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ORIGINAL PAPER

Cross-ecosystem trophic subsidies to sandy beaches support surf zone fish

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Abstract

Food webs in ecotones linking adjacent ecosystems may depend on cross-ecosystem subsidies. In surf zones of temperate sandy beaches, higher-level consumers often rely on intertidal prey that utilize allochthonous primary production. We evaluated the importance of phytoplankton and kelp-based prey, as well as physical characteristics of beaches, to diet of a surf zone fish, barred surfperch (*Amphistichus argenteus*), through stomach content and stable isotope analyses. Our results suggested that barred surfperch rely on prey from both phytoplankton and kelp-based subsidies, but their relative contribution to diet varied widely across beaches. Sand crabs (*Emerita analoga*), which depend on phytoplankton, were abundant at every beach, but their contribution to diet in stomach contents varied from 2 to 87% among sites. At the majority of beaches, $\delta^{13}C$ values of fish muscle tissue, which reflects diet integrated over time, were within 0.5 ‰ of sand crab values, suggesting a reliance on phytoplankton-based prey. However, kelp-dependent prey associated either with beach wrack or subtidal reefs was also present in surfperch stomachs from all beaches (up to 41–72%). The notable enrichment in ^{13}C of juvenile surfperch at two beaches and adults at one beach relative to sand crabs suggested a longer-term contribution of kelp-based prey to fish diet. The detection of kelp-based prey in surfperch diets also indicates the potential for reciprocal subsidies in these ecotones. Our results suggest trophic connectivity between surf zones and kelp forests and sandy beaches is spatially variable and that opportunistic higher-level consumers can shift their diet in response to the availability of phytoplankton and kelp-based food resources.

Keywords Barred surfperch · Allochthonous subsidy · Macroalgal wrack · Kelp · Phytoplankton · Intertidal macroinvertebrates · California Channel Islands

Introduction

Ecotones that connect adjacent ecosystems may benefit from and, in some cases, require cross-ecosystem allochthonous subsidies to sustain populations and drive the dynamics of recipient communities (Polis et al. 1997; Marczak et al. 2007; Leroux and Loreau 2008; Spiller et al. 2010). Often cited examples of cross-ecosystem subsidies include terrestrial organic matter provided to streams in the form of leaf litter that supports detritivore populations and lotic food webs (Cummins and Klug 1979; Doucett et al. 2007; Collins et al. 2016) and marine subsidies that support terrestrial food webs, a phenomenon well described on the desert islands of the Gulf of California, where a wide disparity exists between low-productivity terrestrial and high-productivity marine environments (Polis and Hurd 1996; Anderson and Polis 1998). In some cases, allochthonous subsidies may be reciprocal, with bidirectional transfers of energy and nutrients flowing between ecosystems (Nakano and Murakami 2001; Romanuk and Levings 2010; Hyndes et al. 2014; Gounand et al. 2018).

Surf zones along open coasts are dynamic, turbulent areas of water at the interface between pelagic and intertidal

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ecosystems, including beaches and rocky platforms (Olds et al. 2018; Jarrin et al. 2022). Sandy beaches experience energetic conditions with shifting sands and a lack of hard substrate that precludes the attachment of kelp and other macroalgae that could support local secondary production (McLachlan and Brown 2006). In situ production by diatoms specifically adapted to the surf zone can be high but is uncommon and usually transient (Odebrecht et al. 2014). Consequently, secondary production in the surf zone is largely sustained through flows of organic material from neighboring ecosystems, including the open ocean and rocky reefs (Morgan et al. 2018; Hyndes et al. 2022). These allochthonous subsidies can include phytoplankton, zooplankton, macrophytes (macroalgae and seagrass), and carrion (Colombini and Chelazzi 2003; McLachlan and Brown 2006; Shanks et al. 2017; Hyndes et al. 2022). However, the relative use of these subsidies by surf zone consumers, and factors affecting their incorporation into surf zone food webs are not well quantified (McLachlan and Brown 2006; Hyndes et al. 2014, 2022; Baring 2015; Olds et al. 2018).

Phytoplankton advected into the surf zone are exploited by populations of suspension feeding macroinvertebrates that extend through the surf zone into the lower intertidal beach (Defeo et al. 2009; Morgan et al. 2018; Jarrin et al. 2022). Along the coast of California, USA, suspension-feeding sand crabs (*Emerita analoga*) are the most important macroinvertebrate species by biomass in these habitats (Dugan et al. 2003; Schooler 2018) for their role as a trophic intermediate between phytoplankton and secondary consumers that include surf zone fish (e.g. surfperch, croakers) (Carlisle et al. 1960; Succow 2017a, b). However, phytoplankton concentrations in surf zones can vary, influenced by oceanographic conditions, nutrient availability, surf zone characteristics, and beach morphodynamic state, potentially affecting the abundance of surf zone consumers and the contribution of phytoplankton to surf zone food webs (Lastra et al. 2006; Odebrecht et al. 2010; Morgan et al. 2018).

Macroalgal-based resources may also be incorporated into surf zone food webs. Macroalgae originating from subtidal rocky reefs supports a diverse upper beach macroinvertebrate community (Colombini and Chelazzi 2003; Dugan et al 2003; Hyndes et al. 2022) potentially available to surf zone fish during high tides. Macroinvertebrates of the upper beach typically include talitrid amphipods, isopods, flies, and beetles, which can be extremely abundant depending on the availability of macroalgal wrack (Dugan et al. 2003; Lastra et al. 2008; Schooler 2018). The use of upper beach macroinvertebrates by surf zone fish could vary among locations and over time, depending on variability in wrack inputs, beach characteristics, and management (Revell et al. 2011; Liebowitz et al. 2016; Schooler et al. 2019; Walter et al. 2024), and the accessibility of these mobile prey to fish (Dugan et al. 2013; Emery et al. 2022). Macroalgal carbon could also enter the surf zone food web through reef-associated grazers that feed on kelp or kelp detritus (e.g., the isopod, *Idotea* spp.) exploited by surf zone fish (Crawley and Hyndes 2007; Andrades et al. 2014; Baring et al. 2018).

In this study, we explored the relative use of phytoplankton and macroalgal-based prey resources by a widely distributed surf zone fish that feeds primarily on macroinvertebrates, the barred surfperch (*Amphistichus argenteus*), across seven beaches of a northern California Channel Island. These beaches are not subject to the watershed impacts and beach management practices prevalent on the mainland coast. We hypothesized that the use of these prey resources by surfperch would vary across beaches and be influenced by physical characteristics and the availability of potential prey that use phytoplankton and kelp wrack resources for food (Lagerloef and Bernstein 1988; Dugan et al. 2000; Otero and Siegel 2004; Page et al. 2021).

Materials and methods

Study sites and species

We sampled seven beach sites across Santa Rosa Island, one of California's Northern Channel Islands, located approximately 40 km south of Santa Barbara, California, USA (Fig. 1, Table S1). Sandy beach comprises > 55% of the shoreline of Santa Rosa Island (Curdts 2011) (Fig. 2A and B). The remaining shoreline on the island is primarily cliff-backed rocky intertidal.

Barred surfperch (*Amphistichus argenteus*) are one of a suite of fish species found in the surf zones of sandy beaches in southern California, and one of only two species of fish specializing in this habitat (Allen & Pondella 2006; Gold et al. 2023) (Fig. 2C). Barred surfperch are widespread and abundant on the mainland and islands of southern and central California (Carlisle et al. 1960; Gold et al. 2023), and are targeted by both recreational and commercial fisheries (Love 1991). Barred surfperch are known to exploit several types of suspension-feeding macroinvertebrates along the mainland coast, particularly sand crabs (Carlisle et al. 1960; Barry et al. 1996); the potential importance of wrack-associated invertebrates to barred surfperch diet is unknown.

Macrophyte wrack, associated environmental variables, and macroinvertebrates

We sampled each study beach once during daytime ebbing tides during 8–14 September 2018, prior to strong late fall and winter storms that cause considerable beach erosion, and several months after the major spring recruitment pulses of many taxa (Table 1). Sampling at each beach was conducted along randomly spaced, and at least 10 m apart, transects

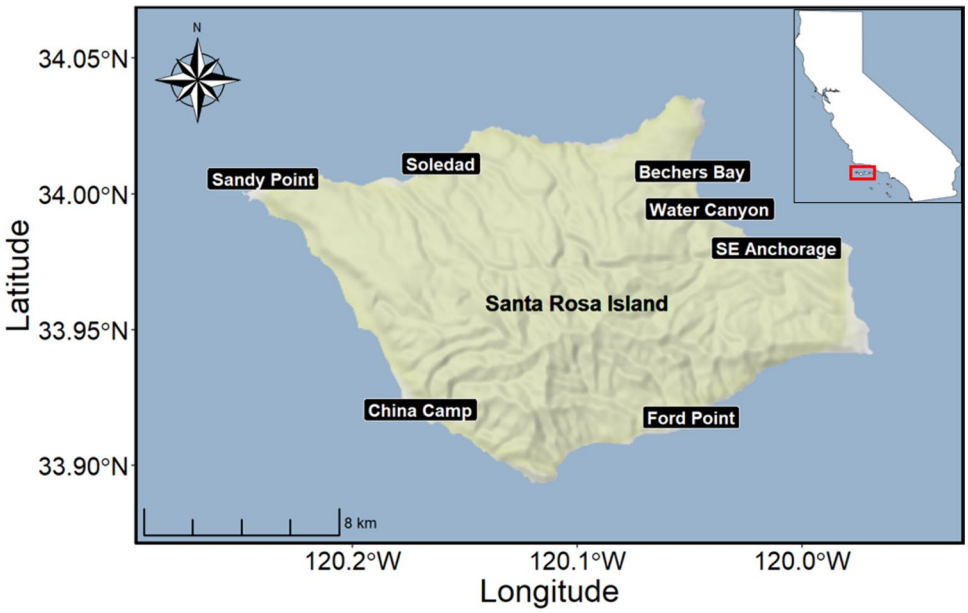

Fig. 1 Map of the seven study beaches on Santa Rosa Island. Inset depicts the location of Santa Rosa Island in California's Northern Channel Islands off the coast of southern California, USA

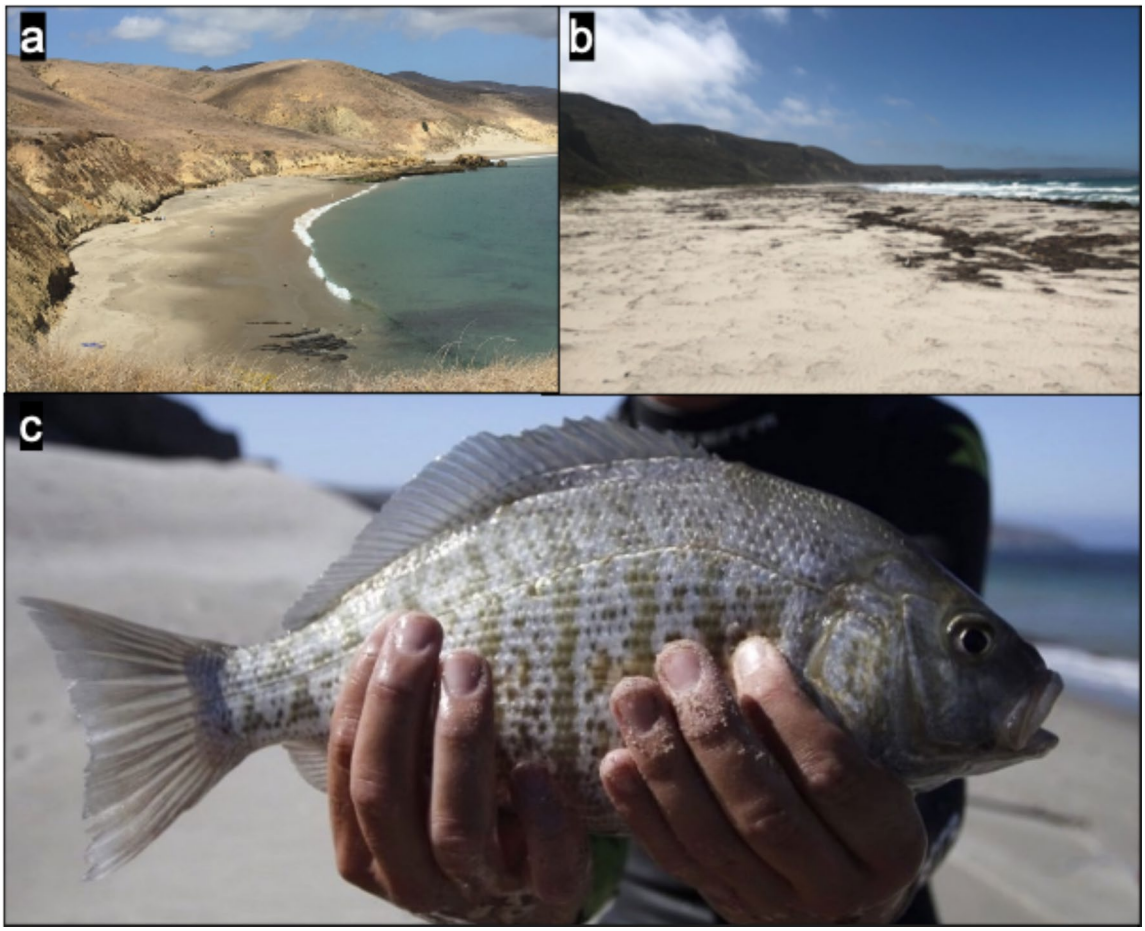

Fig. 2 Two study beaches on Santa Rosa Island, Ford Point (**a**) and Soledad (**b**), and an adult barred surfperch (*Amphistichus argenteus*) (**c**). Note the accumulation of wrack on the upper beach of Soledad

Table 1 List of prey items identified in the stomachs of barred surfperch

Beach endemic taxa	**Marine taxa**
Sand crabs	**Subtidal mesograzers**
Crustacea	Crustacea
Decapoda	Isopoda
Emerita analoga	*Idotea* sp.
Wrack-associated taxa	**Other marine taxa**
Crustacea	Crustacea
Amphipoda	Amphipoda
Megalorchestia spp.	Caprellidae
Isopoda	Decapoda
Alloniscus perconvexus	*Cancer* sp.
Insecta	*Pugettia producta*
Coleoptera	*Pleuroncodes planipes*
Akephorus marinus	*Crangon nigricauda*
Thalasselephas testaceus	Caridea
Cercyon fimbriatus	Other Decapoda
Phaleria rotundata	Isopoda
Staphylinidae	Other Isopoda
Histeridae	Cirripedia
Diptera	*Pollicipes polymerus*
Anthomyiidae	Ostracoda
Coelopidae	Cumacea
Other Diptera	Mysida
Other beach taxa	Annelida
Crustacea	Polychaeta
Amphipoda	Cnidaria
Atylus tridens	Actinearia
Gammaridae	Mollusca
Isopoda	Bivalvia
Excirolana sp.	Patellidae
Gnoremosphaeroma noblei	*Mytilus* sp.
Ancinus granulatus	Other Bivalvia
	Gastropoda
	Other
	Teleost eggs
	Algae

Grouped into prey categories (**bold**) used in analyses

run perpendicular to the shoreline following Dugan et al. (2003). Sampling was conducted along five transects for all but one beach (Southeast Anchorage, n = 3) for wrack and invertebrates and three transects for environmental variables.

We measured the cover and composition of shore-cast macrophytes (kelps, macroalgae, seagrasses) using a line-intercept method (Dugan et al. 2003), and grouped measurements into two categories, *Macrocystis pyrifera* and total macrophyte wrack (kelps, macroalgae, and seagrasses). Mean values for *Macrocystis pyrifera* and total macrophyte wrack at each beach were calculated using transects as replicates and expressed as the area (m^2) of wrack per meter wide strip of beach ($m^2\ m^{-1}$). Beach physical characteristics were measured on three transects and averaged (± SE) for each site. Beach-surf zone width was measured as the distance from the landward boundary of the upper beach to the low swash limit using a survey-grade metric measuring tape and estimating the distance in meters from the low swash limit to the outer edge of significant breakers by eye. Intertidal slope was measured at the water table outcrop using a digital level. Beach length [the sandy shoreline distance between two boundaries (e.g., headlands)] and beach orientation (compass degrees of the shore-normal line) were measured in Google Earth. Beach-surf zone width represents the habitat available to surfperch and their prey and may affect the capacity for the system to accumulate and store subsidies (Dugan and Hubbard 1996; Revell et al. 2011; Jaramillo et al. 2021). Intertidal slope is an integrative measure of habitat area which reflects the long-term wave regime and sediment grain size (Kemp 1960; McLean and Kirk 1969). Beach length is a measure of habitat area and proximity to adjacent ecosystems as shorter beaches are closer to rocky reefs or other coastal habitats (George et al. 2015; Liebowitz et al. 2016). Beach orientation interacts with wind and ocean current directions to affect inputs of marine subsidies (Lastra et al. 2014; Liebowitz et al. 2016).

To estimate abundance and biomass of upper intertidal wrack-associated macroinvertebrates, we divided the upper intertidal portion of the beach, where macrophyte wrack accumulates, into mid and high levels (Olabarria et al. 2007; Garrido et al. 2008; Schlacher et al. 2008; Beeler 2009). The mid-level extends from the seaward to landward boundary of talitrid amphipod burrows and includes crustaceans and insects that depend on recently stranded macrophyte wrack for shelter and food. The high-level extends from the landward boundary of the mid-level to the landward boundary of the beach (i.e., dune vegetation, bluffs, cobble berm) and includes taxa that inhabit older and drier macrophyte wrack. We sampled invertebrates along the same transects used to survey wrack abundance and other beach variables using a series of 10 cores (diameter: 10 cm, depth: 20 cm) spaced at uniform intervals within each of the two levels (20 cores per transect). The 10 cores from each level were combined and sieved through mesh bags (aperture: 1.5 mm) to remove as much sand as possible. The sieved contents were frozen for later processing in the laboratory where all retained macroinvertebrates were counted and identified to the lowest taxonomic level possible and weighed to the nearest milligram blotted wet weight. Abundance and wet biomass values were summed for each transect (mid and high levels combined for upper beach wrack-associated species) and expressed as mean (± SE) values per meter wide strip of shoreline at each study beach (McLachlan and Brown 2006).

We estimated the abundance and biomass of suspension feeding sand crabs (*Emerita analoga*), which were likely to be an important component of surfperch diet (Carlisle et al. 1960). Twenty uniformly spaced cores (10 cm depth) were taken along each transect across the low beach level, combined for each transect, and sieved through mesh bags. The low beach level extends from the seaward to landward boundary of sand crab distribution and did not overlap the mid and high levels. The upper limit of their distribution was identified by excavating and examining a series of closely spaced shallow cores of sand from the upper limit of the visible sand crab aggregation up the beach until sand crabs were no longer present in cores. The lower limit was identified by estimating the lowest position of sand crabs present in the swash zone (generally around the low swash step). Size-frequency distributions were determined for each sample by measuring the carapace lengths of live crabs by hand or with a series of graded sieves in the field or laboratory (Dugan et al. 1991). Crabs were enumerated and measured to the nearest 1.0 mm carapace length (CL). Additionally, we measured the relationship between carapace length and weight for 309 sand crabs collected across study beaches to enable the calculation of sand crab biomass. To estimate biomass from carapace length, we plotted weight as a function of carapace length and fit a nonlinear regression ($R^2 = 0.96$). We used the following equation to estimate sand crab wet biomass for each study beach from carapace length (*CL*):

$$\text{wet biomass (g)} = 0.0003CL^3 - 0.00008CL^2 + 0.0004CL$$

Samples of sand crabs (*E. analoga*) were also collected and frozen at − 20 °C for isotopic analysis (see below).

Sampling barred surfperch for diet analysis

We sampled barred surfperch across the seven study beaches (Fig. 1) using a beach seine and hook and line. The seine was 1.8 m × 15.3 m (10 mm knotless nylon mesh, 2 m poles, 20 m leader ropes) with a bag, floats, and weighted lead line. To execute a haul, two people opened the beach seine parallel to shore in ~ 1.5 m of water in the surf zone. Keeping the weighted line flush with the bottom, the seine was dragged perpendicular to the shore until it reached the beach. On the beach, fish were immediately removed from the seine and placed in aerated live wells. Four hauls were conducted at each study beach. We also used hook and line from the shore to collect a sufficient number of larger barred surfperch, which are more adept at avoiding the seine.

All surfperch collected were counted, measured (standard length), and grouped into two size classes by standard

Table 2 (**A**) Results of One-way PERMANOVA comparing diet composition by category using counts for juvenile and adult surfperch among study beaches. See Materials and Methods for diet categories. (**B**) Results of One-way PERMANOVA comparing diet composition by category using wet weights for juvenile and adult surfperch among study beaches

A					
Source	df	SS	MS	Pseudo-F	p
Juvenile					
Site	5	41,718	8343.6	4.6264	< 0.001
Residual	56	1.01E + 05	1803.5		
Total	61				
Adult					
Site	4	40,446	10,112	8.094	< 0.001
Residual	38	47,470	1249.2		
Total	42	87,917			
B					
Source	df	SS	MS	Pseudo-F	p
Juvenile					
Site	5	48,963	48,963	3.3492	< 0.001
Residual	56	1.64E + 05	1.64E + 05		
Total	61	2.13E + 05			
Adult					
Site	4	49,775	12,444	6.1356	< 0.001
Residual	38	77,069	2028.1		
Total	42	1.27E + 05			

length – juvenile (< 130 mm) and adult (≥ 130 mm). Barred surfperch are considered mature at approximately two years of age or 130 mm standard length (Carlisle et al. 1960). Juvenile surfperch were available for stomach content and isotope analysis from six of seven study beaches. Adult surfperch were available from five of seven study beaches for stomach content analysis and four beaches for isotope analysis.

Surfperch used for diet analysis were immediately euthanized in accordance with protocols approved by the Institutional Animal Care and Use Committee (IACUC Protocol #943) at UC Santa Barbara. Stomachs were removed immediately from euthanized fish and white dorsal muscle tissue was dissected from a subset of those fish for stable isotope analysis. Stomachs were excised and placed into labeled canvas bags and preserved in 10% buffered formalin for later analysis in the laboratory. Dissected muscle tissue was wrapped in labeled aluminum foil and stored in a − 20 °C freezer for later stable isotope analysis (see below). Isotope values of white muscle tissue are widely used in dietary studies of fishes (Hesslein et al. 1993; Post 2002; Vander Zanden and Vadeboncoeur 2002).

Stomach content prey composition and analysis

In the laboratory, we identified, to the lowest taxonomic level possible, and enumerated, the preserved stomach contents under a dissecting microscope (Table 2). Individual prey items were aggregated by taxa, blotted, and weighted wet to the nearest 0.01 g. Empty stomachs were not included in this analysis.

Prey items were assigned to five categories based on habitat (beach or non-beach) and/or probable main source of basal carbon (Table 1): (1) suspension feeding sand crabs (*Emerita analoga*), (2) wrack-associated grazers, detritivores, and predators dependent on beach cast kelp (or other macrophyte) wrack for food and shelter (e.g., talitrid amphipods, upper beach isopods, beetles, and flies), (3) other beach endemics (occurring intertidally on beaches such as isopods, amphipods, and decapods–excludes *E. analoga* and wrack-associated species), (4) subtidal mesograzers that rely on kelp-based resources (e.g., *Idotea* sp.), and (5) other marine taxa that do not inhabit beaches or were not identified to a low enough taxonomic level to determine their habitat preference and/or feeding mode. For each fish, we computed the percent composition by count and weight of each prey item and category. For each study beach, we calculated the mean percent composition of each prey item and category for juvenile and adult fish. We excluded fish size classes from sites where the number of stomachs available was fewer than three.

Variation in the five diet categories described above among beach sites was explored using multivariate analyses in PRIMER 7 (Clark and Gorley 2015) and PERMANOVA + (Anderson et al. 2008) unless indicated otherwise. Prior to analysis, faunal prey counts or blotted wet weights from stomach contents were log (x + 1) transformed to reduce the influence of dominant prey (Clark and Gorley 2015), and these values were used to compute Bray–Curtis dissimilarity matrices. Multivariate permutational analysis of variance (PERMANOVA) analysis was run with beach site as a fixed factor using Type III error and unrestricted permutation of raw data as recommended by Anderson et al. (2008). We used analysis of similarity (ANOSIM) to explore pairwise variation in diet categories of juvenile and adult surfperch between beaches (Clarke and Warwick 1994).

We used the nonparametric, distance-based multivariate linear model DistLM on Bray–Curtis dissimilarity matrices to explore the potential influence of environmental variables on surfperch diet. A number of environmental variables were assessed for collinearity and outliers prior to analysis using pairwise Pearson correlation coefficients (R-values) and draftsman plots. We transformed beach orientation for use as a predictor variable in our models by taking the sine and the cosine of the compass direction in radians (Cox 2006). The sine and cosine terms were taken as paired terms and used as two predictor variables in the models. Cosine terms can be considered as explaining effects operating north to south and sine terms as east to west (Evans & Cox 2005). If two or more variables were significantly correlated ($P < 0.05$), the variable retained in the model was considered to best reflect local habitat conditions, but served as a proxy for the other excluded variables. Environmental variables considered and excluded were: *Macrocystis* wrack abundance, water table outcrop (WTO) slope, beach length, and beach orientation (sine). Environmental variables included were: macrophyte wrack abundance, *Emerita analoga* (sand crab) abundance, beach orientation (cosine), and beach-surf zone width.

We ran sequential DistLM analysis separately for juvenile and adult fish that included all five prey categories, and then each category separately by count and weight. Environmental variables with non-normal distributions were log (n + 1) transformed to reduce skew, but not normalized (Anderson et al. 2008). For each model run, we used a step-wise selection procedure and adjusted-R^2 selection criterion (9999 permutations) to identify the environmental variables that best explained the composition of prey by category in surfperch diet.

Preparation of tissue samples for ^{13}C isotope analysis

To further explore spatial variation in surfperch diet, we supplemented fish stomach content analysis with stable carbon isotope analysis of fish muscle tissue. Whereas stomach content analysis provided a snapshot of recently consumed foods, stable isotope analysis integrates diet over time (weeks) and should reflect the longer-term use of prey dependent on kelp or phytoplankton-based production.

In the laboratory, the white muscle tissue excised from each fish was rinsed in de-ionized water, dried in new glass scintillation vials without caps at 60 °C, and ground to a fine powder using a mortar and pestle. We also prepared three composite samples (Soledad Beach, n = 2) of five individual sand crabs (*E. analoga*) each, per beach, consisting of leg muscle tissue. Muscle tissue was removed from sand crab legs, rinsed, dried, and ground as above. Due to inorganic carbonates in crustaceans, such as sand crabs, samples were processed as recommended by Carabel et al. (2006) and Schlacher and Connolly (2014). Each sand crab sample for carbon isotope analysis was acidified to remove to remove inorganic carbonates by adding a minimum of 190 µl 6% sulfurous acid or more until bubbles ceased forming, and re-dried at 60 °C without rinsing to minimize loss of DOM (dissolved organic matter). Fish muscle tissue samples were not acidified.

Stable carbon isotope analysis was conducted in the Marine Science Institute Analytical Laboratory, University of California, Santa Barbara, using a Thermo Finnigan DELTAplus Advantage isotope mass spectrometer interfaced with a Costech EAS elemental analyzer. Instrument precision, as standard deviation, determined from replicate analyses (n = 16) of the same standard (L-glutamic acid USGS40) was ± 0.10‰ for ^{13}C. The natural abundances of carbon isotopes are expressed relative to the Pee Dee Belemnite (PDB) standard for carbon in standard δ notation and calculated as follows for element *X*:

$$\delta X_n = 1000 \times \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}}$$

where $R = X_n/X_{n-1}$ expressed per mil (‰) relative to the PDB standard for carbon. We calculated mean $\delta^{13}C$ values (± 95% confidence intervals, CI) for surfperch at each study beach and adjusted these values downward ($\Delta^{13}C = 0.5 \pm 1.4$‰, Post 2002) to account for trophic discrimination by surfperch. Adult and juvenile surfperch values were compared across beach sites using one-way ANOVA and Kruskal–Wallis (for non-normally distributed data).

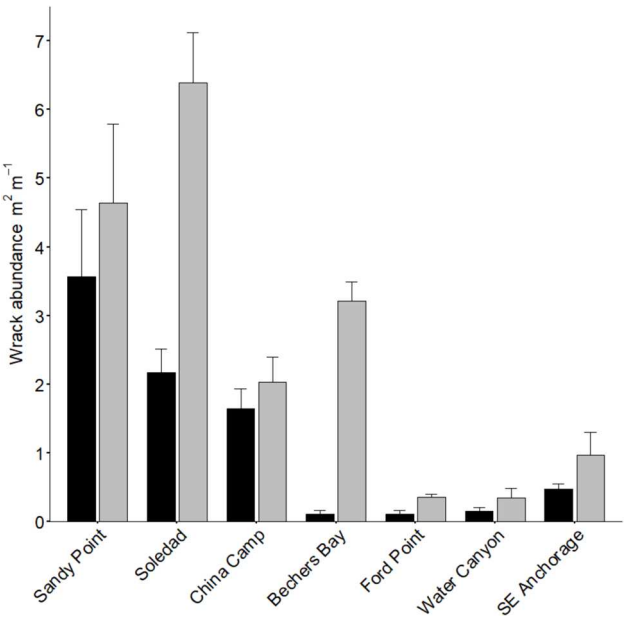

Fig. 3 Spatial patterns in mean (± SE) abundance of *Macrocystis pyrifera* (black bars) and macrophyte (grey bars) wrack as cover. Study beaches arrayed west to east (left to right)

Use of phytoplankton and kelp-based dietary sources

To qualitatively assess the longer-term use of phytoplankton-based prey by surfperch, we employed an approach recommended by Post (2002) in the use of a lower-level consumer, sand crabs (*Emerita analoga*), that integrate the isotope value of phytoplankton over time and focused on this resource since sand crabs were present across all sites at the time of our sampling, whereas wrack and wrack-associated prey were not. The types and abundances of macroalgal wrack and wrack-associated prey (e.g., flies, beetles, amphipods) were variable across beaches and our sampling was insufficient to capture potential variability in the mean isotope value of these resources. However, giant kelp typically has more positive carbon isotope values (− 12.5‰) than phytoplankton, based on longer-term published data from the mainland (Page et al. 2008; Koenigs et al. 2015), which should be reflected in more positive $\delta^{13}C$ values of surfperch using kelp-based resources.

We calculated mean $\delta^{13}C$ values (± 95% CI) for sand crabs at each study beach and adjusted these values downward ($\Delta^{13}C = 0.5 \pm 1.4$‰, Post 2002) to account for trophic discrimination by sand crabs. The overlap of fish and sand crab 95% CI was used to qualitatively assess adult and juvenile surfperch use of sand crabs relative to kelp-dependent prey resources. When consumer and prey confidence intervals overlap, we can infer that surfperch diet is not significantly different from sand crabs, whereas when they diverge

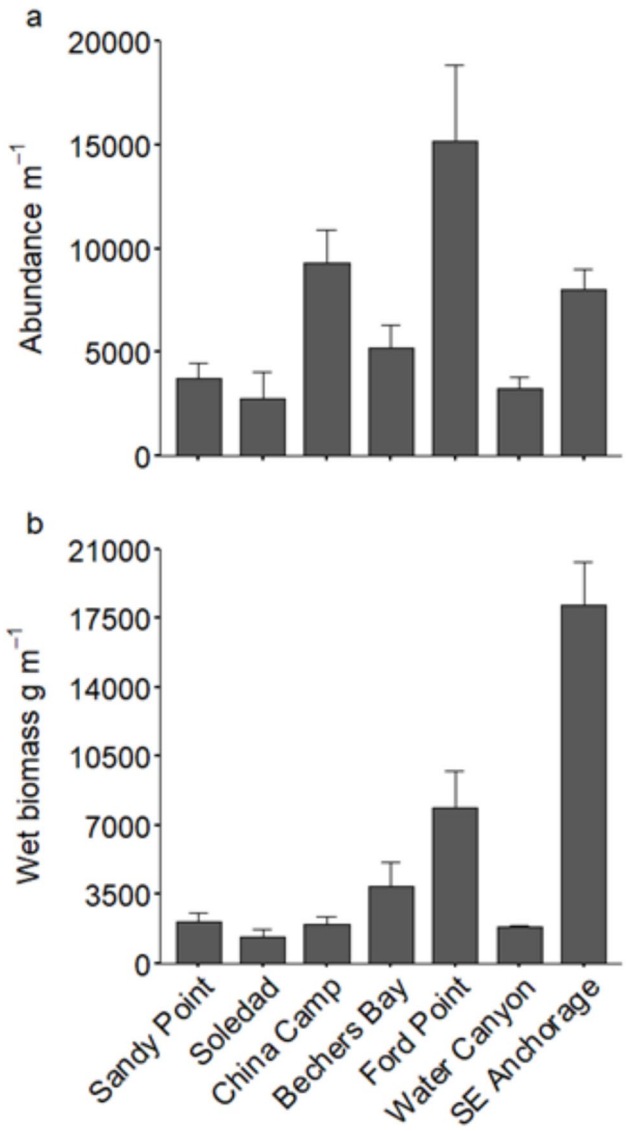

Fig. 4 Mean (±SE) abundance (**a**) and biomass of sand crabs (*E. analoga*) on the beaches sampled (**b**). Beaches are arrayed from west to east (left to right) as in Fig. 1. Biomass was estimated from the carapace length—body weight relationship, and estimates of abundance at each beach (see Methods section)

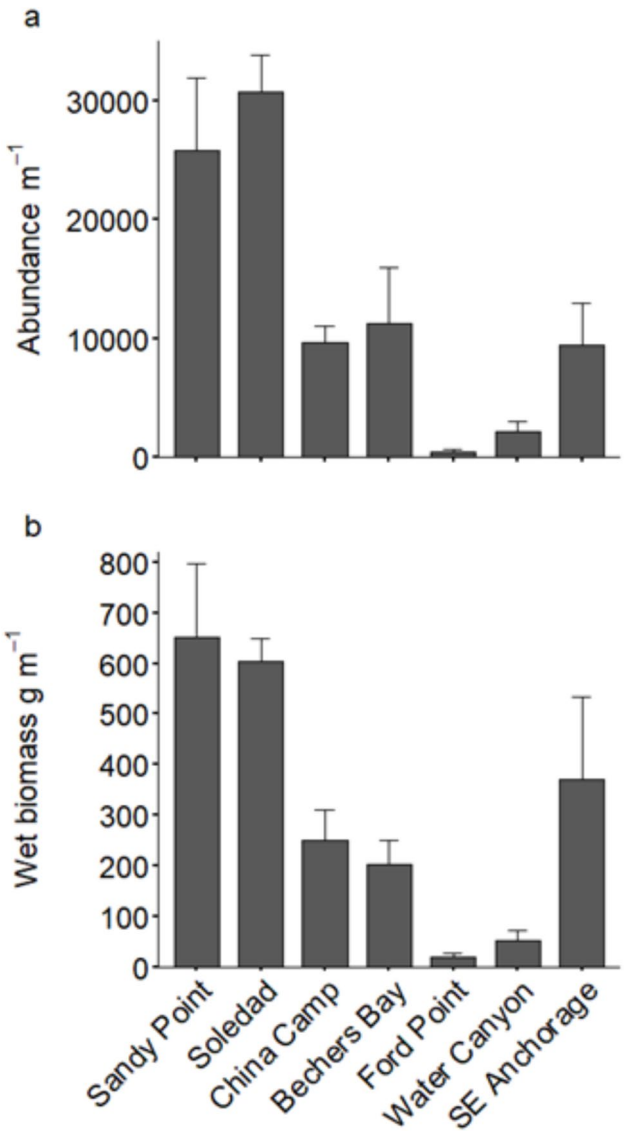

Fig. 5 Mean (±SE) abundance (**a**) and biomass of upper beach wrack-associated macroinvertebrates sampled from Santa Rosa Island sandy beaches (**b**). Study beaches arrayed west to east (left to right) as in Fig. 1

and surfperch values are more positive (i.e., similar to published values for kelp) these fish are likely more reliant on kelp-supported prey resources.

Results

Beach and surf zone characteristics

Beach and surf zone characteristics varied widely across study beaches (Table S1). Beaches ranged in length from 0.16 km at Southeast Anchorage to 2.25 km at Water Canyon. Beach-surf zone width varied almost three-fold from 45.0 m (±0 m SE) at Water Canyon to 146.7 m (±3.3 m SE) at Sandy Point. Intertidal slope measured at the water table outcrop (WTO), which is steepest on reflective beaches, varied over two-fold (3.0°–6.7°) across beach sites. The abundance (areal cover) of giant kelp, *Macrocystis pyrifera*, wrack also varied over an order of magnitude across beaches from 0.11 m^2 m^{-1} at Ford Point and Becher's Bay to 3.6 m^2 m^{-1} at Sandy Point (Fig. 3). Similarly, the abundance of macrophyte wrack, which included seagrass and all algal taxa, varied almost two orders of magnitude across beaches from 0.34 m^2 m^{-1} at Water Canyon to 6.4 m^2 m^{-1} at Soledad (Fig. 3).

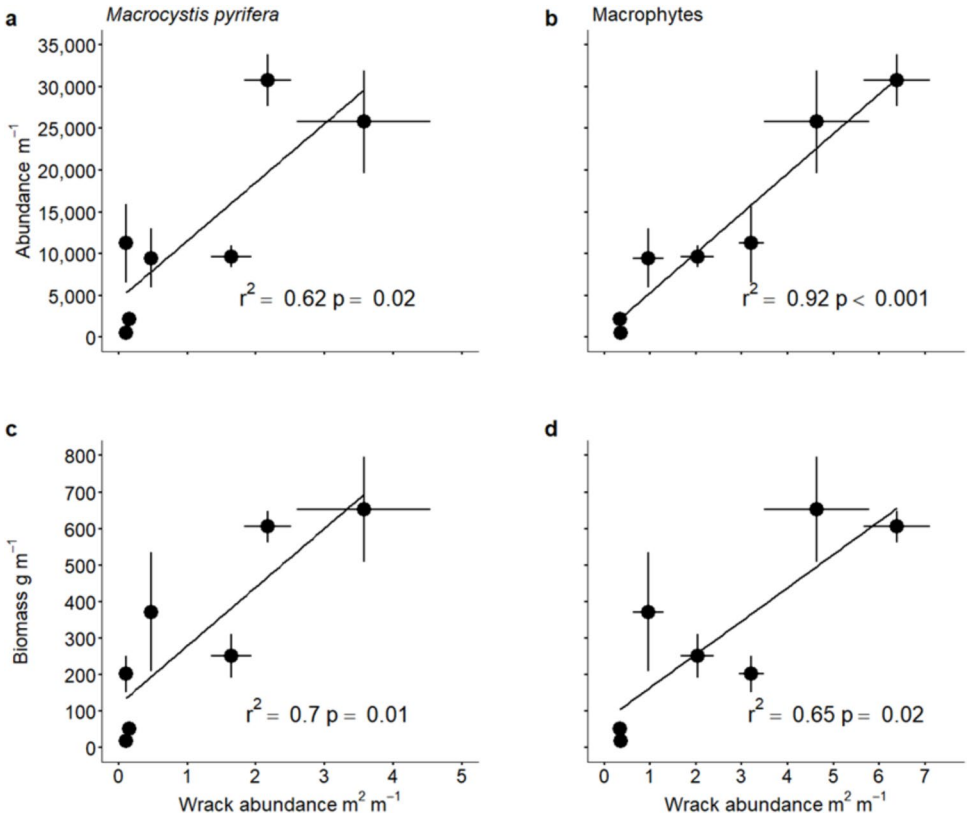

Fig. 6 Relationship between the abundance (**a, b**) and biomass (**c, d**) of wrack-associated macroinvertebrates and the abundance of *Macrocystis pyrifera* and total macrophyte wrack for Santa Rosa Island study beaches. Data presented are mean and standard error for all variables

Beach macroinvertebrate prey resources

Sand crabs (*Emerita analoga*) were present at all sites, varying over six-fold in abundance from 2773 crabs m^{-1} at Soledad to 15,180 crabs m^{-1} at Ford Point (Fig. 4a). Sand crab wet biomass, estimated from carapace length, ranged over an order of magnitude from 1321 to 18,167 g m^{-1} across beaches (Fig. 4b).

The abundance and biomass of upper beach, wrack-associated macroinvertebrates that included talitrid amphipods, isopods, beetles, and fly larvae, potential surfperch prey, varied over an order of magnitude across beaches (Fig. 5). There was a strong correlation between macroinvertebrate abundance or biomass and both the cover of *M. pyrifera* (abundance: $R^2 = 0.62$, $P = 0.02$; biomass: $R^2 = 0.70$, $P = 0.01$) and total macrophyte wrack (abundance: $R^2 = 0.92$, $P < 0.001$; biomass: $R^2 = 0.65$, $P = 0.02$) (Fig. 6).

Stomach content analysis

Thirty-seven prey items (or taxa) were identified in surfperch guts and categorized into one of the five groups described above: (1) sand crabs, (2) upper intertidal wrack-associated taxa, (3) subtidal mesograzers, (4) other beach taxa, and (5) other marine taxa not typically associated with the beach (Table 1). Multivariate analyses revealed that the contribution of these five prey groups to diet, both in terms of count and weight, varied significantly across beach sites for juvenile and adult fish ($P < 0.001$, One-way PERMANOVA, Table 2). ANOSIM analyses found that nine of 10 pairwise comparisons across beach sites were significantly different for adult fish by prey count, and six of 10 comparisons were different by prey weight (Table S2). Although there was also a significant effect of beach on diet category for juvenile surfperch (Table 2), a smaller proportion of pairwise comparisons were significantly different compared with adult fish: nine out of 15 comparisons by prey count and eight of 15 by prey weight (Table 2) (Table S3).

The average contribution of sand crabs to juvenile surfperch diet varied widely among beaches from < 14% by count and weight at Sandy Point to > 72% by count at Southeast Anchorage and 87% by weight at Ford Point (Figs. 7 and S1). Upper intertidal wrack-associated fauna (e.g., talitrid amphipods, oniscid isopods, beetles, flies) were exploited by surfperch at four of the six sites (Figs. 7 and S1). However, these taxa constituted a minor component of juvenile surfperch diet (< 5% of prey by count and weight) except at Soledad where they comprised 17–18% by count and weight of stomach contents (Figs. 7 and S1).

Subtidal mesograzers were not widely found in juvenile surfperch stomachs (< 15% by count and weight) but comprised nearly 40% of contents by count and weight at one beach (Water Canyon) (Figs. 7 and S1). Here, the subtidal kelp mesograzer, *Idotea* sp., contributed substantially

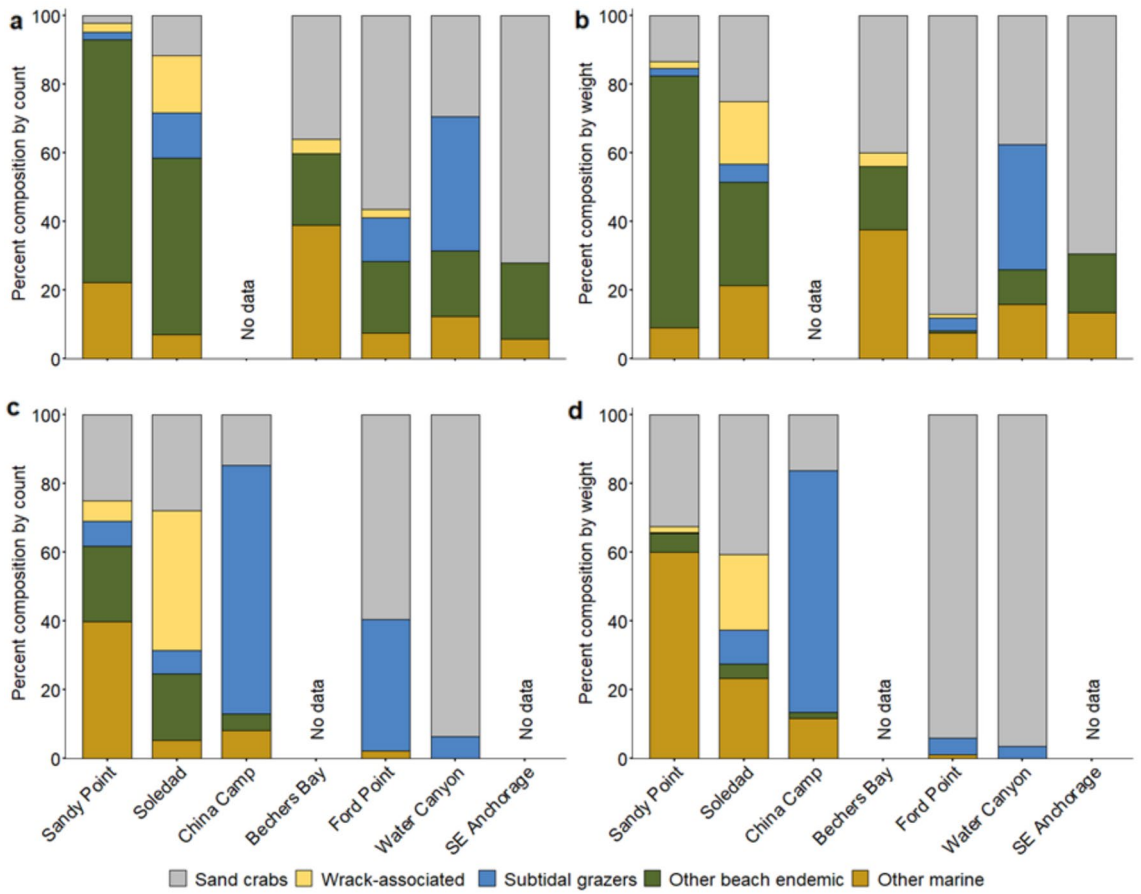

Fig. 7 Stacked mean percent composition of prey items in the stomachs of juvenile (< 130 mm) barred surfperch by count (**a**) and weight and adult (≥ 130 mm) (**b**) barred surfperch by count (**c**) and weight (**d**). Colors correspond to the prey categories prey in the legend. Beaches excluded when fish n < 3. Study beaches arrayed west to east (left to right)

(> 30% by weight) to juvenile surfperch diet (Figs. 7 and S1). Of the two remaining prey categories, other beach taxa, comprised a notable portion of juvenile surfperch diet by count or weight at two beaches, Sandy Point (73%) and Soledad (51%), where this prey category included the low intertidal omnivorous scavenging isopods *Excirolana* sp. and *Gnorimosphaeroma* sp.

Adult surfperch exploited sand crabs, which comprised > 90% of stomach contents by count or weight at two beaches (Ford Point and Water Canyon). However, sand crabs were a smaller component < 25% of stomach contents by count and weight at the other beach sites (Figs. 7 and S1). Wrack-associated taxa were present in adult fish stomachs at two sites (Soledad and Sandy Point), comprising 41% by count and 22% by weight of contents at Soledad, but 6% by count at Sandy Point (Figs. 7 and S1).

Subtidal mesograzers were heavily exploited by adult surfperch at China Camp (> 70% of stomach contents by count and weight), with moderate use at Ford Point (38% by count) and minimal use (< 8%) at the remaining beaches (Figs. 7 and S1). Adult surfperch from China Camp differed from the other sites in consuming a high proportion (> 45% by weight) of the grazing isopod, *Idotea* sp. Of the two remaining prey categories, other marine taxa notably comprised the largest prey category in adult surfperch diet at Sandy Point (40% by count, 60% by weight) (Figs. 7 and S1). Surfperch at this site were feeding on a large aggregation of the filter-feeding pelagic red crab (*Pleuroncodes planipes*) that drifted inshore.

Environmental variables and surfperch diet

For juvenile surfperch, the abundance of macrophyte wrack on the beach explained a significant proportion of variation in prey use when all prey categories were combined (by both prey count and weight, $P < 0.05$, Table 3 and S4). When prey categories were considered individually, this analysis also suggested the importance of beach-surf zone width in the use of other taxa (by prey count) and sand crabs (by prey weight), and beach orientation in the use of other beach taxa (by prey weight). The remaining environmental variables did

not explain a significant amount of variation in the use of prey by juvenile fish (Table 3 and S4).

For adult surfperch, macrophyte abundance on the beach also explained a significant proportion of variation in prey category use when all prey categories were combined (by both prey count and weight, $P < 0.05$, Table 3 and S4). Beach orientation also explained a significant amount of variation in prey category use when all prey categories were combined (by prey count). When prey categories were considered individually, the analysis suggested the importance of beach orientation (by prey count) and macrophyte wrack abundance (by prey weight) in the use of subtidal mesograzers, and the abundance of macrophyte wrack in the use of other marine taxa (by prey weight). The remaining environmental variables did not explain a significant amount of variation in the use of prey by adult fish (Table 3 and S4).

Fish and prey stable isotope analysis

To evaluate the relative importance of phytoplankton-based prey to surfperch diet over longer timescales across beach sites, we compared the $\delta^{13}C$ value of surfperch muscle tissue to the $\delta^{13}C$ value of sand crabs, a proxy for a phytoplankton-based diet. Values were adjusted for anticipated trophic enrichment (see Methods). Mean $\delta^{13}C$ values for surfperch muscle ranged from − 16.2 to − 14.6 ‰ for juveniles (n = 6 sites) and from − 16.1 to − 14.8 ‰ for adults (n = 4 sites) (Fig. 8) and differed significantly among beaches

Table 3 Results from stepwise DistM analysis showing significant relationships only ($P < 0.05$) between environmental variables and diet categories. Results presented for juvenile and adult surfperch across study beaches using stomach contents assessed by count and wet weight. See Materials and Methods for specifics on the diet categories. Models that could not be calculated because the Bray–Curtis dissimilarity matrices were undefined are also shown

Diet category	Environmental variable	Adjusted R^2	Pseudo-F	P	Cumul
Juvenile fish (prey count)					
Five diet categories combined	Macrophyte abundance (log)	0.224	2.444	0.017	0.379
Wrack associated taxa	undefined				
Other beach taxa	Beach-surf zone width	0.989	448.990	0.005	0.991
Subtidal mesograzers	undefined				
Juvenile fish (prey weight)					
Five diet categories combined	Macrophyte abundance (log)	0.224	2.444	0.014	0.379
Sand crabs	Beach-surf zone width	0.697	12.514	0.020	0.758
Wrack associated taxa	undefined				
Other beach taxa	Orientation (cos)	0.833	26.107	0.053	0.867
Subtidal mesograzers	undefined				
Adult fish (prey count)					
Five diet categories combined	Macrophyte abundance (log)	0.611	7.276	0.025	0.708
	Orientation (cos)	0.954	23.573	0.018	0.977
Wrack associated taxa	undefined				
Subtidal mesograzers	Orientation (cos)	0.967	117.930	0.043	0.975
Other beach taxa	undefined				
Adult fish (prey weight)					
Five diet categories combined	Macrophyte abundance (log)	0.592	6.813	0.025	0.694
Wrack associated taxa	undefined				
Other beach taxa	undefined				
Subtidal mesograzers	Macrophyte abundance (log)	0.670	7.032	0.050	0.473
Other marine taxa	Macrophyte abundance (log)	0.298	2.696	0.017	0.473

Cumul = cumulative amount of variation explained by each significant model

(juveniles: one-way ANOVA $F_{8,36} = 65.3$, $P < 0.0001$; adults: Kruskal–Wallis chi-squared = 23.7, $P < 0.0001$). Because mean $\delta^{13}C$ values of sand crabs varied significantly among beaches, we compared $\delta^{13}C$ isotope values of surfperch from each beach to the mean $\delta^{13}C$ isotope values of sand crabs from the same beach.

Mean $\delta^{13}C$ values of juvenile surfperch were enriched relative to sand crabs at all the study beaches (Fig. 8). Mean $\delta^{13}C$ values of adult surfperch were comparable to sand crabs (95% CI overlapping mean values) at three beaches (Sandy Point, Soledad, and Water Canyon) and enriched at one beach (China Camp) (Fig. 8). We observed consistent trends between mean $\delta^{13}C$ values for juvenile and adult surfperch and stomach contents. On beaches where the mean $\delta^{13}C$ values of juvenile surfperch were most enriched in ^{13}C, the mean percent composition of kelp-dependent prey in stomachs was > 5% (Figs. 7 and 8). At the two beaches, Soledad and Sandy Point, where juvenile surfperch had elevated $\delta^{13}C$ values, sand crabs were a lesser component of the stomach contents (< 25%) (Figs. 7 and 8). Similarly, adult surfperch from Soledad and China Camp had the highest ^{13}C values, and the highest contribution of kelp-dependent prey in stomachs among beaches (Figs. 7 and 8). At one beach, Water Canyon, where the mean $\delta^{13}C$ value for fish was the lowest, the mean composition of sand crabs in adult surfperch stomachs was > 90% (Figs. 7 and 8).

Discussion

Trophic transfer of phytoplankton-based carbon to surfperch

Phytoplankton is considered an allochthonous subsidy that supports surf zone and intertidal suspension feeders, including large aggregations of sand crabs (*Emerita analoga*) present on the beaches of California (Wenner et al. 1993; Dugan et al. 2000; 2003; Morgan et al. 2018). Our results and those of others (Carlisle et al. 1960; Barry et al. 1996) show that this widespread and abundant crustacean is an important prey resource exploited by barred surfperch. Carlisle et al. (1960) estimated that sand crabs made up 92.9% of surfperch stomach content by volume on mainland beaches in southern California, similar to our highest values for this prey based on count and weight. Since sand crabs feed almost entirely on phytoplankton, with smaller contributions of zooplankton and other organic matter (Efford 1966), carbon assimilated from sand crabs by surfperch can be considered largely of phytoplankton origin. While the exploitation of sand crabs feeding on particulate kelp detritus could provide a potential pathway for kelp-based carbon to enter the surf zone food web, this contribution is likely trivial because *M. pyrifera* does not produce enough particles of the right size to be useful to suspension feeders relative to the availability of phytoplankton (Yorke et al. 2013, 2019; Miller et al. 2015).

Trophic transfer of kelp-based carbon to surfperch via upper beach taxa

Although the diet of surfperch on most beaches consisted largely of sand crab prey supported by phytoplankton-based production, the use of prey supported by giant kelp (*M. pyrifera*), either as wrack deposited on the beach or in situ on nearshore rocky reefs, also occurred. This pathway was particularly notable at Soledad Beach, where an average of 41% of the stomach contents by count and 22% by weight of adult surfperch consisted of upper beach, wrack-associated species, a pattern also observed to a lesser extent at Sandy Point. The longer-term use of kelp-based prey was also suggested by the elevated $\delta^{13}C$ values of surfperch muscle from these two beaches, indicative of the incorporation of kelp-derived carbon. Interestingly, adult surfperch from China Camp also had elevated $\delta^{13}C$ values, consistent with the use of a kelp-derived carbon source, however in this case it was likely the subtidal grazing isopod *Idotea* sp. (discussed below). Since the $\delta^{13}C$ values of consumers reflect diet integrated over time, results from stomach content analysis, which reflects recent feeding, may not match expectations from $\delta^{13}C$ values. However, stomach content analysis generally agreed with inferences from $\delta^{13}C$ values in this study, suggesting that the relative use of phytoplankton-based versus kelp-based food resources inferred from diet analysis reflected longer term, site-specific patterns. Tag-recapture studies indicate that surfperch in California generally exhibit limited dispersal, perhaps because of natural barriers like rocky headlands (Carlisle et al 1960; Pruden 2000).

Trophic transfer of kelp-based carbon to surfperch via subtidal mesograzers

Predation on subtidal macroinvertebrates that directly graze on giant kelp is another pathway that could facilitate the transfer of kelp-based carbon to surfperch. Predation on subtidal kelp grazing macroinvertebrates is a well-documented pathway for the trophic transfer of kelp-based carbon to reef fish (Koenigs et al. 2015). Kelp grazing isopods, *Idotea* sp., are strongly associated with *M. pyrifera* fronds (Bernstein & Jung 1979) and have carbon isotope values similar to *M. pyrifera* (Koenigs et al. 2015). These isopods made up the majority of prey items in the stomachs of surfperch from Water Canyon (juveniles) and China Camp (adults).

Two potential pathways for the transfer of kelp-based carbon from nearshore rocky reefs to the surf zone may occur here. First, surfperch may leave the surf zone and forage in kelp forests. This possibility, although plausible,

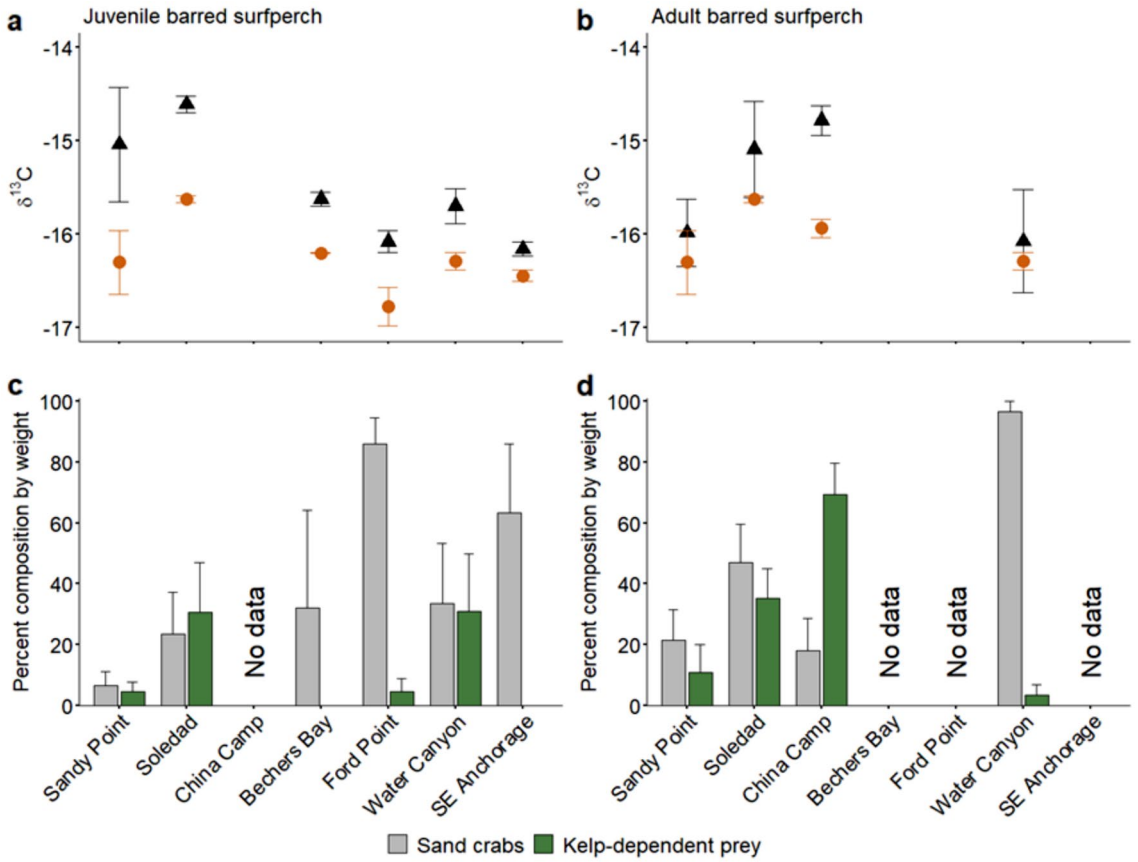

Fig. 8 The top two panels show the mean (±95% confidence interval) $\delta^{13}C$ values (**a**, **b**) for juvenile (**a**) and adult barred surfperch (**b**) (*Amphistichus argenteus*) (black triangles) and sand crabs (*Emerita analoga*) (orange circles). A trophic discrimination factor of 0.5‰ for $\delta^{13}C$ has been added to sand crab $\delta.^{13}C$ values (Post 2002). The bottom two graphs contrast mean (±SE) percent composition by weight of sand crabs (grey bars) and kelp-dependent (green bars) prey items in the stomachs of juvenile (**c**) and adult barred surfperch (**d**). Not all prey categories included in panels (**c**) and (**d**). Beaches excluded when fish n < 3. Study beaches arrayed west to east (left to right)

seems unlikely considering that barred surfperch prefer sandy bottoms and are rarely reported in kelp forests (DeMartini 1969), and are often mistakenly reported in kelp forests for black perch (*Embiotoca jacksoni*) assuming a light color (Feder et al. 1974). At Water Canyon, where *Idotea* sp. were a dominant component in juvenile surfperch stomachs, the surf zone encroaches on subtidal rocky reefs during low tide, making foraging in kelp forests conceivable.

Another and perhaps more likely possibility when rocky reefs are located further offshore involves foraging by surfperch on mesograzers such as *Idotea* spp. attached to kelp dislodged from reefs and advected into the surf zone (Cartraud et al. 2021). We observed but did not quantify *Idotea* sp. attached to *M. pyrifera* in the surf zone during sampling. However, Hobday (2000) found that *Idotea resecata* was an abundant rafting species and found on every *M. pyrifera* raft surveyed in the Santa Barbara Channel. Furthermore, several studies from southwestern Australia and northeastern Brazil found evidence that amphipod mesograzers associated with kelp rafts in the surf zone constituted a major (> 75%) component of the diet of surf zone fish (Robertson and Lenanton 1984; Crawley et al. 2006; Santos et al. 2021).

Availability of kelp and phytoplankton-based subsidies to surfperch

The DistLM analysis suggested that the abundance of macrophyte wrack on the beach was an important driver of the use of wrack-associated taxa by surfperch of both age classes. Talitrid amphipods, which reached high abundances on some study beaches, depend primarily on macroalgal wrack stranded on the beach during ebbing tides for food and shelter. The abundance of these amphipods was positively correlated with the abundance of both *Macrocystis* and total macroalgal wrack, which varied greatly across the study beaches. Talitrid amphipods grow rapidly on *M. pyrifera* (Lastra et al. 2008), which was the main macroalgal

component of wrack on our study beaches, and on other island and mainland beaches in the region (Dugan et al. 2000, 2003). Other upper beach wrack-associated taxa (isopods, flies, and beetles) were also found in surfperch stomachs. Although upper beach wrack-associated macroinvertebrates can attain high abundances as shown in this study and others (e.g. Dugan et al. 2003; Schooler et al. 2019), we report the first exploitation of this diet category by surf zone fish.

There are three possible mechanisms by which upper beach wrack-associated macroinvertebrates are accessible to surf zone fish. First, kelp that has been deposited on the beach and colonized by upper beach macroinvertebrate species could be resuspended as the tide rises and advected back into the surf zone where biota adhering to the wrack become available to foraging fish. Evidence for this pathway is largely speculative (Hyndes et al. 2014; Baring 2015) and based on the role that rafting plays in dispersing upper intertidal taxa (Thiel and Gutow 2005). Second, wrack-associated taxa may also become available to surf zone fish during high tides and wave events that transport surface or burrowed upper beach wrack-associated macroinvertebrates directly into the surf zone independently of wrack (Craig 1973).

Finally, during high tide, fish could forage in and around wrack piles on the beach where upper intertidal macroinvertebrates are burrowed. For example, in salt marshes, the vegetated marsh surface provides important foraging habitat for a number of fish species during high tide (e.g., West and Zedler 2000). Observations of foraging by barred surfperch in shallow (~ 10 cm) intertidal zones, particularly during flooding tides, supports this possibility for sandy beaches (Love 1991). Whatever the mechanisms, our results indicate that beaches with large accumulations of wrack can provide wrack-dependent prey subsidies to barred surfperch and perhaps other surf zone fish as well.

Beach-surf zone width was predictive of the use of sand crabs and other beach taxa by juvenile surfperch when those diet categories were considered separately. On narrow beaches, sand crabs and other beach taxa aggregate in concentrated bands (Klapow 1972; Jaramillo et al. 2000) which may create better foraging opportunities for juvenile surfperch than wide beaches where these macroinvertebrate prey are distributed across a larger area. Not only does beach-surf zone width affect foraging area and access to macroinvertebrate prey (e.g., wave runup), it also affects the composition and abundance of prey communities by influencing productivity of surf zones and resources available to sandy beach suspension feeders (Bergamino et al. 2011; Morgan et al. 2018).

Orientation (cosine) also explained a significant amount of variation in the use of other beach taxa by juvenile surf perch. This was also the case for adult surfperch when all diet categories were combined and when considering subtidal mesograzers only (by prey count for both). Orientation (cosine) is a spatial variable that can explain effects varying on north to south gradients (Evans & Cox 2005). Beach orientation relative to prevailing currents and wind may strongly influence the delivery of subsidies to surf zones and sandy beaches (Orr et al. 2005; Lastra et al. 2014; Liebowitz et al. 2016). The study region is characterized by northwesterly winds and prevailing currents (Fewings et al. 2015) that could move subsidies directly to or past study beaches, thus influencing the availability of subsidies to beaches (Lastra et al. 2014). Similarly, beach orientation explained a significant proportion of variation in wrack-associated species in the diet of endemic island foxes that forage on Channel Islands sandy beaches (Page et al. 2021).

Subsidies and dynamics of surf zone ecosystems

The use of upper beach wrack-associated taxa by surfperch may be considered a reciprocal subsidy. A reciprocal subsidy occurs when a bidirectional flux of allochthonous energy occurs between ecosystems (Nakano & Murakami 2001; Bartels et al. 2012). Typically, this involves the reciprocal exchange of material such as invertebrates and detritus between terrestrial and freshwater ecosystems (e.g., Baxter et al. 2005), but this exchange can occur between terrestrial and marine ecosystems (Romanuk & Levings 2010). In this case, upper beach wrack-associated macroinvertebrates use giant kelp and other macrophytes deposited on the upper shore for food and shelter. These taxa develop and reproduce within the terrestrial-marine ecotone and, in turn, provide a food resource subsidy to fully marine surfperch. For sandy beaches where upper beach habitat has been lost or modified by armoring (Jaramillo et al 2021) or beach management activities, like grooming that remove wrack (Schooler et al. 2019), the importance of this reciprocal subsidy to surf zone fish diets would be greatly reduced.

We have highlighted the role of variation in beach physical characteristics and prey resources in determining surfperch diet. Climate change will alter both environmental conditions (Harley et al. 2006; Halpern et al. 2007; Ruttenberg & Granek 2011) and the availability of allochthonous subsidies that support surf zone and sandy beach food webs (Defeo et al. 2009; Revell et al. 2011; Morgan et al. 2018). Although the myriad anthropogenic threats facing surf zones and sandy beaches need addressing (Defeo et al. 2009), our results suggest that surfperch can shift their diet in response to changing environmental conditions and resource availability as has been observed for beach-foraging ghost crabs (*Ocypode* sp.) (Gül & Griffen 2020). In fact, the highly dynamic nature of surf zones and beaches, including the supply of food resources to these ecosystems, is likely the driver of the generalist diet behavior of organisms endemic

to these ecosystems (Bessa et al. 2014; Santos et al. 2021; Carcedo et al 2024; Mosman et al. 2023).

Increasing sea surface temperature could result in the loss or reduction of some diet staples for surfperch as well as beach habitat zones. Ocean warming is negatively impacting kelp (Krumhansl & Scheibling 2012; Cavanaugh et al. 2019; Rogers-Bennett & Catton 2019; Lowman et al. 2021) and could affect surfperch prey that depend on kelp. The upper beach zones that support kelp-based intertidal prey for surfperch are also highly vulnerable to loss from sea level rise (Myers et al. 2019; Barnard et al. 2021) and coastal armoring (Jaramillo et al 2021). However, changing environmental conditions could also introduce new resource subsidies to foraging surfperch. For example, while the majority of surfperch diet was comprised of benthic prey, we observed the opportunistic consumption of water column-based prey in the southern affinity, filter feeding pelagic red crabs (*Pleuroncodes planipes*) by adult surfperch at Sandy Point. Once rarely found near shore in California, pelagic red crabs have been washing into these habitats including beaches more frequently during El Niño Southern Oscillation cycles or marine heat waves (Zuercher & Galloway 2019), as have other more tropical species into the northeast Pacific (Sutherland et al. 2018; Morgan et al. 2018). These results are both promising and concerning for conservation and management of an economically and ecologically important fish species, highlighting the need to further evaluate the effects of climate change and other anthropogenic disturbances on coastal ecosystems and food webs.

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Author contributions Henry Page, Jenifer Dugan, Donna Schroeder, and Robert Miller contributed to the study conception and design. All authors contributed to data collection. Sample analyses were performed by Jessica Madden, Nicholas Schooler, and Kyle Emery. Data analyses were performed by Nicholas Schooler, Henry Page, and Kyle Emery. The first draft of the manuscript was written by Nicholas Schooler and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets generated for this study will be made available in an online repository upon publication.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

Ethical approval All activities involving animals met the ethical and legal requirements for the humane care and use of animals as set forth by the PHS Policy, the Animal Welfare Act, AAALAC International standards, and UCSB policies and guidelines (IACUC Protocol #943).

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