits (e.g., relatively higher lipids when adjacent to *N. luetkeana* kelp forests). Overall, the largest YOY recruitment in the seagrass meadow was observed adjacent to *N. luetkeana* kelp forests. Adjacent sand habitats, on the other hand, had little effect on YOY rockfish in the seagrass meadows. In sum, neighboring kelp forests within the seascape played a key role in the nursery effects of the seagrass meadow to YOY rockfish by increasing access to areas of greater habitat quality, as well as allochthonous subsidies.

Spatially mediated bottom-up subsidies from kelp forests

Our results reinforce the role of kelp forests as an important and pervasive allochthonous source of energy to nearshore marine food webs. Benthic macroalgae can become available to seagrass food webs by recruiting and growing within the same substrate used by seagrasses and/or, after detachment from nearby rocky substrates, accumulating in meadows with currents and tides (Hyndes et al. 2012, 2014). With higher nutritional content than seagrass leaves and high rates of consumption by grazers (Thayer et al. 1984, Smit et al. 2006, Doropoulos et al. 2009), macroalgae in general has the potential to make substantial contributions to seagrass food webs. Previous feeding trials (Doropoulos et al. 2009) and isotopic studies (Smit et al. 2006) have demonstrated a preference for macroalgae over seagrass by grazers, but could not distinguish between allochthonous or autochthonous (i.e., epiphytic) macroalgae. With distinct macroalgae isotopic signatures in this system (Appendix S2: Table S1), we were able to discern these differences and their relative contributions: *N. luetkeana* from adjacent kelp forests contributed more than epiphytic *S. naiadum* (found at high biomass within the seagrass meadow) and understory kelps (found at low biomass within the meadow).
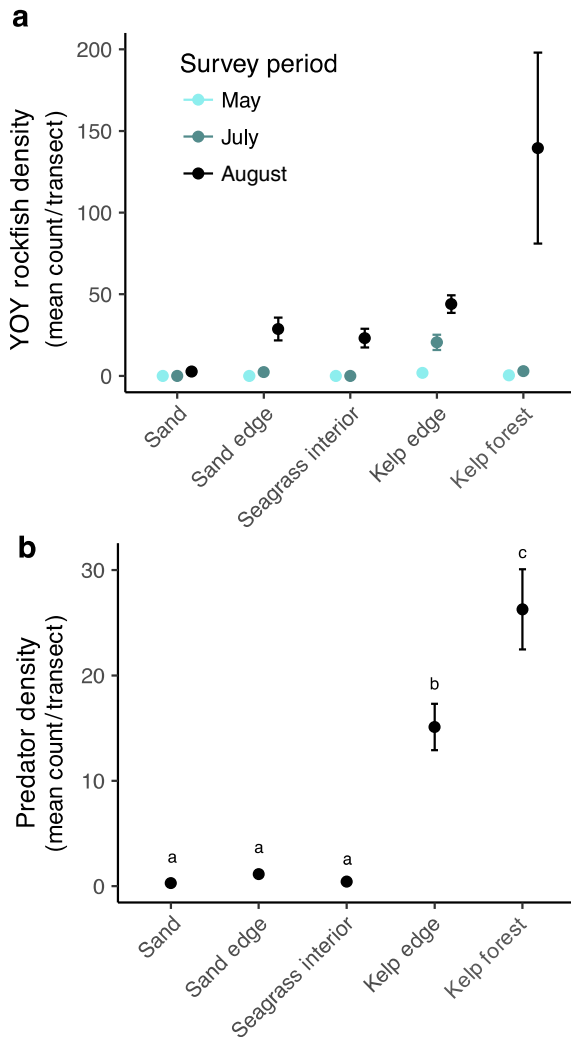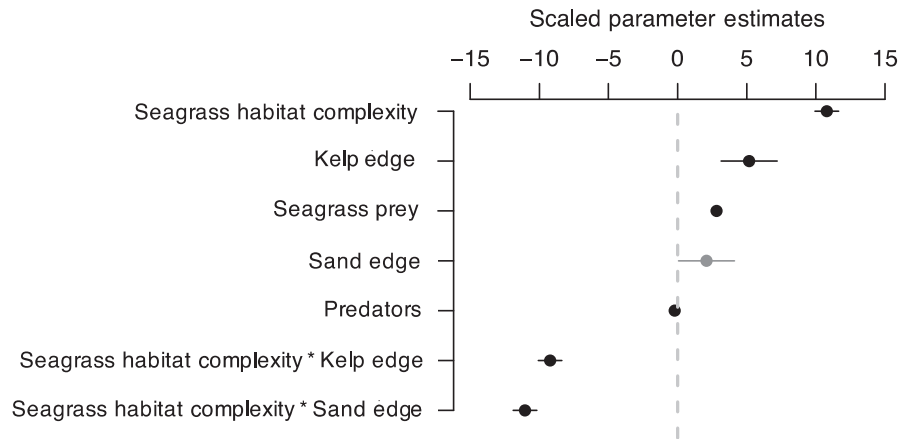

FIG. 5. (a) YOY copper-quillback rockfish densities (mean ± SE) observed across sites and time. (b) Predator densities (mean ± SE) pooled across the study period. Significant site differences among predator densities are distinguished by letters, while differences in YOY densities were reserved for model testing (Fig. 6).

Fig. 6. Scaled parameter estimates (±SE) of seagrass nursery factors (seagrass habitat complexity and seagrass prey) and seascape factors (kelp edge, sand edge, and predator density) influencing YOY copper-quillback rockfish densities within the seagrass meadow. Significant parameter estimates (black) have error bars that do not cross zero (gray dashed line).

High contributions by *N. luetkeana* suggest that this allochthonous macroalgae is preferred by YOY rockfish prey (i.e., invertebrate grazers) over autochthonous sources, and this energy is transferred to top consumers. Differences in grazer preference for macroalgae species and traits are prevalent, and can depend on the chemical defenses, palatability, and/or morphology of macroalgae (Leighton 1966, Duffy and Hay 1994, Cox and Murray 2005). By utilizing *N. luetkeana* subsidies, seagrass meadow grazers may use epiphytic *S. naiadum* as habitat rather than food, as this behavior has been seen in low-mobility grazers (Duffy and Hay 1991) or in those under threat of predation (Boström and Mattila 1999). Preference for *N. luetkeana* may also be a function of its widespread distribution and availability in temperate nearshore environments (Kaehler et al. 2006, Krumhansl and Scheibling 2012, Ramshaw et al. 2017), but feeding trials are needed to test this hypothesis.

While *N. luetkeana* energy fueled YOY rockfish in the seagrass meadow, small-scale differences in the assimilation of *N. luetkeana* were nevertheless observed across sites. YOY rockfish diets adjacent to unvegetated sand habitats (i.e., sand edge sites) had the highest contribution of *N. luetkeana* subsidies. Although seagrass meadows are highly productive ecosystems, productivity can vary within a single meadow due to seascape configuration and environmental conditions (Fourqurean et al. 2001), which may lead to disproportionate effects of subsidies. Moreover, unvegetated sand shorelines tend to accumulate high rates of detrital macroalgae from adjacent reefs leading to important subsidies for invertebrate grazers in these habitats (Hyndes et al. 2014). As in other studies, areas of lower production and/or accumulation of drift macroalgae may benefit most from broadly available allochthonous kelp subsidies (Lastra et al. 2008, Gonçalves and Marques 2011, Kelly et al. 2012).

In addition to the provision of primary production, our results provide empirical support for spatially mediated trophic dynamics in seagrass meadows. Here, the structural complexity of adjacent habitats (high-complexity kelp forests vs. low-complexity unvegetated sand) altered prey availability and/or consumption in seagrass meadows. Small, juvenile fish in seagrass meadows have been found to select areas of high habitat complexity for shelter from predators without a compromise in foraging (Yeager and Hovel 2017). Increased habitat complexity in the water column with *N. luetkeana* forests (i.e., added vertical structure) may facilitate access to better prey. The prey of YOY rockfish adjacent to *N. luetkeana* forests was of higher quality than adjacent to sand, due to the dominance of lipid-rich, pelagic-associated calanoid copepods (Sargent and Falk-Petersen 1988) relative to bottom-associated harpacticoid copepods (Gee 1989), respectively. This dietary contrast indicates different feeding behavior (e.g., more pelagic) with increased habitat complexity and/or an alteration in zooplankton availability by the kelp forest (Pakhomov et al. 2002, Atilla et al. 2005).

Patterns in fish recruitment and trade-offs with habitat complexity

Three-dimensional habitat structure is a critical attribute promoting the nursery function of seagrasses (Heck et al. 2003, McDevitt-Irwin et al. 2016). We found that seagrass habitat complexity had the largest, positive effect on YOY rockfish recruitment density (~4× larger than prey provision). Yet, connectivity to structurally complex adjacent habitats can provide an additional enhancement of fish densities (Baltz et al. 1993, Dorenbosch et al. 2005, Valentine-Rose et al. 2007, Gilby et al. 2018). Adjacency to kelp forests had a large positive effect on YOY rockfish recruitment. Because habitat complexity is a key driver of juvenile recruitment

success, edges occurring between two vegetated habitats may be optimal nursery areas in the seascape. However, habitat adjacency may also come with trade-offs such as predation. Because elevated predator densities were associated with both *N. luetkeana* and high seagrass habitat complexity (Figs. 5, 6), predator spillover from neighboring habitats is likely (Johnson 2006, Casini et al. 2012).

Access to multiple habitats is essential for many species during adult life stages and during ontogenetic shifts (Gillanders et al. 2003, Rand et al. 2006, Sheaves 2009). Incentives exist for predators to move into intermediate areas of habitat complexity (e.g., seagrass and kelp forest ecotones) to increase foraging success (Crowder and Cooper 1982, Johnson 2007). There, predators can cause increased mortality and/or shifts in habitat use by juveniles due to predation risk (Holbrook and Schmitt 1988, Persson and Eklov 1995), thereby dampening nursery benefits in these regions despite augmented refuge and subsidies. In this study, despite elevated predation risk at seagrass meadow edges, we found that other components of seascape connectivity largely controlled the observed rockfish nursery effects. Considering seascape composition and arrangement can reveal important trade-offs between optimizing foraging habitat and reducing predation (Lima and Dill 1990), factors that ultimately shape nursery function (Fig. 1).

Planning for seascape connectivity

Globally, human activity is accelerating the loss of seascape connections by fragmenting and altering habitats in nearshore areas. In British Columbia, anthropogenic disturbances are degrading seagrass habitats, in which rockfish species may be particularly sensitive (Iacarella et al. 2018). To counter these trends, our findings support the inclusion of a mosaic of nearshore habitats in protection zones where preserving and/or elevating nursery function is a primary goal of coastal conservation or management.

Based on this study, the ideal habitat mix should include habitat types that (1) increase structural complexity, fostering maximum access to resources and refugia and (2) augment productivity by increasing flows of production across habitat edges and seascape scales. Planning for habitat types that incorporate these components should also include an understanding of their temporal dynamism. For instance, kelp forests are strongly influenced by regional drivers (Krumhansl et al. 2016), where human-induced activities (removal of top predators, climate change, marine diseases) can influence declines in biomass (Watson and Estes 2011, Filbee-Dexter et al. 2016, Burt et al. 2018). As such, we advocate for the inclusion of a portfolio of habitat types when planning for seascape connectivity, including the incorporation of low complexity substrates capable of augmenting water column structural complexity in the future (e.g., rocky reef urchin barrens transitioning to

kelp forests), as well as an understanding that future seascape composition may change as a result of habitat loss.

Our findings also indicate that the arrangement of habitats within a seascape matters, particularly as a result of edge effects and composition of adjacent habitats. In this study, edge effects promoted access and use of seagrass edges, with trade-offs between predation, refuge, and provision of food. Overall, the observed edge effects had positive influences on nursery function for rockfish species, but varied by adjacent habitat type. Edge effects are ubiquitous across landscapes and seascapes, but can foster both positive and negative effects, depending on the ecological context and mechanisms at play (Ries et al. 2004). This study focused on the nursery function of a large, continuous seagrass meadow. But, nursery function may vary when habitat patches are smaller or seagrass meadows are fragmented, resulting in larger relative edge areas. Smaller seagrass patch sizes may illuminate different trade-offs with predation and subsidies (Smith et al. 2010). Moreover, fragmentation and/or habitat loss (Valentine-Rose et al. 2007), eutrophication (Deegan et al. 2002), and infrastructure additions (Bulleri and Chapman 2010), may further degrade the structure and function of coastal nursery habitats for juvenile fishes. As such, future research should also investigate the response of nursery function in areas of higher disturbance or in smaller seagrass meadows, which are often the management focus of coastal restoration or habitat mitigation.

The general application of these findings also depends on local and regional environmental factors influencing spatial connectivity, as well as the life history and traits of the focal fauna. Although not the focus of this study, tidal effects (Rangeley and Kramer 1995, 1998), upwelling dynamics (Bjorkstedt et al. 2002), and turbidity (Blaber and Blaber 1980) can alter juvenile habitat use and influence the physical connectivity between seascape habitats.

Fish species may also respond differently to local and regional environmental forcing, which may differentially affect recruitment, foraging behaviors or predatory avoidance strategies (Beukers and Jones 1998, Hammerschlag et al. 2010). While this study focused on rockfishes, more research is needed to investigate seascape nurseries across a wider range of fish species.

In general, seascape connectivity has been found to improve the efficacy of marine reserves (Halpern et al. 2010, Olds et al. 2011, 2015) and can increase the resilience of marine ecosystem functions (Mumby and Hastings 2007, Olds et al. 2012). For temperate coastal seascapes, where connectivity is most at risk by habitat loss and climate change (Hyndes et al. 2014), our findings illustrate how the inclusion of habitat mosaics, and connectivity between habitats, can be utilized advantageously by marine planners and managers to promote fish nurseries. In BC, Rockfish Conservation Areas (RCAs) have been established coast-wide to protect

declining rockfish populations (Yamanaka and Logan 2010, Haggarty et al. 2016). Although a long recovery time for rockfish populations is expected due to their life-history characteristics, overall positive reserve effects have not yet been found and RCAs are being evaluated for their effectiveness (Haggarty et al. 2016). Evaluation of habitat in and around RCAs (Haggarty and Yamanaka 2018) should consider connectivity to seascape nurseries, including seagrass meadows, kelp forests, and high-relief rocky reefs to improve RCA effectiveness and the recovery of rockfish abundances.

Our research also emphasizes the importance of seascape connectivity in a large-scale Marine Protected Area (MPA) Network planning processes such as the one ongoing in Canada's Northern Shelf Bioregion, which aims to protect 10% of its coastal and marine areas by 2020 (DFO 2017). Although kelp and seagrass habitats are considered Ecologically and Biologically Significant Areas (EBSAs; Rubidge et al. 2018) and receive conservation priorities within MPA network design (DFO 2017), little empirical evidence currently informs design guidelines aimed at promoting connectivity among these habitats. Our research provides support for the prioritization of connected seascape habitats in these protected area networks.

Conclusion

Concurrent with emerging evidence (Nagelkerken et al. 2013, Perry et al. 2018), our findings highlight the importance of temperate seascape connectivity in positively influencing seagrass nursery function. We recommend the protection and management of nearshore habitats mosaics to maintain and/or enhance nursery function and value of coastal ecosystems for commercially and biologically important fish populations.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1897/full

DATA AVAILABILITY

Data are available in the Hakai Metadata Catalogue: https://doi.org/10.21966/exy6-1k58