



## Evaluating eelgrass site quality by the settlement, performance, and survival of a marine fish

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### ABSTRACT

The quantity of habitat can be defined by the distribution and abundance of organisms, but it is the quality of the habitat that may have more direct demographic consequences. Habitat quality is best assessed by determining demographic rates and the performance of the focal species residing within a habitat. Using this framework to develop a method for evaluating habitat quality among sites, we used two demographic rates (settlement and survival) and two performance measures (growth and condition) of the giant kelpfish (*Heterostichus rostratus* Girard) to determine whether eelgrass (*Zostera marina* L.) habitat quality varies spatially (i.e., site quality) within San Diego Bay, California, USA. Seven sites were selected that encompass the northern and central areas of the bay. Settlement was estimated bi-weekly from May to July 2009 with artificial seagrass units (ASUs) and standard monitoring units for the recruitment of fishes (SMURFs). Eelgrass habitat complexity (shoot height and density) was measured at each site, and three complexity treatments were replicated with ASUs in large mesocosms to estimate survival of giant kelpfish after exposure to kelp bass (*Paralabrax clathratus* Girard), a common predator. Growth and condition were derived from juvenile giant kelpfish collected from sites two months after the settlement period using otolith daily growth increments and total lipid content, respectively. Settlement, growth, and condition were evaluated using a multivariate analysis to provide an assessment of habitat quality among sites and a framework for which site quality can be evaluated in different marine habitats. Combined with habitat-dependent survival from predators in laboratory trials that reflected site-specific habitat attributes, sites were ranked along a gradient of habitat quality. The multivariate analysis of site quality based on demographic and performance variables was then overlaid with a similar analysis of environmental variables. Environmental variables that would serve as proxies for habitat quality were not concordant with the suite of demographic and performance variables used to differentiate site quality, suggesting that a pluralistic approach using demographic rates and individual performance is a potentially more appropriate method for evaluating habitat quality, whether among different habitats or among sites of the same habitat.

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## 1. Introduction

The quantity of habitat can be defined by the distribution and abundance of organisms across spatial scales (Bell et al., 1991; Bunnell and Houde, 2010; Holbrook et al., 2000). The quality of habitat, however, is important in the dynamics of populations and is more difficult to assess. For example, several variables, including food availability, predator abundance, habitat structure, and environmental measures may determine high quality habitat for flatfishes (Gibson, 1994). Moreover, a single component alone does not necessarily represent higher habitat quality (Van Horne, 1983), and specific parameters as to what constitutes higher quality have not been clearly defined. These parameters often include population density (Meng et al., 2004) and fecundity (Skagen and Adams,

2011), but they may not necessarily indicate higher habitat quality if, for instance, these parameters are subject to density-dependent processes. Habitat quality may also be species-specific in that higher habitat quality for one species may represent lower habitat quality for another.

Taking these issues into account, we have developed a framework with which to evaluate habitat quality by providing a common currency among disparate variables in a multivariate context. The variables measured that truly reflect habitat quality should be based on the performance of the organisms living within it, “where growth, survival, and future reproductive potential are optimized” (Gibson, 1994). Our framework takes a pluralistic approach by incorporating both demographic (i.e. settlement, survival) and individual performance (i.e. growth, condition) measures to assess quality at the species-specific level. Thus, this approach allows us to determine the combination of variables that contribute to differences in habitat quality.

Recent studies have taken a more pluralistic approach in evaluating habitat quality using multiple parameters. The growth and condition of flatfishes, for example, have been used to estimate habitat quality

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among estuaries (Amara et al., 2007, 2009), with chemical contaminants measured at each estuary providing a gradient of anthropogenic impact that is positively related to lower growth and condition and thus a range in estuarine habitat quality. Moreover, spatial variation in the quality of the same habitat has been applied across sites. For example, the survival of a reef fish at a common density and size structure has been used to evaluate the quality of coral heads spatially (Shima et al., 2008).

Seagrass beds constitute a critical habitat in near shore ecosystems, serving as a nursery ground for many fishes and invertebrates and providing numerous ecosystem services, including sediment stabilization, filtration of pollutants, and carbon storage (Larkum et al., 2006). Because of global declines in seagrass habitats (Short and Wyllie-Echeverria, 1996), it is crucial that we more fully understand how these ecosystems function. In previous studies that have evaluated the quality of seagrass habitats in comparison to other marine habitats (e.g., marsh, sand, macroalgae), the importance of one or two variables that could contribute to the relative quality of the more suitable habitat has been emphasized (Meng et al., 2004; Phelan et al., 2000; Sogard, 1992). Using drop nets to measure the density and biomass of nekton among five habitats, higher habitat quality for the target species was assumed to correspond with the highest population densities (Meng et al., 2004). However, in areas with higher densities, density-dependent processes through a reduction in individual growth, performance (e.g., nutritional condition), and survival may actually indicate lower overall habitat quality. In caging experiments used to determine individual growth rates of three estuarine fishes in vegetated vs. unvegetated habitat, higher growth as an important demographic rate was a proxy for more suitable habitat (Sogard, 1992). However, growth rates may not completely mirror habitat quality because of potential differences in the nutritional condition and the survival of organisms.

Eelgrass (*Zostera marina* L.) forms highly productive beds that function as important nursery habitats for a diverse variety of organisms (Beck et al., 2001), including economically important fishes and invertebrates in southern California (Allen et al., 2002; Hoffman, 1986). The objective of our study was to use a framework encompassing multiple variables to assess habitat quality for a common macrophyte-associated fish across a spatial gradient of eelgrass beds in San Diego Bay, California by addressing five questions: (1) Does settlement (input of young) of the giant kelpfish (*Heterostichus rostratus* Girard: family Clinidae) differ among eelgrass beds in San Diego Bay? (2) Is there variation in the growth and condition of giant kelpfish among eelgrass beds? (3) Are there differences in predator-mediated survival of giant kelpfish based on variation in structural habitat complexity among eelgrass beds? (4) Does the combination of these variables (settlement, growth, condition, survival) contribute to differences in site quality among eelgrass beds? (5) Are environmental variables concordant with the demographic and performance variables used to evaluate site quality?

## 2. Methods

### 2.1. Study system and species

San Diego Bay covers approximately 46 km<sup>2</sup> and contains eelgrass beds throughout much of its waters. This provides an ideal system for studying the habitat quality of eelgrass beds spatially (i.e., site quality). Eelgrass beds were once widespread in San Diego Bay prior to 1940 (Browning and Speth, 1973), but urban development greatly reduced this habitat. Multiple restoration attempts with varying levels of success have reestablished some eelgrass beds, and eelgrass currently covers approximately 6.6 km<sup>2</sup> (14%) of San Diego Bay (U.S. Navy, 2000). Many aspects of these regional eelgrass beds have been studied, including the genetic diversity of eelgrass (Williams, 2001; Williams and Davis, 1996), the effects of smothering by sessile epifauna on eelgrass performance (Sewell, 1996), the effects of habitat configuration, loss, and restoration on invertebrate communities (Healey and Hovel, 2004; Moore and Hovel, 2010; Reed and Hovel, 2006; Sirota and

Hovel, 2006), habitat use and recruitment of fishes (Allen et al., 2002; Hoffman, 1986; Lipski, 2005), and trophic interactions that affect eelgrass production (Lewis and Anderson, 2012). Many fishes occur in the bay (Allen et al., 2002), and several of them are associated with eelgrass in southern California, often as juveniles that use this habitat as a nursery ground. To provide a potential spatial gradient of site quality, we selected seven eelgrass beds in the bay (Fig. 1): Shelter Island South (SIS), Shelter Island North (SIN), Harbor Island Central (HIC), Marriott (MAR), Coronado Golf Course (CGC), Silver Strand North (SSN), and Silver Strand South (SSS).

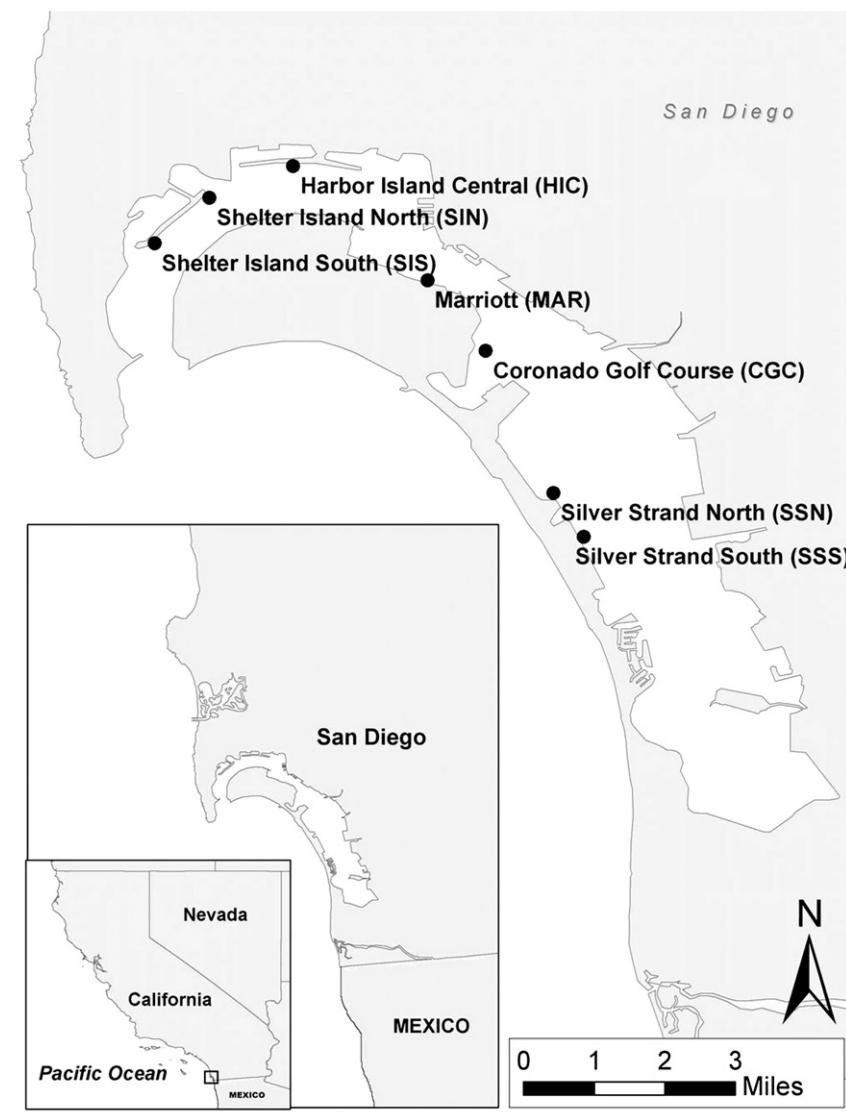
The giant kelpfish was selected to evaluate habitat quality. Giant kelpfish are closely associated with macrophytes (Stepien, 1986), including eelgrass and the giant kelp, *Macrocystis pyrifera* (L.). The giant kelpfish is a common coastal species in southern California, and competent larvae settle to eelgrass and giant kelp at ~30–35 mm total length (TL) (Stepien, 1986). Once settlement has occurred, juveniles begin to feed on macrophyte-associated invertebrates (Coyer, 1979).

### 2.2. Settlement of giant kelpfish

Two devices were used to estimate settlement of giant kelpfish in eelgrass beds within San Diego Bay: (1) artificial seagrass units (ASUs; Bell et al., 1985) and (2) standard monitoring units for the recruitment of temperate reef fishes (SMURFs; Ammann, 2004). These devices allow for the standardization of structural habitat complexity to estimate settlement among sites independent of differences in habitat attributes. Both devices were used in the event that there was differential settlement between SMURFs deployed on buoyed lines in the water column and ASUs positioned on the sea floor. Two ASUs and two SMURFs were placed at each site haphazardly, each deployed at least 10 m apart. Each ASU or SMURF was considered to be an independent estimate of settlement at a site. ASUs and SMURFs were sampled every 14 days from 22 May to 17 July, 2009. During every sampling period, SMURFs, ASUs, and mesh on cages were replaced to minimize the amount of algae and invertebrates settling onto the devices. Giant kelpfish were measured (mm TL) immediately after collection, with the maximum size of a settler set at 50 mm TL, accounting for post-settlement growth over a maximum 2-wk period (Stepien, 1986).

ASUs consist of green polypropylene ribbon tied to black plastic mesh and have been used extensively in various studies of seagrass-associated fauna (Bell et al., 1995; Healey and Hovel, 2004; Levin et al., 1997), and they are comparable to natural seagrass in observed species richness and diversity of fishes (Upston and Booth, 2003). To estimate settlement, ASUs were deployed 5 m in front of a natural eelgrass bed. Each ASU was 1 m<sup>2</sup> with 500 "shoots", 40 cm long and tied uniformly to the black plastic base. This density of shoots was within the range of values commonly observed in eelgrass beds in San Diego Bay (Lipski, 2005). Each ASU was enclosed by a square cage (1.5 m height × 1.1 m length) constructed of PVC with clear plastic mesh (6-mm mesh size). Cages were used to allow settlement of competent larvae, but to exclude entry by larger fishes to prevent predator-induced post-settlement mortality. ASUs were staked to the substratum using rebar and placed on top of a sewn (2-mm mesh size) bag. To collect the ASU, two divers removed the cage and the mesh bag was lifted and cinched closed as divers swam upward in the water column. During collection, fish were observed to dart downward into the ASU, consistent with other studies (Kenyon et al., 1999; Lipski, 2005) and an indication that this method did not result in the loss of recently settled fish.

SMURFs were constructed of 1.07 m<sup>2</sup> of green plastic garden fencing (2.5 cm mesh size), stuffed with five, 1.85-m<sup>2</sup> sections of construction fencing (4.4 × 5.4 cm mesh size) and have been used to study settlement of temperate reef fishes (Ammann, 2004). This design allows for the settlement of young fish without entrance by their piscine predators so that the accumulation of fish effectively represents settlement and not post-settlement mortality. Each SMURF was deployed on a buoyed line 5 m in front of the natural eelgrass bed. SMURFs were attached to



**Fig. 1.** Map of San Diego Bay, California, and the seven sites used in this study: Shelter Island South (SIS), Shelter Island North (SIN), Harbor Island Central (HIC), Marriott (MAR), Coronado Golf Course (CGC), Silver Strand North (SSN), and Silver Strand South (SSS).

the line using releasable cable ties and placed so that the center of the SMURF was ~2 m above the substratum. To collect a SMURF two weeks after deployment, a diver used a BINCKE net (Anderson and Carr, 1998) to enclose the SMURF and slowly swam upward in the water column while releasing the cable ties.

### 2.3. Growth and condition

A total 25 or more juvenile giant kelpfish were collected using dip nets on SCUBA from each of five sites (SIS, SIN, HIC, MAR, and CGC; no fish were found at SSN and SSS) in September 2009, approximately two months after the settlement period. Collection of these individuals provides for an estimate of site-specific growth and condition (total lipid content). To determine individual growth, sagittal otoliths were extracted from fish, cleaned with reverse-osmosis water, and mounted on glass microscope slides. To make growth increments more visible, otoliths were sanded on each side using 3M® diamond lapping film (1–30 µm) and remounted onto the slide. Digital images of otoliths were analyzed with digital imaging software (Media Cybernetics ImagePro Plus® ver. 5.1) and a compound microscope. A linear transect was drawn from the otolith core to the edge of the otolith along the

longest radius. The mean distance (µm) between daily growth increments was determined from the settlement mark to the outer edge of the otolith. Growth increments have been validated as being laid daily in giant kelpfish (M. Steele, unpublished data).

Site-specific nutritional condition was determined by quantifying the amount of total lipids extracted from each fish. Lipid extraction followed the methods of Bligh and Dyer (1959) using a chloroform-methanol mixture. For each fish, the head, fins, and stomach were removed, and approximately 3 g of tissue from the remainder of the fish was placed into a 50 ml Nalgene® centrifuge tube with the chloroform-methanol mixture. The centrifuge tube was refrigerated at 4 °C overnight, allowing for complete separation of chloroform and methanol. The chloroform layer (containing lipids) was then pipetted into a glass test tube (10 ml) and dried using nitrogen gas. The remaining orange viscous layer was then weighed and divided by the initial amount of fish tissue used to obtain total lipids (mg) per gram of tissue (g wet weight).

### 2.4. Predator-induced mortality

Because of low visibility, expected movement of giant kelpfish from experimental units, and our judgment that tethering of individuals

would induce artifacts in reliably estimating predator-induced mortality of giant kelpfish in the field, a laboratory mesocosm experiment was employed to estimate site-specific, habitat-dependent survival. To obtain site-specific estimates of eelgrass structural complexity, surveys of eelgrass shoot density and shoot height were conducted in July 2009 at each of the seven sites. A 30-m transect tape was haphazardly placed in the center of each eelgrass bed, and twenty 0.06-m<sup>2</sup> (0.25 m × 0.25 m) quadrats were sampled randomly. In each quadrat, the total number of eelgrass shoots was counted, and 10 shoots from the bottom right corner of each quadrat were measured. Mean shoot density and height were calculated for all seven sites (see **Results**). The data obtained were categorized into three distinct treatments with combinations of shoot density and shoot height that reflected habitat structural complexity at these sites: (1) low density, high height (LDHH; 500 shoots per m<sup>2</sup>, 50-cm height), (2) low density, low height (LDLH; 500 shoots per m<sup>2</sup>, 25-cm height), and (3) high density, low height (HDLH; 1100 shoots per m<sup>2</sup>, 25-cm height). ASUs (1 m<sup>2</sup>) with green polypropylene ribbon and black plastic mesh were used to constitute the three treatments of habitat structural complexity.

An array of six 1766-l (1 m height × 1.5 m diameter) mesocosms located at the Coastal and Marine Institute Laboratory, San Diego State University, was used to conduct predation trials from 23 Jun to 14 Jul 2010. A separate mesocosm held a pool of 100–200 recently settled giant kelpfish collected by beach seine off Shelter Island in San Diego Bay. Fourteen kelp bass (*Paralabrax clathratus* Girard; family Serranidae, 18–28 cm TL) collected by hook and line were allocated into seven pairs of predators. All kelp bass used in a particular trial were starved for ~48 h so that their stage of hunger was similar among trials.

For a given trial, two replicates of each habitat treatment were placed randomly among the six mesocosms. A pair of kelp bass was randomly selected and placed within a 1-m high × 0.4-m diameter black plastic mesh cylinder (10-mm mesh size) to allow them to acclimate to the mesocosm for 2 h but not feed on young giant kelpfish. After two predators were placed in each tank, ten giant kelpfish (41–59 mm TL) were haphazardly selected, measured, and placed into each mesocosm for a 2-h acclimation period before the trial began.

Trials were begun at 1700 PDST when the plastic mesh cylinder was removed, allowing kelp bass to feed on young giant kelpfish. Each trial lasted for 15 h, covering two crepuscular periods when kelp bass forage most actively. At 0800 the next day, all kelp bass were removed and the remaining recruits were collected and measured to determine the proportion of fish that survived. After each trial was completed, the habitat treatments and pairs of predators were again randomly assigned, and both kelp bass and giant kelpfish were allowed to acclimate in mesocosms before the next trial. For each habitat treatment, 14 replicate trials were conducted.

## 2.5. Environmental variables

A set of common environmental variables (predator density, density of juvenile giant kelpfish, eelgrass shoot height, eelgrass shoot density) that could be used as proxies of habitat quality were measured to determine how they might influence differences in habitat quality among sites. Data on structural habitat complexity (shoot height and shoot density) were taken from surveys conducted for the laboratory predation trials. Surveys of fishes using SCUBA were conducted in September 2009 to estimate the numerical densities of juvenile giant kelpfish and piscivores at all seven sites. Two transects were positioned 10 m apart in the middle of the eelgrass bed at a site and parallel to shore. Two divers swam along each transect (2-m wide × 2-m high × 30-m long; 120 m<sup>3</sup>) simultaneously and recorded the size of all common piscivores (kelp bass, spotted bay bass (*Paralabrax maculatusfasciatus* Steindachner), and barred sand bass (*Paralabrax nebulifer* Girard)) >15 cm TL and juvenile giant kelpfish <10 cm TL. The next set of transects was placed 30 m from the previous set. This process was completed three times (n = 6 transects) at each site. Observers were trained in sizing of fish

before initiating surveys, including practice in comparing the size of fish among observers.

## 2.6. Statistical analysis

The mean settlement of giant kelpfish among sites was compared using one-way analysis of variance (ANOVA). To determine whether there were differences in survival from site-specific habitat attributes used in predation trials, the mean proportion of survivors among treatments was compared using a one-way ANOVA. For significant differences among treatments, a Tukey's post-hoc multiple comparison test was performed to determine which treatments differed from each other. The assumptions of normality and homogeneity of variances were met through examination of normal probability plots and applying Levene's test, respectively.

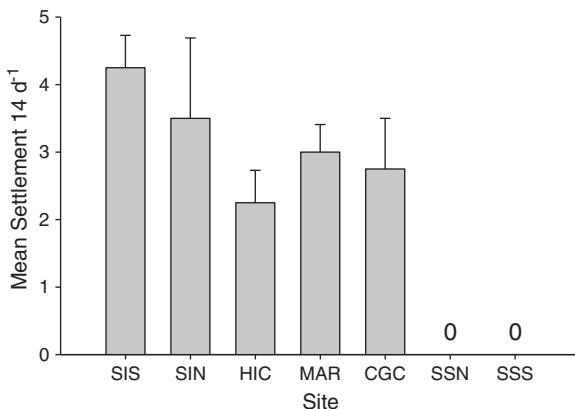
Mean growth and condition (total lipid content) of individual fish were compared among sites using a permutational multivariate analysis of variance (PERMANOVA). Growth and condition were measured from the same fish and so do not meet the assumption of statistical independence. PERMANOVA normalizes data in multivariate space, allowing for an assumption-free test. SYSTAT, ver. 12 and PRIMER, ver. 6 (Clarke and Gorley, 2006) were used to conduct all univariate and multivariate analyses.

Biological variables (settlement, growth, and condition) were grouped among sites, and Linkage Tree (LINKTREE; PRIMER, ver. 6) analysis was used to compare site quality. LINKTREE creates a resemblance matrix based on the Euclidean distances between sites. Using the means of each variable, it groups sites based on two values; correlation coefficients (r) and B% values describe similarities and differences among sites, with higher B% values representing greater dissimilarity among sites. Because site-specific survival rates were not measured directly in the field, they were not included with the LINKTREE analysis but assessed separately in the context of the multivariate analysis. The output of LINKTREE analysis with demographic and performance variables was overlaid with measured environmental variables (predator biomass, juvenile giant kelpfish density, eelgrass shoot height, and eelgrass shoot density) in the same resemblance matrix. Incorporating the same output with environmental data allowed for an assessment of the concordance of assumed habitat quality from environmental variables with demographic and performance variables among sites.

## 3. Results

A total 63 giant kelpfish settlers was collected (43.6 ± 0.7 mm TL (mean ± SE)) at five of the seven sites over four 2-wk sampling periods. After the fourth sampling period, settlement of giant kelpfish was not observed at any of the seven sites. Two sites (SSN and SSS) received no settlement and a near absence of juveniles, so they represent the lowest habitat quality; these sites were excluded from further analysis. There was no statistical difference ( $F_{4, 75} = 0.792$ ,  $p = 0.53$ ) in settlement among the five sites that received settlers, and of these five sites, SIS and SIN had nominally higher settlement than HIC, MAR, and CGC (Fig. 2).

Estimates of individual growth and condition of giant kelpfish collected ~2 months after the settlement period (87.5 ± 2.0 mm TL) revealed a significant difference among sites (PERMANOVA:  $F_{4, 120} = 3.3898$ ,  $p = 0.003$ ; Fig. 3). Results of a permutation multiple comparison test revealed that SIS was significantly different from SIN, HIC, MAR, and CGC, with no difference in growth and condition among these latter sites. When settlement, growth, and condition among sites were examined with a multivariate perspective using LINKTREE, two distinct breaks in output among the five sites analyzed (Fig. 4) were observed. In the first break (A), SIS was separated ( $R = 1.00$ ,  $B\% = 100$ ) because of lower condition (<14.6 mg/g), but higher settlement (>4.25 settlers/14 days) than at the other four sites (>18.4 mg/g and <3.5 settlers/14 days). The second break (B) distinguished HIC from SIN, MAR, and CGC ( $R = 1.00$ ,  $B\% = 59$ ) based on lower settlement



**Fig. 2.** Mean (+ 1 SE) settlement of giant kelpfish per 14-day sampling period among seven sites in San Diego Bay (see Fig. 1 for site names).

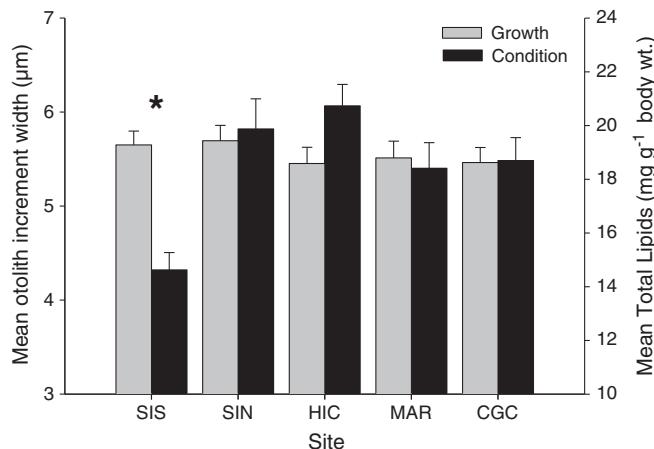
(<2.25 settlers/14 days), higher condition (>20.7 mg/g), and lower growth (<5.45 µm) than SIN, MAR, and CGC (>2.75 settlers/14 days, <19.9 mg/g, and >5.46 µm).

The assessment of predation risk by exposing juvenile giant kelpfish to kelp bass under three regimes of eelgrass shoot height and density that categorized all sites (Fig. 5) showed differences in survival of giant kelpfish. Mean proportional survival differed significantly among treatments ( $F_{2,39} = 31.840$ ,  $p < 0.001$ ; Fig. 6). A Tukey's multiple comparison test showed that survival was significantly lower in the low density, low height (LDLH) treatment of eelgrass habitat than in the other two treatments (LDHH and HDLH). The LDLH treatment is representative of CGC as having the highest predation risk among all sites.

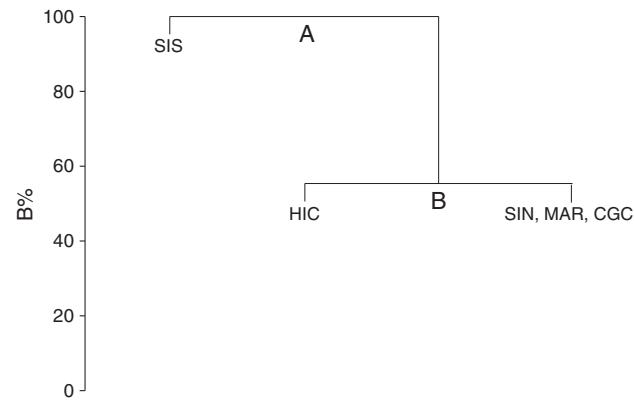
Environmental variables (predator density and juvenile giant kelpfish density (Table 1), eelgrass shoot height and eelgrass density (Fig. 5)) were examined with LINKTREE based on the output from settlement, growth, and condition (Fig. 4). The first break (A) shows SIS separating from other sites ( $R = 1.00$ ,  $B\% = 100$ ) because of a higher density of juvenile giant kelpfish (>4.83/120 m<sup>3</sup>) than at the other four sites (<3.83/120 m<sup>3</sup>). The second break (B) shows HIC ( $R = 1.00$ ,  $B\% = 59$ ) with higher shoot height (>56.2 cm) and lower predator density (2.5/120 m<sup>3</sup>) than SIN, MAR, and CGC (<31.3 cm and  $\geq 3/120$  m<sup>3</sup>).

#### 4. Discussion

In this study, we employed a pluralistic framework to address habitat quality spatially (i.e., site quality). Understanding habitat quality is

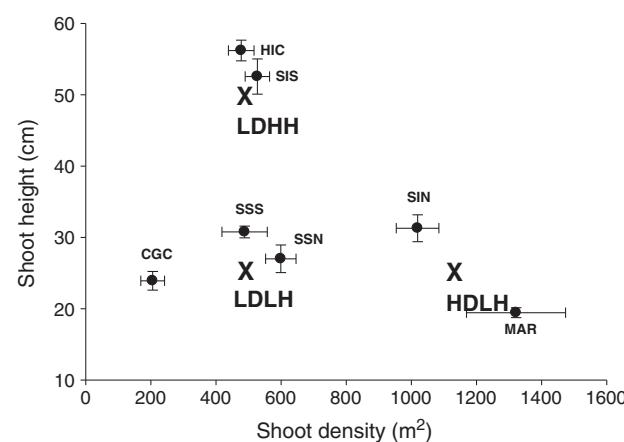


**Fig. 3.** Mean (+ 1 SE) growth (gray bars) and condition (black bars) of giant kelpfish at five sites in San Diego Bay (see Fig. 1 for site names). The asterisk denotes that growth and condition combined were significantly different at SIS than at the other four sites.

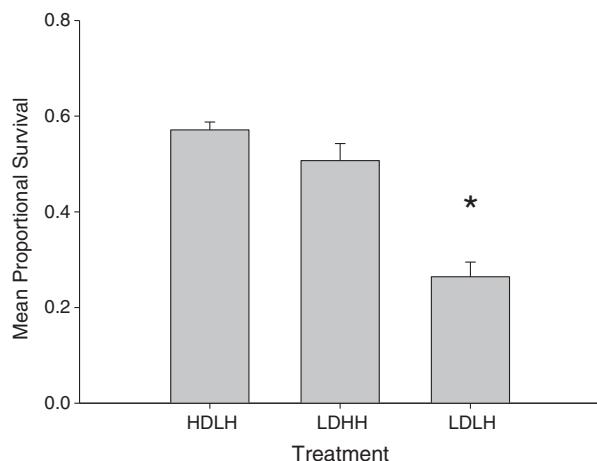


**Fig. 4.** LINKTREE analysis for mean settlement, growth, and condition. The first break (A) shows SIS having lower condition (<14.6 mg/g) and higher settlement (>4.2 settlers/14 days) than SIN, HIC, MAR, and CGC (>18.4 mg/g, <3.5 settlers/14 days) (see Fig. 1 for site names). The second break (B) shows HIC having lower settlement (<2.2 settlers/14 days), higher condition (>20.7 mg/g), and lower growth (<5.45 µm) than SIN, MAR, and CGC (>2.75 settlers/14 days, <19.9 mg/g and >5.46 µm).

becoming increasingly important, particularly with respect to fishes (Able et al., 1999; Lloret and Planes, 2003; Tarpgaard et al., 2005). At issue, however, is that habitat quality is not well defined, and a particular set of parameters used to evaluate habitat quality is subject to interpretation. Previous studies have independently focused on the density (Meng et al., 2004), growth (Able et al., 1999), growth and condition (Amara et al., 2007), and survival (Shima et al., 2008) of fishes to assess habitat quality. Performance and survival may be related to organism density, so the strength of density dependence is important with respect to these metrics of habitat quality. For example, site quality for the six-bar wrasse (*Thalassoma hardwicke*) has been assessed in which habitat and the density and size of recruit fish were standardized through an experimental assay on coral reef heads, with quality based on mean survival time (Shima et al., 2008). Their results show that the structural complexity of the coral *Pocillopora* sp. not only increases settlement of *T. hardwicke* but also attracts greater densities of predators, resulting in increased density-dependent mortality from predation. Consequently, an intermediate level of structural habitat complexity provided the highest survival of the six-bar wrasse and thus should represent the highest habitat quality. This is a pertinent example of the importance of incorporating multiple variables when evaluating habitat quality.



**Fig. 5.** Mean ( $\pm 1$  SE) shoot density and shoot height for seven sites in San Diego Bay. The "x" placed on the graph in three locations denotes the combination of shoot density and height used for three treatments of habitat structural complexity in predation trials. The three treatments used are low shoot density, high shoot height (LDHH), low shoot density, low shoot height (LDLH), and high shoot density, low shoot height (HDLH). See Fig. 1 for site names.



**Fig. 6.** Mean (+1 SE) proportional survival of giant kelpfish recruits from predators under three treatments of eelgrass habitat complexity. HDLH (high shoot density, low shoot height) represents the sites SIN and MAR, LDHH (low shoot density, high shoot height) represents the sites SIS and HIC, and LDLH (low shoot density, low shoot height) represents the site CGC. The asterisk denotes that survival in the LDLH treatment was significantly lower than in the two other treatments. See Fig. 1 for site names.

Settlement is indicative of the replenishment of local populations with new individuals as they transition from a pelagic to benthic existence. That a site receives sufficient input of new individuals is an important measure of site quality. In this study, settlement of giant kelpfish was not particularly high among eelgrass beds, but settlement was nominally higher at sites closer to the mouth of San Diego Bay, suggestive of differences in larval delivery to eelgrass beds. Certainly habitat structural complexity can play a role in settlement and recruitment variability in seagrass beds (Jenkins et al., 1998), but our use of standardized habitat allowed us to estimate larval input independently at each site. Settlement did not occur at the two sites farthest from the mouth of the bay, and surveys of those eelgrass beds revealed a near absence of giant kelpfish, relegating these sites to having the lowest habitat quality. Higher settlement and subsequent recruitment that would result in higher densities of resident local populations in eelgrass, however, may not simply reflect higher site quality because of density-dependent effects on growth, condition, and the survival of fishes (e.g., Anderson, 2001; Johnson, 2008; Shima et al., 2008). Consequently, it is important to incorporate settlement, growth, condition, and survival as demographic and performance measures into an evaluation of habitat quality for any focal species.

Individual growth and nutritional condition are reasonable metrics for evaluating habitat quality, based on the assumption that faster growing fish with higher energy reserves reflects higher food resources or foraging rates. Here, although individual growth of giant kelpfish was nominally higher at SIS and SIN, growth did not vary appreciably among the five sites in which settlement of fish occurred. With respect to nutritional condition, however, SIS exhibited sufficiently lower condition relative to the four other sites. Although lipids have been widely used

to estimate condition in fishes (Berg and Bremset, 1998; Booth and Hixon, 1999; Floyd and Anderson, 2010; Post and Parkinson, 2001), growth and condition in fishes are not necessarily correlated (Gilliers et al., 2004), and these two measures of performance may have differential responses to temporal changes in environmental factors (Suthers, 1998). As a result, when possible, it is useful to incorporate both somatic growth and condition when evaluating habitat quality. Lower nutritional condition could reflect a number of processes, including environmental conditions such as higher current velocity that is more commonly observed near the front of the bay (pers. observation), which might incur higher metabolic costs in fish maintaining position within eelgrass habitat. Lipid depletion in fish has been linked as a general metabolic response to stress (Lemly, 1993), and perhaps environmental conditions at this site such as higher tidal flux caused higher stress. Alternatively, fish with higher nutritional condition can experience higher survival vs. those with lower condition (Booth and Hixon, 1999; Floyd and Anderson, 2010; Hoey and McCormick, 2004; Johnson, 2008). Our results and these past studies suggest that nutritional condition is an important measure of performance that can influence the demography of fishes.

Survival is certainly an important measure of habitat quality. If a particular site incurs disproportionately higher mortality, populations at a particular site may be compromised and thus represent lower site quality. Survival of many fishes from predators is often related to structural habitat complexity, especially in vegetated habitats (e.g., Anderson, 2001; Johnson, 2006, reviewed by Steele and Anderson, 2006). For giant kelpfish, survival as a result of predation was significantly lower within the LDLH treatment that was representative of the site CGC. Lower structural complexity should result in higher rates of predation, and structural habitat complexity plays an important role in the survival of giant kelpfish, with higher survival rates at sites with dense and long eelgrass shoots. This is not surprising given the cryptic nature of the giant kelpfish and its ability to change coloration in different habitats (Stepien, 1985). We acknowledge the possible issues in conducting a laboratory experiment instead of a field-based estimate of survival, and our lab experiment using large mesocosms does not take into account differences in predator density or predator foraging behavior (e.g., Anderson, 2001). For example, greater seagrass habitat structure may decrease predation by pursuing predators but increase predation by ambushing predators (Flynn and Ritz, 1999; James and Heck, 1994), and when there is an increase in the densities of prey and predators that reflect increasing habitat structure, there may be little difference in predation rates (Canion and Heck, 2009). However, given the logistical difficulties in estimating mortality in the field and the likely artifacts of tethering (e.g., mobile prey have limited movement to escape a predator), we conclude that our estimates of habitat-dependent survival are representative of eelgrass structural complexity among specific sites in San Diego Bay and are an appropriate measure of survival in evaluating site quality in this case.

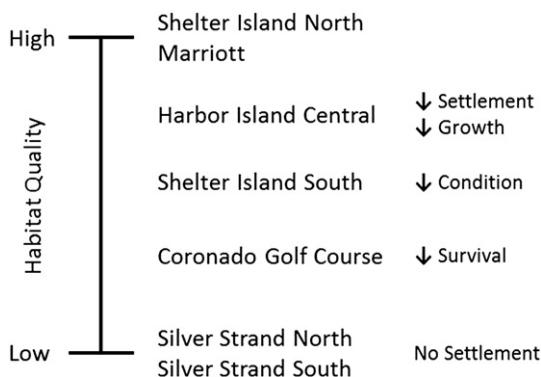
There is a growing body of work that suggests that larval traits in fishes play a subsequent role in the survival of older life stages (McCormick and Hoey, 2004; Shima and Findlay, 2002). If individuals among sites were to differ intrinsically in their quality (e.g. growth and condition), higher quality sites may simply reflect, at least in part, the survival of individuals of higher quality. For instance, larval growth has been used as a measure of 'quality' in individual fish (Shima and Sweare, 2009). To explore this possibility, we measured larval (pre-settlement) growth of all juvenile giant kelpfish collected in San Diego Bay and found that there was no significant difference in growth among sites (C. Jones unpublished data).

The multivariate analysis conducted in this study provides a common currency with which to evaluate the contribution of disparate multiple variables to site quality. We evaluated and ranked sites from low to high quality based on measured demographic and performance variables (Fig. 7). Sites were ordered based on its evaluation with the site(s) ranked directly below it. Because settlement is an important demographic rate in

**Table 1**

Mean ( $\pm$ SE) densities of giant kelpfish and their predators at seven sites in San Diego Bay (see Fig. 1 for site names).

Site	Juvenile giant kelpfish density	Predator density
SIS	4.8 $\pm$ 1.17	3.5 $\pm$ 0.85
SIN	3.7 $\pm$ 1.28	3.5 $\pm$ 0.67
HIC	3.2 $\pm$ 0.91	3 $\pm$ 0.63
MAR	3.8 $\pm$ 1.66	2.5 $\pm$ 0.63
CGC	1.2 $\pm$ 0.48	3.5 $\pm$ 0.62
SSN	0	1.0 $\pm$ 0.37
SSS	0.2 $\pm$ 0.17	1.3 $\pm$ 0.49



**Fig. 7.** Diagram of a gradient in eelgrass site quality for giant kelpfish based on seven sites in San Diego Bay. Sites were ranked based on demographic rates (settlement, survival) and performance measures (growth, condition).

replenishing local populations, we relegated SSS and SSN as sites with the lowest quality. There is a general lack of settlement of giant kelpfish in the back half San Diego Bay (Lipski, 2005, this study), and SSS and SSN eelgrass beds are frequently overgrown by the red alga *Gracilaria* sp. (Greville) (pers. observation). Altered habitat and the apparent absence of settlement obviated any measures of performance or survival. Survival as a critical demographic rate is an important component of habitat quality, and predator-induced mortality was highest in the low shoot density, low shoot height treatment of eelgrass habitat. This treatment corresponds to eelgrass habitat at CGC, and this site was ranked just above SSS and SSN along a gradient of site quality. SIS was ranked next highest in site quality because fish from this site exhibited lower condition than fish at SIN, HIC, and MAR, even though there was nominally higher settlement. Among the remaining sites, HIC had relatively lower settlement, higher condition, and lower growth than SIN and MAR, and having lower values in two of these three variables (settlement and growth), HIC was considered to be of lower site quality. Finally, after considering both demographic rates and performance measures at all seven sites, SIN and MAR eelgrass beds were deemed as sites with the highest habitat quality for giant kelpfish because of higher settlement, growth, and survival.

A suite of environmental variables (eelgrass shoot height and shoot density, juvenile giant kelpfish density, and predator density) at each site were selected as proxies of habitat quality as a comparison with the demographic rates and performance measures used in this study. The quantity of habitat and density of organisms are potential measures that can be used to estimate habitat quality. Using LINKTREE output with an analysis of environmental variables, SIS was distinguished as a site with a higher density of juvenile giant kelpfish than the remaining four sites (Table 1). However, the condition of fish at this site was lower than at any other site, demonstrating that the density or abundance of fish in itself is not necessarily the most relevant predictor of site quality. This comparison provides an example concerning the importance of incorporating the performance of organisms in an assessment of habitat quality. For the second LINKTREE break, HIC had higher eelgrass shoot height and lower predator density, which can be attributed to higher survival from predators at this site. With lower eelgrass shoot height and an increase in predator density at SIN and MAR, one could conclude that these sites would have lower survival, but the dense eelgrass beds found there contribute to higher survival observed in this study. From the LINKTREE analysis, CGC has lower eelgrass shoot height and higher predator density. Because this site had the lowest measured density of eelgrass, it is not surprising that this site contributes directly to the lowest observed survival from predators. The lack of correspondence between the demographic and performance variables with environmental variables one might use as proxies of habitat quality strongly suggests that such environmental variables are often not sufficient by

themselves in evaluating habitat quality. Consequently, it is important to identify sites with higher quality as this may inform resource managers charged with their conservation and restoration. This study provides a model of eelgrass habitat quality spatially based on demographic rates and the performance of a macrophyte-associated fish. However, because habitat quality is relevant for a particular species or perhaps a guild of species, future work using multiple organisms as indicators of habitat quality evaluated across multiple years may provide greater context for this approach, especially as it may relate to community structure and ecosystem-based management.

A pluralistic approach is useful in addressing habitat quality, which can be applied to an assessment among different habitats or the same type of habitat spatially (site quality). Because the complexity of relationships between organisms and the habitat in which they reside may result in different demographic rates and measures of individual performance, it is difficult to predict differences in habitat quality. Here, by including several potentially important variables, we offer a framework and approach for evaluating habitat quality in marine ecosystems.

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