Secondary Production of Kelp Bass Paralabrax clathratus in Relation to Coastal Eelgrass Zostera marina Habitat in a Southern California Marine Protected Area

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Abstract.—Seagrasses are an important refuge for fishes and provide ecosystem services worldwide. Along the Pacific Coast, however, quantitative assessments of the ecological role of seagrass habitats with limited anthropogenic impacts are lacking despite their value to resource management. To address these issues, the ecological function of the eelgrass *Zostera marina* Linnaeus in a protected area off Santa Catalina Island, California, USA was quantified using estimates of secondary production in the kelp bass *Paralabrax clathratus* (Girard, 1854). Monthly assessments of *Zostera* structural complexity, as well as the size and abundance of juvenile kelp bass were used to establish a baseline of fish biomass and recruitment associated with *Zostera* habitat. The greatest number of kelp bass was recorded in the summer and fall months and the fewest during the winter and spring. Secondary production in kelp bass (0.1 to 0.59 g m^{-2} mo^{-1}) followed monthly changes in *Zostera* habitat structure throughout the 24-month study period. Seasonal changes in the structural complexity of coastal *Zostera* beds may influence the flow of energy to adjacent reef environments through the transfer of fish biomass. These findings help define the potential role of *Zostera* habitat within the larger context of nearshore coastal ecosystems in the Southern California Bight.

Coastal seagrass beds are an important nursery habitat for fishes and provide a variety of ecosystem services worldwide (Worthington et al. 1992; Heck et al. 2003; Burkholder et al. 2007; Warren et al. 2010; Parsons et al. 2015). Given the significance of this resource, the protection of seagrass habitat has received considerable attention (Coles et al. 2014; Bas Ventín et al. 2015; Schultz et al. 2015). The National Oceanic and Atmospheric Administration's National Marine Fisheries Service (NOAA Fisheries) recognizes seagrasses as habitat areas of particular concern, which are defined as subsets of essential fish habitat under the Pacific Coast Groundfish Fishery Management Plan. Such areas are considered high priorities for conservation and management, and warrant special attention during the regulatory process set forth by the Magnuson Stevens Fishery Conservation and Management Act in 1976. Nevertheless, the management of seagrasses has proven challenging in some areas, particularly those with remote coastlines that are difficult to access, and in other cases due to a paucity of information on seagrass resources altogether (Long and Thom 2001). For example, because of their isolation from the Southern California mainland, the distribution and habitat function of seagrass beds off the California Channel

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Islands are poorly known; this is in contrast to the many long-term studies of shallow rocky reefs and kelp forests from the same region (Engle and Miller 2005).

One of the most common species of seagrass found along the Southern California coast is the eelgrass *Zostera marina* Linnaeus 1753, which forms extensive beds in shallow bays and estuaries with low to moderate current exposure (Dawson and Foster 1982; Engle and Miller 2005). Many of the areas inhabited by *Zostera* are subject to anthropogenic stressors such as dredging, eutrophication and development that decrease the ecological function and stability of these communities (Obaza et al. 2015; Shelton et al. 2017). While studies of *Zostera* beds found in these locations offer information on habitat function in a stressed environment, data from protected areas provide an upper bound of the behavioral response by fishes that are dependent on seagrass as a refuge from predators (Jackson et al. 2001; Gillanders et al. 2003). Such is the case for populations of *Zostera* around the California Channel Islands, which are separated from many of the anthropogenic stressors found along the mainland coast and thus are an ideal location to collect ecological and environmental data (Findlay and Allen 2002; Davis 2005; Mason and Lowe 2010; Saarman and Carr 2013). Of particular interest is information on habitat use and movement patterns of ecologically and economically important populations of reef fishes living in these areas (NOAA 2014). Accordingly, estimates of secondary production are used to quantify the biological benefit of different habitats by accounting for both changes in fish biomass and population parameters that include fish mortality, recruitment, immigration and emigration (DeMartini et al. 1994; Johnson et al. 1994; Love et al. 1996; Faunce and Serafy 2008; Jeong et al. 2009; Kamimura et al. 2011; Yeager et al. 2012; Williams et al. 2013; Claisse et al. 2014).

Here, we compare secondary production in juvenile kelp bass *Paralabrax clathratus* (Girard 1854), a temperate serranid fish, in relation to the three-dimensional (= structural) complexity of *Zostera* habitat in a protected area off Santa Catalina Island, California, USA. *Zostera* forms highly productive beds (Risgaard-Petersen et al. 1998) that function as an important nursery habitat for kelp bass (Mendoza-Carranza and Rosales-Casian 2002; Altstatt et al. 2014), as well as other common and economically important fishes such as rockfish (*Sebastes* sp.) and surfperch (*Embiotocidae*) (Hoffman 1986; Allen et al. 2002). Our findings provide an important baseline of fish biomass and recruitment associated with *Zostera* habitat in the absence of significant anthropogenic impacts. By integrating multiple metrics for evaluating *Zostera* habitat function, such as species use and secondary production, we aimed to improve conservation and management efforts by evaluating the role of *Zostera* habitat in a Southern California marine protected area.

Material and Methods

Study Site and Natural History

Field surveys were conducted monthly from September 2013 to August 2015 in Big Fisherman's Cove (33°26′38.85″N, 118°29′6.86″W) in the Blue Cavern State Marine Conservation Area (SMCA) on Santa Catalina Island, ~35 km off the coast of Southern California, USA (Fig. 1). Neither anchoring nor fishing is allowed in Blue Cavern SMCA, and all commercial and recreational take of marine life is prohibited as outlined by California's Marine Life Protection Act of 1999. The subtidal habitat of Big Fisherman's Cove extends seaward from a northwest facing, boulder and rock cobble beach as a sloping, sandy bottom that steadily descends to depths >35 m that lie towards the center and mouth of the cove. The northeast and southwest borders are comprised of semi-vertical rocky reef (5-20 m depth)
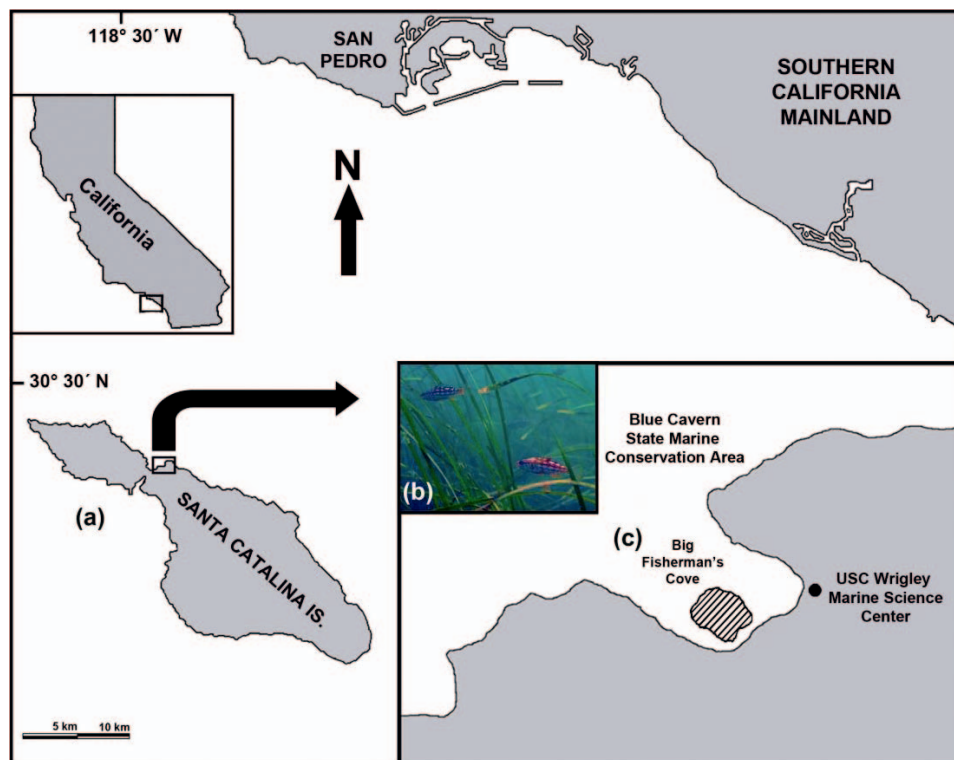
Fig. 1. Map showing the location of (a) Santa Catalina Island relative to the Southern California mainland. Surveys of (b) eelgrass *Z. marina* and kelp bass *P. clathratus* were conducted in (c) Big Fisherman's Cove, which is part of the Blue Cavern State Marine Conservation Area. Hatched area indicates survey site and extent of *Zostera* areal coverage (∼0.24 hectares). Map adapted from Froeschke et al. (2006).

covered with macroalgae and kelp that provides a forest habitat for fishes and invertebrates (Abbott and Hollenberg 1992; Parnell et al. 2010). The sandy, inner reaches of the cove (4-12 m depth) support a *Zostera* bed that covers an area ∼0.24 ha in size (Obaza and Ginsburg unpublished data). Areal coverage of *Zostera* in Big Fisherman's Cove was estimated using a Trimble® R1 Global Navigational Satellite System (GNSS) receiver held at the water surface in which a scuba diver was tracked while swimming along the perimeter of the bed at depth. Patches of *Zostera* were first documented at this site in 1996 and are likely the result of natural colonization from nearby populations (Engle and Miller 2005).

Fish surveys targeted kelp bass, which are one of the most important recreational species of reef fish off Southern California (Young 1963; Erisman et al. 2011). Typically found in shallow water (3-25 m depth), juveniles feed on benthic invertebrates and switch to a mostly piscivorous diet as adults (Hobson and Chess 1976; Eschmeyer and Herald 1999). Mature individuals form breeding aggregations in the late spring to early fall in which larvae enter the plankton and settle after 28-30 days onto *Zostera* beds (Valle et al. 1999; Allen et al. 2002) and shallow, rocky reefs (Carr 1994; Love et al. 1996; Cordes and Allen 1997; Erisman and Allen 2006). Adult kelp bass exhibit high levels of site fidelity (Mason and Lowe 2010). However, catch and release studies by Carr (1994) and Hartney (1996)

indicate that juveniles are unlikely to return to the reef in which they settled (home) after moving to a new location.

Zostera and Kelp Bass Surveys

The structural complexity of *Zostera* habitat, as well as the size and abundance of juvenile kelp bass was measured by scuba divers. Surveys were conducted along four separate, 30-m long benthic transects spaced ~4 m apart. The beginning of each transect was marked with a semi-permanent sand anchor and surveyed along a northwest compass heading of 310 degrees. Structural complexity was defined using three key measurements of *Zostera* habitat: shoot frequency, shoot density and canopy height. Frequency was estimated using a point-intercept approach in which *Zostera* leaf shoots were recorded as either present or absent along each meter interval (from 1 to 30 m) directly beneath the transect line. Density was measured as the total number of leaf shoots counted within four quadrats (0.25 m^2) placed at 10-m intervals (0-30 m) along each transect. Lastly, *Zostera* canopy height was recorded (to the nearest cm) as 80% of the mean length of ≥10 haphazardly selected leaf shoots (Short and Durate 2001) within each of the quadrats described above. The product of each of these metrics (i.e., frequency, density and canopy height) was used to create an eelgrass structural index in order to view the collective changes in *Zostera* habitat over time.

Juvenile kelp bass were surveyed visually from 1 m above the benthos and within a 2 m wide swath along each 30 m transect line. Given the importance of *Zostera* habitat to new recruits (Jackson et al. 2001), visual surveys focused on juvenile kelp bass (2.1–10 cm TL; Love et al. 1996) and not adults that may have migrated from other areas. The size and abundance of juveniles was recorded by divers as they swam the length of each transect line. The TL of an individual was recorded to the nearest cm following the methods of Bell et al. (1985). Kelp bass abundance was measured as the total number of juvenile fish recorded on a given transect. Visual estimates of fish length and density are known for a range of different reef fishes and habitats (Sale 1980; Brock 1982; Coyer and Witman 1990; Ebeling and Hixon 1991) and are frequently used to monitor subtidal marine life off Southern California (Pondella et al. 2006; Gillett et al. 2012; Coates et al. 2018).

Kelp Bass Secondary Production

Secondary production was based on visual surveys of length and abundance of juvenile fish using a modified version of the model developed by Claisse et al. (2014). Specifically, secondary production rates were estimated for individual kelp bass observed on a given survey by determining changes in biomass after one month of growth using a weight–length relationship specific to this species. A linear growth function was used, rather than an exponential growth curve, as the former provides a better fit for modeling the growth of young-of-the-year (YOY) fishes (Faunce and Serafy 2008; Yeager et al. 2012; J.T. Claisse pers. comm.).

Fish biomass (i.e., mean wet body weight, W) was calculated from the observed length of kelp bass using the weight-length relationship: $W = a\,TL^{\,b}$, where TL is the total length of individual kelp bass from visual surveys and the constants *a* and *b* (0.00813 and 3.03, respectively) are specific growth rates reported for this species (see Froese et al. 2014). The age (months-old) of individual kelp bass was determined using empirical age-at-length values for juveniles (2.1 to 10 cm TL) reported by Love et al. (1996). From these data, a linear growth rate of 1.17 cm TL mo^{-1} was calculated for post-settlement (>2.1 cm TL) kelp bass ≤1 year old. Individual kelp bass, whose TL was recorded (to the nearest cm)

on dive surveys in Big Fisherman's Cove, were then sorted into one of the following age-at-length bins (AL_1–AL_6): 1 month old, 2.1–3.27 cm TL; 2 months old, 3.28–4.45 cm TL; 3 months old, 4.46–5.63 cm TL; 4 months old, 5.64–6.81 cm TL; 5 months old, 6.82–7.99 cm TL; 6 months old, 8.0–9.17 cm TL). The growth (G) of individual kelp bass from each length bin was calculated using visual survey data as the difference between changes in biomass, estimated by TL, after one month of growth ($\Delta TL = 1.17$ cm mo^{-1}) using the equation: $G = a(TL + \Delta TL)^b - W$.

The instantaneous rate of fish mortality (M) was calculated monthly with the TL of individual kelp bass from each age-at-length bin using the empirical formula reported by Gislason et al. (2010) as follows: $\ln (M) = 0.55 - 1.61 [\ln (TL)] + 1.44 [\ln (L_\infty)] + \ln (k)$, where L_∞ and k (69.8 cm TL and 0.06, respectively) are key life-history parameters specific to kelp bass reported by Love et al. (1996). We selected this approach because it is the best-supported estimator for determining the number of individuals that survive to successive life stages (Lv and Pitchford 2007; Claisse et al. 2014). Fish mortality rates were estimated on a monthly basis (as opposed to an annual schedule). Survivorship (S) of kelp bass was then calculated using the monthly length- and species-specific exponential rate of fish mortality for each month sampled using the equation: $S = e^{-M}$.

Accumulated biomass (i.e. somatic production, P_s) of kelp bass was calculated on a monthly basis as the product of fish growth (G), survivorship (S) within a given age-at-length bin and fish density (N; number of juvenile kelp bass recorded within a 2 m wide swath along each of the four, 30 m transects [= 240 m^2 total survey area]) using the equation: $P_s = (G) (S) (N)$. Total secondary production (P_T) was calculated as the monthly sum (Σ_m) of recruitment (P_R, accounts for YOY fish growth) and somatic production (P_S) for each of the six post-settlement age-at-length bins (AL_1-AL_6) recorded over the course of the study as follows: $P_T = \Sigma_m (P_R + P_{AL1} + P_{AL2} + P_{AL3} + P_{AL4} + P_{AL5} + P_{AL6})$.

Data Analysis

The relationship between the structural complexity of *Zostera* habitat and the abundance of juvenile kelp bass was analyzed using a multiple regression model. Visual estimates of fish density were tested for heteroscedasticity and treated as individual, monthly events. Interactions among the different predictor variables of *Zostera* habitat (leaf shoot frequency, density and canopy height), measured across different months, were presumed to have at least one common variable between them. Temporal autocorrelation among covariate months and years was accounted for by applying a generalized least squares (GLS) and maximum likelihood (ML) estimation procedure to all statistical models tested. Akaike's Information Criterion (AIC) was used to determine the model of best fit. Comparisons between the different predictor variables were tested for multicollinearity using a Farrar chi-square test. Although the relationship between *Zostera* shoot frequency and canopy height was collinear ($\chi^2 = 2.39$, $p < 0.05$), the relationship between each of these factors in addition to shoot density was not strong enough to warrant a statistical correction. Furthermore, variance inflation factors for each of the *Zostera* predictor variables were not statistically significant (critical value < 2). Therefore, multicollinearity was unlikely to pose an issue (Graham 2003) for estimating the relationship between the structural complexity of *Zostera* and the presence of kelp bass.

Comparisons between the abundance of kelp bass and each of the predictor variables of *Zostera* habitat structure were analyzed separately using a GLS approach, and subsequently evaluated by AIC using the information-theoretic approach for analyzing
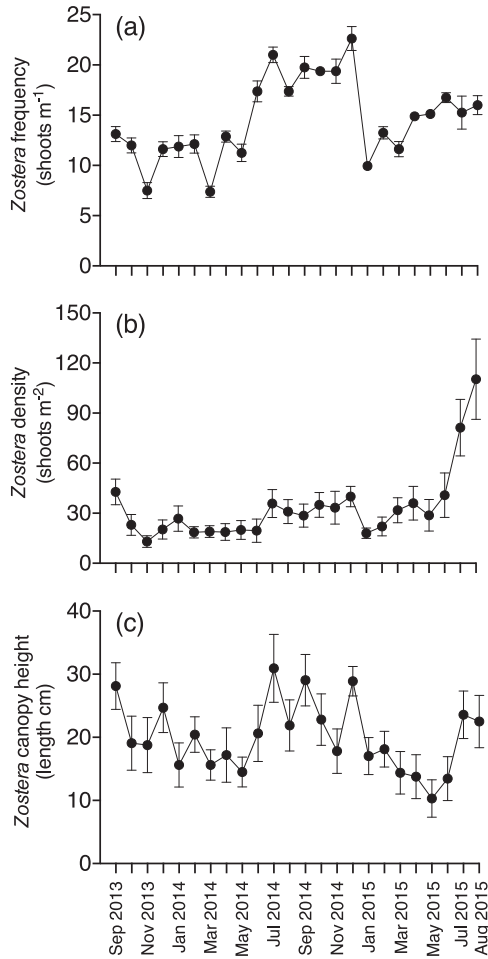
Fig. 2.   Monthly changes in (a) frequency, (b) density and (c) canopy height of eelgrass *Zostera marina* recorded from September 2013 to August 2015 in Big Fisherman's Cove. Values are means ± 1 SE. Where not shown, errors fell into the graphical representation of the data point.

ecological data developed by Burnham and Anderson (2002). Given the relatively low sample sizes, a second-order (i.e., corrected) information criterion (AICc) approach was used in place of the general AIC estimator. These values were, in turn, compared to kelp bass abundance and secondary production using a GLS approach. Error values reported are ± 1 SE of the mean. All data were analyzed using R Statistical Software (R Core Team 2015) with the *dplyr* (Wickham et al. 2015) and *nlme* (Pinheiro et al. 2015) packages.

Results

The frequency of *Zostera* leaf shoots (Fig. 2a) increased nearly 3-fold from March to July 2014 (average = 7.4 ± 0.6 to 21.0 ± 0.78 shoots m^{-1}, respectively; ANOVA, $F_{1, 9} = 8.13$, $p < 0.05$) and remained relatively unchanged until December 2014 (average = ANOVA, $F_{1, 11} = 26.9$, $p = 0.0004$). Shoot frequency then dropped 32% from an average of

Table 1. Factor type (ψ), AICc scores, AICc differences (Δ) and Akaike weights (ω) for predicting the use of *Zostera* habitat structure by juvenile kelp bass *Paralabrax clathratus*. The model with the smallest ΔAICc value was selected as the best fit: ℓ are the maximized log likelihoods, Cumul (ω) are the cumulative Akaike weights and Coeff (ψ) are the factor coefficients.

ψ	AICc	ΔAICc	ω	ℓ	Cumul (ω)	Coeff (ψ)
Canopy height	257.48	0	0.37	-122.08	0.37	1.56
Shoot density						0.84
Canopy height	258.55	1.06	0.21	-124.22	0.59	1.81
Canopy height	259.45	1.97	0.14	-123.06	0.73	1.43
Shoot frequency						0.97
Canopy height	259.85	2.37	0.11	-121.46	0.84	1.33
Shoot density						0.72
Shoot frequency						0.69
Shoot density	260.96	3.47	0.07	-123.81	0.90	0.87
Shoot frequency						1.52
Shoot density	261.31	3.83	0.05	-123.60	0.96	0.32
Shoot frequency	261.90	4.42	0.04	-125.90	1.00	1.81

19.9 ± 0.4 shoots m^{-1} between July and December 2014 to 13.6 ± 0.33 shoots m^{-1} between January and August 2015 (ANOVA, $F_{1,13} = 26.1$, $p = 0.0003$). Alternatively, the density of *Zostera* leaf shoots (Fig. 2b) increased 39% from an average of 22.2 ± 2.54 shoots m^{-2} between September 2013 and June 2014 to 30.9 ± 1.93 shoots m^{-2} between July 2014 to May 2015 (ANOVA, $F_{1,20} = 7.7$, $p < 0.05$). From here, shoot density more than tripled in December 2015, reaching a peak value of 110.3 ± 24.1 shoots m^{-2} (ANOVA, $F_{1,13} = 21.5$, $p = 0.0006$). Finally, despite month-to-month fluctuations in the canopy height of *Zostera* (Fig. 2c), the overall length of leaf shoots did not significantly change throughout the study period (average = 20.0 ± 1.13 cm; ANOVA, $F_{1,23} = 0.33$, $p = 0.57$).

A total of 1,419 kelp bass were recorded within the *Zostera* study site in Big Fisherman's Cove (Fig. 3). Nearly 87% of fish were identified as juveniles (2.1 to 10 cm TL; Love et al. 1996) with 84% of individual kelp bass estimated as younger than 6 months of age (<9.18 cm TL). Kelp bass were not observed in the *Zostera* study area on the following dates: February 2014, April 2014, January 2015 and May 2015. The number of kelp bass recorded for each age-at-length bin ranged from 124 to 311 individuals (average = 202.7 ± 26.8 kelp bass) over the course of the study (Fig. 3a-g). Kelp bass abundance across all age-length bins varied seasonally with the greatest number of fish recorded in the summer and fall months (June to November) and the fewest during the winter and spring (December to May) averaging 98.3 ± 14.9 and 19.9 ± 9.3 kelp bass mo^{-1}, respectively (ANOVA, $F_{1,23} = 19.9$, $p = 0.0002$).

Seasonal changes in *Zostera* habitat structure (Fig. 4a) were observed throughout the study period reaching its peak in the summer and fall (June to November, average = $15,519 \pm 3,099$) and dropping to its lowest point in the winter and spring (December to May, $6,381 \pm 1,838$; ANOVA, $F_{1,23} = 6.34$, $p < 0.05$). Likewise, seasonal changes in *Zostera* habitat structure were significantly correlated with juvenile kelp bass abundance ($\beta_{GLM} = 0.015$, $p < 0.001$; Fig. 4a). Results of the AICc goodness-of-fit model selection are shown in Table 1. The model that best approximated the use of *Zostera* habitat structure by kelp bass, as indicated by the smallest ΔAICc score, included eelgrass shoot density and canopy height as the predictor variables (AICc = 257.5). Two other models accepted by the AIC$_c$ statistic (ΔAICc < 2) also included *Zostera* canopy height as a predictor
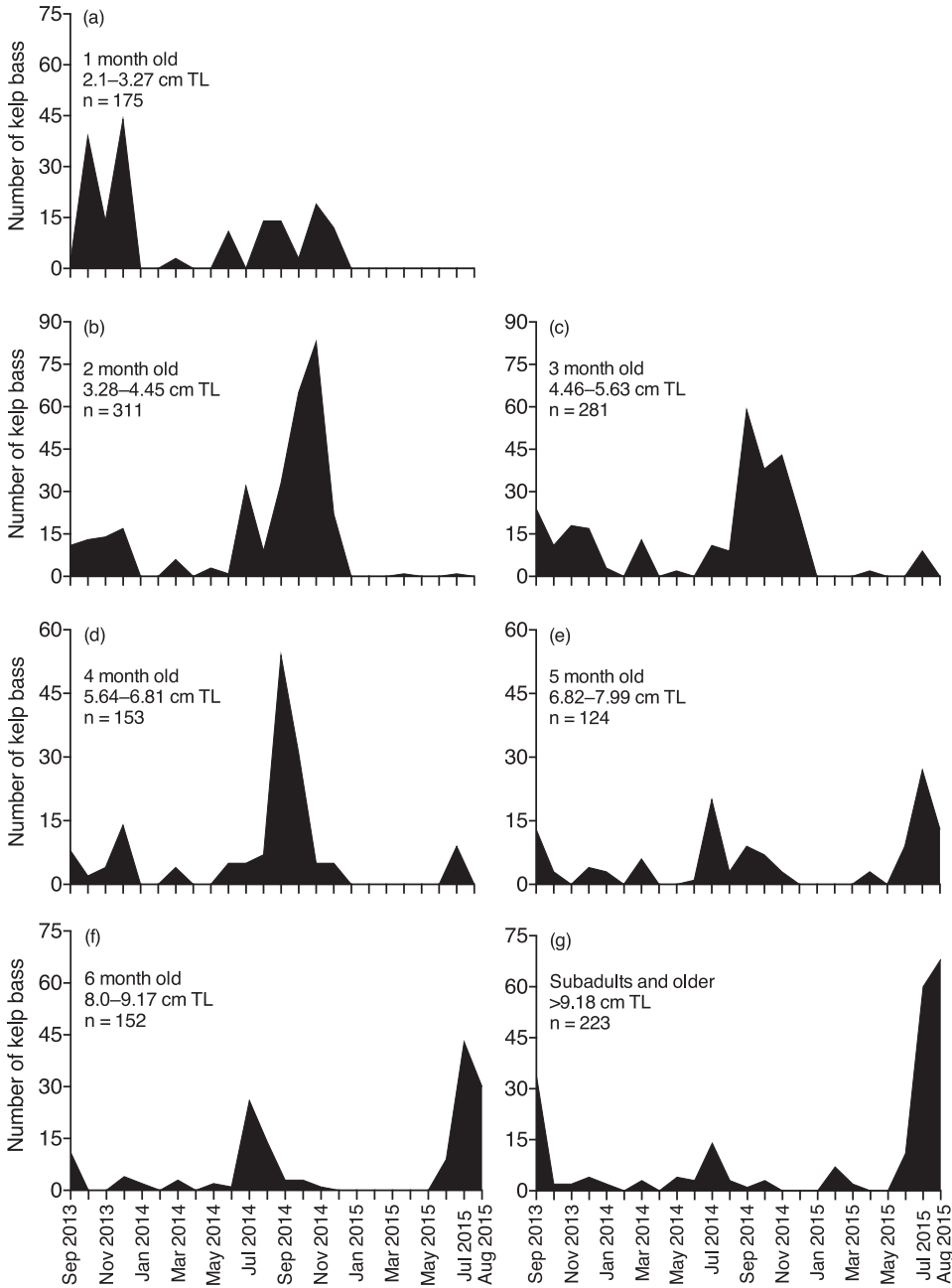
Fig. 3.   Monthly abundance of kelp bass *P. clathratus* observed amongst eelgrass *Z. marina* habitat in Big Fisherman's Cove. A total of 1,419 kelp bass were recorded from September 2013 to August 2015. Kelp bass observed during visual surveys were sorted into different age-at-length bins as follows: (a) 1 month old, 2.1–3.27 cm TL, (b) 2 month old, 3.28–4.45 cm TL, (c) 3 month old, 4.46–5.63 cm TL, (d) 4 month old, 5.64–6.81 cm TL, (e) 5 month old, 6.82–7.99 cm TL, (f) 6 month old, 8.0–9.17 cm TL and (g) > 9.18 cm (subadult stage and older). On February and April 2014 and January and May 2015, no kelp bass were observed in the *Zostera* study area.
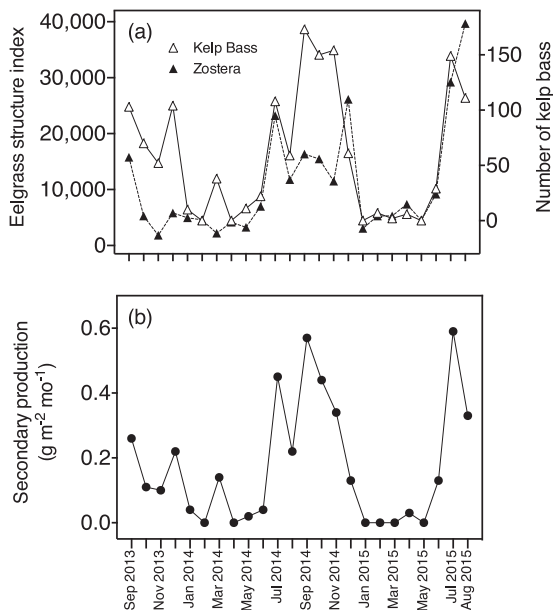
Fig. 4.   Relationship between the (a) structural complexity of eelgrass *Z. marina* habitat and kelp bass *P. clathratus* abundance, and (b) rates of secondary production in juvenile kelp bass surveyed monthly from September 2013 to August 2015 in Big Fisherman's Cove. Eelgrass structure index defined as the product of the mean leaf shoot frequency, density and canopy height of *Zostera*.

variable: both on its own (AICc = 258.6) and when combined with leaf shoot frequency (AICc = 259.5). ΔAICc scores for the remaining candidate models exceeded the threshold value for the best-fit model (ΔAICc < 2) and, therefore, were not considered an accurate predictor of the relationship between kelp bass and *Zostera* habitat structure.

Rates of secondary production calculated for juvenile kelp bass (range = 0.1 to 0.59 g m^{-2} mo^{-1}) in Big Fisherman's Cove were significantly correlated with monthly changes in *Zostera* habitat structure throughout the study (β_{GLM} = 0.21, p = 0.0005; Fig. 4, Table 2). Secondary production in kelp bass was 6-times higher in the summer and fall months (June to November, average = 0.3 ± 0.05 g m^{-2} mo^{-1}) than in the winter and spring (December to May, average = 0.05 ± 0.02 g m^{-2} mo^{-1}). However, interannual shifts in fish secondary production from 2013 to 2015 were not observed (range = 1.62 ± 0.92 to 2.39 ± 0.70 g m^{-2} yr^{-1}; β_{GLM} = 0.56, p = 0.07; Table 2).

Discussion

Data presented here provide an important baseline of fish biomass and recruitment associated with *Zostera* habitat in the absence of significant anthropogenic impacts, and will help to define the role of seagrass within the larger context of nearshore coastal ecosystems. Because juvenile fishes are known to seek refuge in areas with structured habitat such as seagrass (Hovel et al. 2002; Pihl et al. 2006), the positive relationship between the abundance of kelp bass and different metrics (shoot frequency, shoot density and canopy height; Fig. 2) used to evaluate *Zostera* structure was expected. In California, eelgrass mitigation policies established by NOAA Fisheries require that measurements of leaf shoot density and areal coverage (frequency, in this study) are used as a proxy for estimating

Table 2.   Monthly estimates of total length (TL) and secondary production recorded for juvenile kelp bass *P. clathratus* in Big Fisherman's Cove. TL values are means ± SE. Zero TL values indicate survey dates in which individual kelp bass were either absent from the *Zostera* study area or >9.17 cm TL (subadult stage and older).

Survey date	TL (cm)	Secondary production $(\text{g m}^{-2}\,\text{mo}^{-1})$
Sept 2013	7.78 ± 0.39	0.26
Oct 2013	4.89 ± 0.68	0.11
Nov 2013	3.97 ± 0.24	0.1
Dec 2013	4.54 ± 0.15	0.22
Jan 2014	6.28 ± 2.40	0.04
Feb 2014	0	0
Mar 2014	5.80 ± 0.37	0.14
Apr 2014	0	0
May 2014	12.0 ± 0.33	0.02
June 2014	8.73 ± 0.21	0.04
July 2014	7.27 ± 0.53	0.45
Aug 2014	5.87 ± 0.45	0.22
Sept 2014	5.04 ± 0.09	0.57
Oct 2014	5.10 ± 0.15	0.44
Nov 2014	4.36 ± 0.07	0.34
Dec 2014	4.32 ± 0.12	0.13
Jan 2015	0	0
Feb 2015	15.2 ± 0.20	0
Mar 2015	7.50 ± 0.01	0
Apr 2015	4.33 ± 0.48	0.03
May 2015	0	0
June 2015	9.39 ± 0.43	0.13
July 2015	9.12 ± 0.25	0.59
Aug 2015	9.12 ± 0.12	0.33

the function of eelgrass habitat. However, a significant finding from the current study is that the canopy height of leaf shoots, by itself, is a better predictor of the use of *Zostera* habitat by kelp bass (Table 1). Similar sets of measurements on the spatial patterns and variability of seagrass-fish assemblages report that canopy height is a key determinant of juvenile fish density (Gullström et al. 2008), and leaf shoot density, on its own, is a poor indicator of the abundance of fishes and decapods associated with a given eelgrass bed (Worthington et al. 1992). In addition to providing essential habitat and protection to fishery species, seagrasses provide a variety of ecosystem services whose economic value, in terms of the abundance and density of seagrass beds as a whole, far outweigh their ecological function (Barbier et al. 2011; Schubert et al. 2015). Survey metrics that capture the three-dimensional complexity of *Zostera* habitat will help to better understand the ecological functions of these communities.

Higher rates of secondary production in juvenile kelp bass coincided with increases in *Zostera* habitat structure (Fig. 4), as does the spawning season for this fish species, which reaches its peak during the summer months from June to August (Love et al. 1996; Cordes and Allen 1997; Erisman and Allen 2006). These findings highlight the need for time series data with seasonal patterns across multiple years to provide a more accurate estimate of variability. A reduction in the sampling frequency of fish at a given location, as dictated by limited access or resource availability, could yield dramatically different estimates of

secondary production on an annual scale. For example, if monthly rates of secondary production for juvenile kelp bass (Table 2) were calculated on a quarterly basis, rates would be either over- or underestimated by as much as 8 to 27%, respectively (quarterly schedule begins on either September or November 2013; average = 2.24 ± 0.97 and 1.52 ± 0.96 g m^{-2} yr^{-1}, respectively; compare to 24-month average = 2.08 ± 0.46 g m^{-2} yr^{-1}). Future studies should utilize both existing patterns of habitat use and spatial variability as a best estimate of the abundance and distribution of animals in a given location. In the case that fish movement patterns are limited to a specific area (cf. blue rockfish *Sebastes mystinus*: Jorgensen et al. 2006), a single sampling event on an annual basis may be sufficient.

Annual rates of secondary production calculated for juvenile kelp bass in this study approximate those reported for adult fishes in seagrass habitat (0.24 to 7.08 g m^{-2} yr^{-1}, Table 2; compare to 3.8 to 14.6 g m^{-2} yr^{-1}: Adams 1976; Edgar and Shaw, 1995; Jeong et al. 2009). Given the increased protection of kelp bass off Catalina Island through enhanced conservation and management plans (essential fish habitat and marine protected areas), coupled with their relatively small home range (< 0.33 ha, Lowe et al. 2003), enhanced settlement and recruitment within coastal *Zostera* beds are likely to play an important role in the export of adult fish to adjacent areas (Domeier 2004; Watson et al. 2010). Claisse et al. (2014) report markedly higher rates of annual secondary production amongst fishes on offshore oil platforms (range = 104.7 to 886.8 g m^{-2} yr^{-1}) in the same region as this study. Although both habitats may perform a nursery function (Love et al. 2006), the complex, hardscape structure of the offshore oil platform itself is distributed throughout the water column and is therefore better suited for intercepting larvae. *Zostera* beds, on the other hand, while associated with low-relief (<1 m above the benthos) nearshore habitats, are an important nursery ground and refuge for a variety of animals and may undergo high rates of species turnover for both reef fishes and invertebrates (Seitz and Ewers Lewis 2018). Nonetheless, research findings presented here indicate that *Zostera* is an important contributor to secondary production in kelp bass, which is one of the most important nearshore recreational species off the Southern California coast (Love et al. 1996; Erisman and Allen 2006; Horning 2009).

A common goal of resource monitoring is the development of biological indicators that provide rapid assessment of ecosystem function. Fish are useful as bioindicators because they are relatively easy to see, can disperse from stressed habitats and are economically important (Whitfield and Elliot 2002). The resources required to monitor secondary production at a level appropriate to detect significant impacts is daunting, but may be comparable, or perhaps less intensive, than other bioindicators (cf. carbon-to-nitrogen ratios, rhizome sugars and above-ground biomass; McMahon et al. 2013) used to assess the quality of *Zostera* habitats and how they might change over time. Further research is required to assess changes in secondary production in response to different impact types such as, sediment disturbance and invasive species encroachment. Kelp bass make for an effective case study of ecosystem function and services because these fish are common throughout the Southern California Bight and are an important component of biomass and recruitment associated with seasonal changes in *Zostera* habitat structure. Results from this study provide a baseline for the use of fish secondary production as an indicator of the health of eelgrass ecosystems.

The seasonal use of coastal *Zostera* habitat as a nursery ground by juvenile kelp bass off Catalina Island during the summer and fall months coupled with the presence of significantly fewer fish in the winter and spring (Fig. 3 and 4) suggests that a substantial amount of biomass could be exported to nearby coastal habitats. These findings support previous

work on the export of energy and nutrients across coastal habitat boundaries through the transfer of fish biomass (Deegan 1993). We postulate this on the assumption that juvenile kelp bass vacate eelgrass beds after reaching a certain ontogenetic stage, but further work is needed to verify the movement of kelp bass throughout their life cycle. While the relationship among juvenile habitats is well defined in tropical areas (Nagelkerken et al. 2000), far less is known in temperate regions such as the Pacific Coast. This study is one of the first in the region to provide quantitative data that support a possible ontogenetic shift in juvenile fish from coastal *Zostera* beds to adjacent habitats. Future studies on the export of fish biomass from seagrass beds (Gillanders 2006) will allow conservation and management efforts to focus on key marine resources such as protected areas around the California Channel Islands, which provide a major contribution to adult populations of ecologically and economically valuable species. Likewise, quantitative assessments of habitat function are beneficial for resource managers to determine the mitigation costs (e.g., habitat equivalency analysis) associated with a loss in natural resource services (Dunford et al. 2004). Further investigations of fish secondary production in nearshore coastal ecosystems are required to provide new insights into the mechanisms that contribute to the growth, dispersal and connectivity among populations and will help to communicate the significance of marine resource conservation with both the general public and stakeholder groups.

Acknowledgements

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