POPULATION CHARACTERISTICS AND TROPHIC INTERACTIONS BETWEEN PACIFIC MOLE CRABS AND REDTAIL SURFPERCH ON NORTHERN CALIFORNIA SANDY BEACHES

By

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CHAPTER 1 ABSTRACT

POPULATION CHARACTERISTICS AND TROPHIC INTERACTIONS BETWEEN PACIFIC MOLE CRABS AND REDTAIL SURFPERCH ON NORTHERN CALIFORNIA SANDY BEACHES

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A network of marine protected areas (MPAs) was established to protect northern California coastal habitats in December 2012. Populations of two indicator species, *Amphistichus rhodoterus* (redtail surfperch) and *Emerita analoga* (pacific mole crabs) were characterized within MPAs and reference sites to provide baseline ecological information for this region. Data were gathered using a series of simple field surveys (hook and line fishing surveys for *A. rhodoterus* along with core and transect surveys for *E. analoga*). Relative abundance, lengths, and sex ratios of *A. rhodoterus* did not differ between MPAs and their respective reference sites, whereas condition (overall health) increased in a north to south trend. Although based on a limited number of tag returns, movement of *A. rhodoterus* within northern California appears to be relatively local. Relative swash zone abundance of *E. analoga* did not differ between the MPA studied and its respective reference sites. Abundance and biomass of small-sized (<10 mm) *E. analoga* greatly increased during the summer months, likely due to recruitment to northern California beaches. A similar trend occurred for medium and large-sized crabs during spring months, likely due to the timing of reproduction in this region. Both species

serve as good indicator species for the northern California region. However, future monitoring for *E. analoga* should be based on timing of reproduction and recruitment.

ACKNOWLEDGEMENTS

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INTRODUCTION

Northern California marine sandy beaches and adjacent surf zones are dynamic environments with great ecological, economic, and cultural value. These shorelines exhibit exceptional biodiversity; sandy beaches in this region support foraging and nesting shorebirds, surf zone fishes that feed and spawn in the adjacent surf, and a diverse assemblage of invertebrates that serve as important sources of food for beach predators (McLachlan and Brown 2006). Sandy beaches also have scenic and aesthetic appeal; they are among the most intensely used coastal ecosystems for recreational activities and are highly important for coastal economies (Klein et al. 2004). Northern California shore-based commercial and recreational fisheries, targeting surfperch and smelt species, contribute to the economy of several communities in the North Coast Study Region (State of California Department of Fish and Wildlife 2014). In addition to recreational and commercial uses, historically, tribes have fished local beaches for salmon, smelt, surfperch, clams, and mussels (Caughman 1987). Today, northern California native tribes, including the Tolowa Dee-Ni' Nation, utilize sandy beaches to practice traditional fishing methods and preserve their heritage (J. Steinruck, pers. comm., 2014). To safeguard the health of marine life, as well as the economy and heritage of coastal California, a statewide network of marine protected areas (MPAs) was established in 1999 by the Marine Life Protection Act.

In northern California, sandy beaches comprise 35% of the 832 km of coastline within the boundaries of the north coast MPA region (California Marine Life Protection

Act Initiative 2010). Since establishment in 2012, approximately 10% of the available sandy beaches in this region (~29 km) have become protected in a network of 17 designated MPAs. Though protection levels of the individual MPAs vary, the overarching goal of the network is to protect the diversity and abundance of marine life and habitats. To evaluate the success of northern California MPAs in achieving this goal, it will be necessary to monitor these MPAs throughout their establishment. Gathering baseline data at the time of implementation is especially crucial, otherwise interpretation of long-term results would be impossible (Edgar et al. 2004).

A common method for assessing the effectiveness of MPAs is monitoring population characteristics of indicator species: a species whose presence denotes either the *composition* or *condition* of a habitat, community or ecosystem (Zacharias and Roff 2001). While *composition* indicator species are used to determine protected area designation (Zacharias and Roff 2001), *condition* indicator species are used to assess the effectiveness of the MPA, post-establishment (Meffe and Carroll 1997). To provide baseline ecological data for northern California sandy beach MPAs, we examined two condition indicator species: *Amphistichus rhodoterus* (redtail surfperch) and *Emerita analoga* (pacific mole crabs). These species were selected due to their abundance on northern California sandy beaches and adjacent surf zones, and because of their recreational, cultural, and economic significance in this region.

Amphistichus rhodoterus is a fish abundantly found in surf zones adjacent to sandy beaches, ranging from Monterey Bay, California to Vancouver Island, British Columbia (Tarp 1952, Clemens and Wilby 1961). The species is greatly sought after by northern California beach recreational anglers and tribal members (J. Steinruck, pers. Comm., 2014). Additionally, the largest commercial landings of *A. rhodoterus* occur through the port of Eureka (northern California), where there is a small commercial hook and line fishery (California Department of Fish and Wildlife 2016). Despite the fishing activities for this species along the north coast, information on population characteristics of *A. rhodoterus* is sparse. In central Oregon, Bennett and Wydoski (1977) examined multiple aspects of *A. rhodoterus* life history, including age, growth, length-weight relationships, age and size at sexual maturity, fecundity, and diet. In addition, they identified several parasites of *A. rhodoterus*. More recently, a study in southern Oregon (Pruden 2000) examined movement, age, sex structure, maturity, and embryonic development. No previous information has been published on population characteristics of *A. rhodoterus* in northern California.

Emerita analoga is an intertidal crustacean that is widespread throughout North and South America. It inhabits many beach types, and typically dominates the total biomass of invertebrates on sandy beaches (Dugan et al. 2000, Dugan et al. 2003). These crabs exhibit a tidal migratory rhythm within the swash zone of beaches (Cubit 1969, Fusaro 1980). As inhabitants of the swash zone, *E. analoga* serve as a food source for surf zone fishes and shorebirds. Limited studies have examined the effect of physical processes upon populations of *E. analoga* in Chile (Jaramillo & McLachlan 1993, Jaramillo et al. 2000, Veas et al. 2013) and southern California (Dugan and Hubbard 1996). Similar to *A. rhodoterus*, no previous information has been published on the population characteristics of *E. analoga* in northern California.

This study provides a baseline regional characterization of these two condition indicator species: *A. rhodoterus* and *E. analoga*, within the northern California MPA bioregion. Populations of these two species, in MPAs and associated reference sites, were studied at seven and four sites for *A.rhodoterus* and *E. analoga*, respectively. Through a series of field surveys (hook and line surveys for *A. rhodoterus*, and core and transect surveys for *E. analoga*), we provide information on abundances, size distributions, sex ratios, condition, and movement patterns of *A. rhodoterus* populations, as well as the swash zone abundance, size distributions, and biomass of *E. analoga* populations. Population abundances are compared to water temperature and salinity (and slope of the beach for *E. analoga* populations) to examine how physical components of sandy beaches impact these sandy shore residents. Finally, these indicator species were evaluated to determine their value for future MPA monitoring.

METHODS

Description of Study Sites

Surveys were conducted at seven sandy beaches (three MPAs and four associated reference sites) in the northern California MPA bioregion (Figure 1, Table 1). All surveyed MPAs are classified as State Marine Conservation Areas (SMCAs), where recreational and/or commercial take of some resources is permitted despite MPA status. All MPAs surveyed do not allow the take of either *A. rhodoterus* or *E. analoga,* consequently, all specimens sampled in MPAs were released during the time of capture.

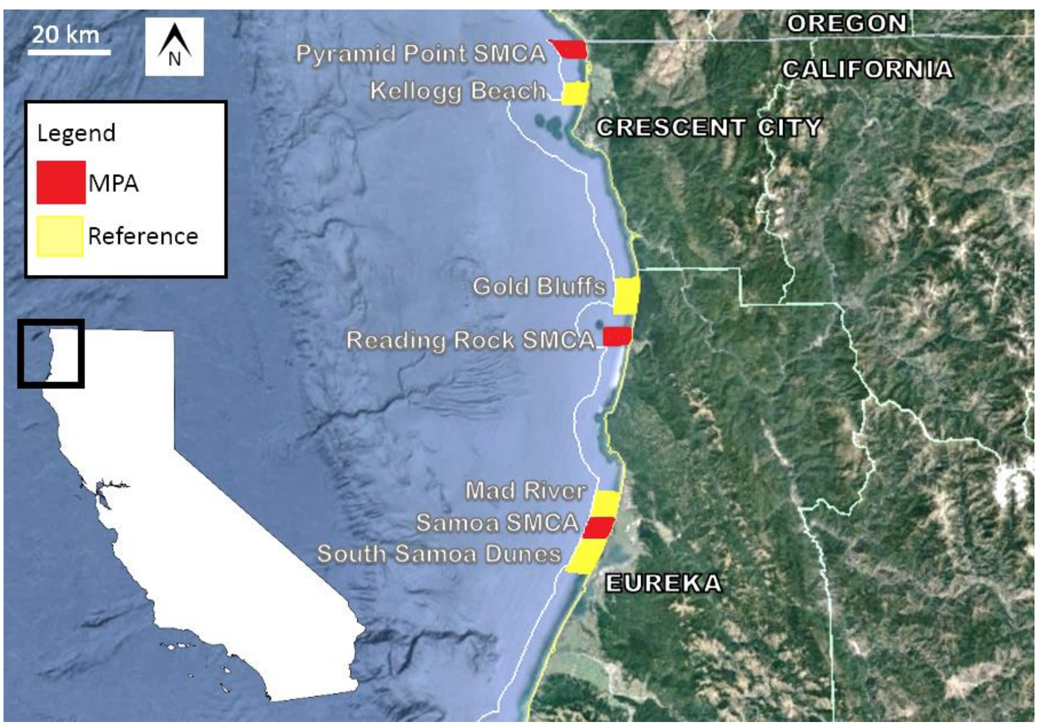


Figure 1. Sandy beach MPA and reference sites located within the northern California marine protected area bioregion, sampled from 2014-2016.

Table 1. Sandy beach sites, site status, and surveys conducted within the northern California MPA bioregion, 2014-2016.

Site Name	Abbreviation	Status	Latitude	Longitude	Survey(s) conducted
Pyramid Point SMCA	PP	MPA	41.97242	-124.20576	*A. rhodoterus* population survey
Kellogg Beach	KB	Reference Site	41.86688	-124.21387	*A. rhodoterus* population survey
Gold Bluffs	GB	Reference Site	41.35954	-124.07685	*A. rhodoterus* population survey *E. analoga* population survey
Reading Rock SMCA	RR	MPA	41.29742	-124.09150	*A. rhodoterus* population survey
Mad River	MR	Reference site	40.92908	-124.13612	*A. rhodoterus* population survey *E. analoga* population survey
Samoa SMCA	SMD	MPA	40.86654	-124.16403	*A. rhodoterus* population survey *E. analoga* population survey
South Samoa Dunes	SSD	Reference Site	40.79938	-124.20521	*A. rhodoterus* population survey *E. analoga* population survey

The two most northern sites studied were Pyramid Point SMCA and its associated reference site Kellogg Beach. Pyramid Point SMCA allows the recreational take of surf smelt and, before it gained MPA status, was a popular surfperch fishing location. South of Pyramid Point SMCA and Kellogg Beach is Reading Rock SMCA and its associated reference site, Gold Bluffs. Reading Rock SMCA permits the recreational and commercial take of salmon, surf smelt, and Dungeness crab. Gold Bluffs has historical and current importance as a major site for commercial and recreational *A. rhodoterus* fishing (D. Barrett, pers. comm., 2014). The most southern sites sampled in this study are Samoa SMCA and two adjoining reference sites: Mad River, north of the Samoa SMCA and South Samoa Dunes, south of the Samoa SMCA. South Samoa Dunes was added as a second reference site in 2015 due to its proximity and ease of access. Like Reading Rock SMCA, Samoa SMCA allows the recreational and commercial take of salmon, surf smelt, and Dungeness crab. Both Mad River and South Samoa Dunes are popular recreational fishing locations.

Amphistichus rhodoterus Population Surveys

Survey Schedule

During 2014, all sites (Table 1, except South Samoa Dunes) were sampled three times each, between the months of June and October. During 2015, a minimum of three sampling events were conducted between April and November at each of the seven sites, with more focused sampling at Samoa SMCA, Mad River, and South Samoa Dunes. During 2016, additional sampling occurred at Samoa SMCA, Mad River, South Samoa

Dunes, and Gold Bluffs between January and April. Strong winter weather conditions between October and December 2015, as well as between January and April 2016, restricting surfperch sampling at some sites during those months. Dates and times of surveys were dependent upon tidal patterns and weather conditions.

Survey Design

All collections were conducted under Institutional Animal Care and Use Committee approval number 13/14.F.10-A (28 May 2014). Upon arriving at a site, three anglers moved up/down the beach selecting sites based on beach slope. Each was equipped with a rod holding two hooks baited with two-inch Gulp™ saltwater sandworms, camo flavor. Within each selected sampling area, the anglers sampled until the "bite" ceased, or for a maximum of 20 minutes if there was no bite, at which time anglers moved to another sampling area. Sampling at each beach lasted four hours with sampling effort being evenly spaced around the timing of low tide. At MPA sites, *A. rhodoterus* were enumerated, measured (total length), sexed, tagged with a T-bar tag, and released at the site of capture. Sexes were determined externally based on the presence or absence of a modified anal fin and by the number of conspicuous openings between the pelvic and anal fins. In mature or maturing males, the anal fin modifies into a bulbous genital organ. Though both male and female surfperch have three openings between their pelvic and anal fins, one of the openings in males is obscured. At reference sites, up to 20 individuals were sacrificed to collect additional data on fish condition and gut contents. Sacrificed fish were kept in coolers and brought back to the Telonicher Marine Lab (TML) in Trinidad, CA for processing. Sacrificed *A. rhodoterus* were dissected within 24 hours of capture to ensure specimen quality. Before dissection, weight, length (total and standard length), and sex of each fish was recorded. The gonads, mesenteric fat, and gut were all removed and weighed separately. All additional fish caught at reference sites (that were not sacrificed) were enumerated, measured (total length), sexed, tagged with a T-bar tag, and released at the site of capture. During sampling events, water quality was monitored by measuring the temperature using a digital thermometer, and the salinity was determined with a refractometer.

Data Analyses

All statistical analyses were completed using R statistical software. Relative abundance (catch-per-unit-effort, or CPUE) of *A. rhodoterus* was calculated for each sampling event by dividing the total number of fish caught by the total number of hours fished. Relative abundance of *A. rhodoterus* at MPAs versus reference sites was compared using a paired t-test. Analysis of Variances (ANOVAs) were performed to determine if the sampling year affected relative abundance, and if relative abundance of *A. rhodoterus* differed among sampling sites. Regression analyses were performed to determine if water quality affected relative abundance of *A. rhodoterus*.

Total lengths of all *A. rhodoterus*, sampled across all sampling years, were measured to the nearest millimeter to determine the size frequency distribution at each site; mean total lengths for each site were compared using ANOVA. Mean total lengths of all fish at MPAs, versus reference sites, were compared using a paired t-test. Mean total length of male versus female fish were compared using ANOVA. A Tukey's post-hoc test was used to examine differences across sites.

The sex of each fish was recorded at the time of sampling. A paired t-test was used to compare sex ratios of *A. rhodoterus* populations between MPAs and reference sites. ANOVA was used to compare sex ratios of *A. rhodoterus* among sites.

The condition (K) for *A. rhodoterus* was determined by the formula $K = \frac{W}{L^3} \times 100$, where W = gut-free fish weight and L = standard length in mm. Mean condition of *A. rhodoterus* was compared among sites using an ANOVA, followed by a Tukeys post-hoc test to examine differences between specific sites. Mean condition of male and female fish were compared over the length of the study.

Tags were deployed on all fish sampled at MPAs and all fish not sacrificed at reference sites. Upon the return of a tag by an angler, information was collected on the tag number, as well as the date and location of capture. This information was used to determine the number of days the fish were at liberty, as well as the distance between release and capture sites.

Emerita analoga Population Surveys

Survey Schedule

Monthly *E. analoga* abundance surveys were conducted at Samoa SMCA and its adjoining reference sites (Mad River and South Samoa Dunes) between May and November 2015, with further sampling in 2016 between January and May. Sampling in 2016 was limited due to unfavorable weather conditions. Additional surveys were conducted at Gold Bluffs between May and August 2015 to add geographical breadth to the analyses. Dates and times of surveys were dependent upon tidal patterns and weather conditions.

Survey Design

At all sites, *E. analoga* was surveyed by taking cores along three transects located within the distributional boundaries of the swash zone: the zone of wave action on the beach between the upper limit of swash and lower limit of backwash. Transects were randomly spaced within one-hundred meters from the beach entry point and cores (10 cm diameter, 10 cm deep) were taken at uniform intervals of 0.25 to 1 meter along the transect line, depending on the width of the swash zone. Cores from each transect were pooled and placed in a mesh bag (mesh size = one mm) for sieving. *E. analoga* obtained in Samoa SMCA were enumerated and assigned to a size category (small <10 mm; medium 10 mm to <15 mm; large ≥15mm), then released at the site of capture. At reference sites, individuals were retained and placed in Ziploc bags, chilled on ice, and processed at the TML. Water temperature and salinity were measured using a digital thermometer and refractometer, respectively. Beach morphology was assessed by measuring the slope of the beach at the water table outcrop (WTO) using a digital level.

Data Analyses

All statistical analyses were performed using R statistical software. ANOVA was performed to determine if sampling year affected *E. analoga* abundance. Relative swash zone abundance of *E. analoga*, at MPAs, was compared to reference sites using a paired t-test. ANOVA, followed by a Tukey's post-hoc test, was used to determine differences between site abundances. Regression analyses were performed to determine if water quality or beach morphology affected the abundance of *E. analoga* in the swash zone.

The carapace and telson lengths of all individual *E. analoga*, collected at reference sites, were measured with electronic calipers to the nearest hundredth of a millimeter. To determine the size frequency distribution at each beach, carapace length measurements were used to place individuals into size categories; these size categories were identical to those used at Samoa SMCA. The mean count of crabs in each size category, averaged across all sites, was plotted over time to determine months of recruitment as well as to examine growth through time. For crabs sampled at reference sites, ANOVA was used to compare mean lengths of crabs among sites.

A subset of 230 randomly-selected (from across all reference sites) crabs was weighed and used in a weight-length model to estimate the biomass of *E. analoga* within the swash zone of each of the sampling sites. ANOVA was used to determine differences among site biomasses. The mean biomass of crabs, averaged across all sites, was plotted to examine swash zone biomass over time.

RESULTS

Amphistichus rhodoterus population characteristics

From 2014 to 2016, a total of 884 *A. rhodoterus* individuals were sampled across all sampling sites. Relative abundance of *A. rhodoterus* was not affected by sampling year [$F_{7,57}$=0.78, P=0.6], therefore, results were compiled across all years for further analyses. The relative abundance of *A. rhodoterus* did not differ between MPAs and reference sites [T_{34}=0.85, P=0.40] (Figure 2), or among individual sites [$F_{6,58}$=0.68, P=0.67] (Figure 3). By comparing relative abundance of *A. rhodoterus* to water quality measurements, it was determined that relative abundance of *A. rhodoterus* increases with increasing salinity, though this trend was not quite significant [$F_{1,33}$=3.949, P=0.055] (Figure 4). Relative abundance of *A. rhodoterus* was unaffected by water temperature [$F_{1,21}$=0.02, P=0.90] (Figure 4)

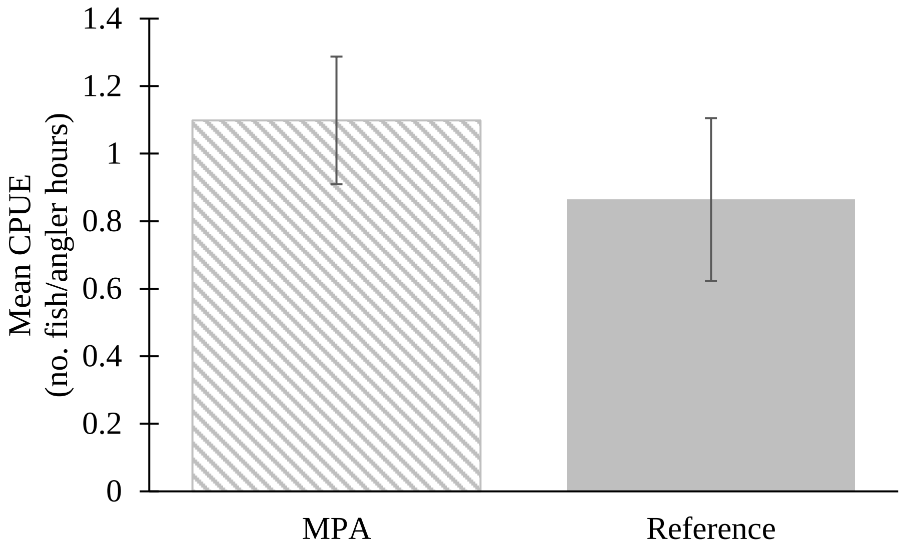


Figure 2. Relative abundance (CPUE) of *A. rhodoterus* sampled at MPAs and reference sites within the northern California MPA bioregion, 2014-2016. All data are averages across all sites and sampling years (±SE).

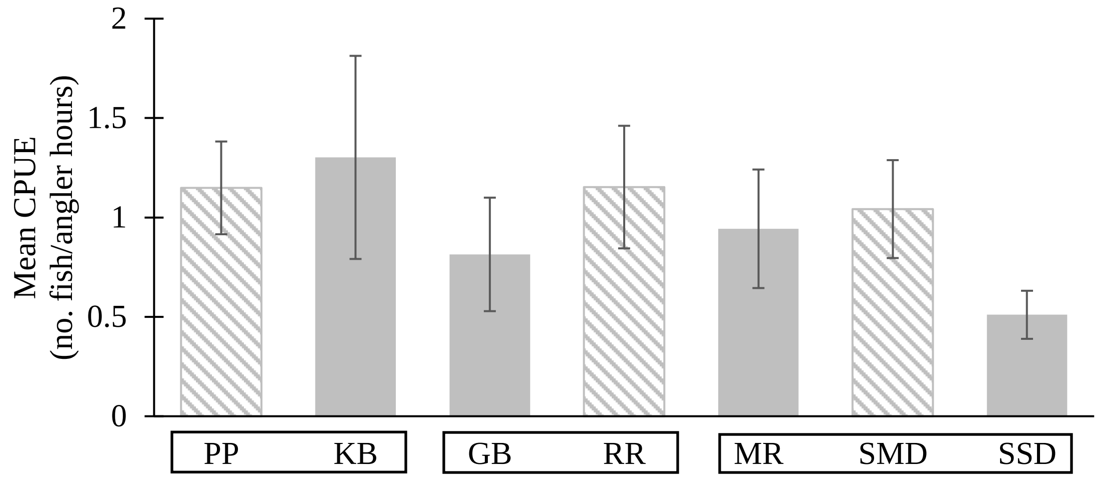
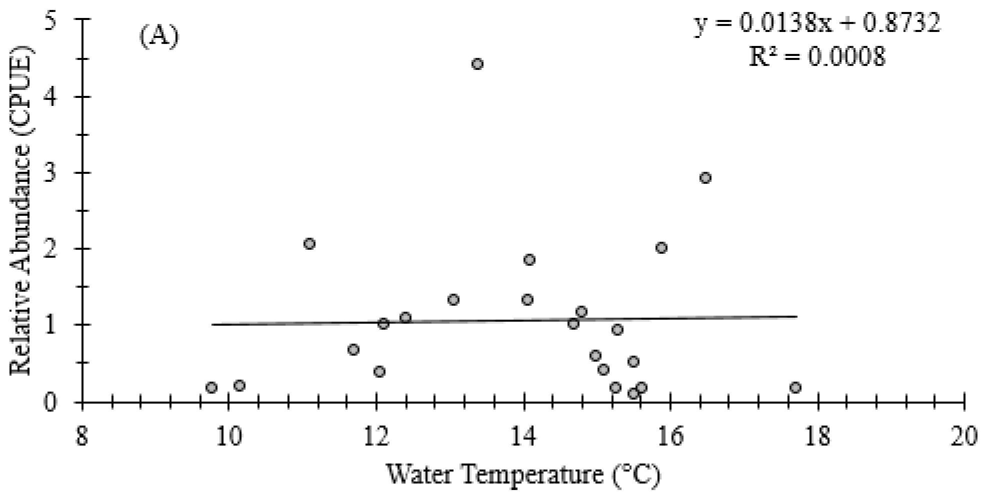


Figure 3. Mean relative abundance (CPUE) of *A. rhodoterus* sampled at the North Coast MPAs and reference sites within the northern California MPA bioregion, 2014-2016. All data are averages across all years (±SE). MPAs indicated by diagonal hatching. MPAs and associated reference sites are indicated by box around site abbreviations. Beaches are arranged from north to south along the horizontal axis. Site abbreviations: PP = Pyramid Point SMCA, KB = Kellogg Beach, GB= Gold Bluffs, RR= Reading Rock SMCA, MR= Mad River, SMD= Samoa SMCA, SSD= South Samoa Dunes.



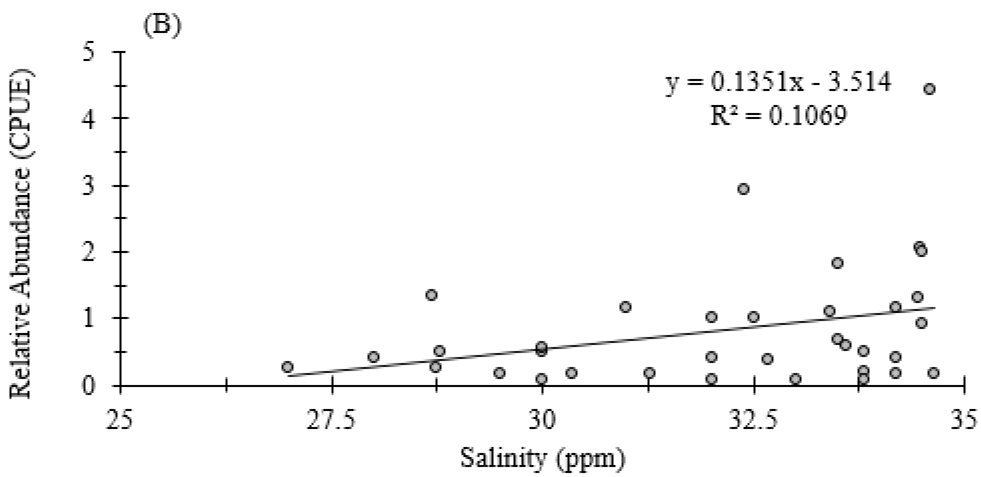


Figure 4. The effect of A) water temperature and B) salinity on the relative abundance (CPUE) of *A. rhodoterus* sampled in the northern California MPA bioregion, 2014-2016.

Sampled *A. rhodoterus* ranged from 140 to 380 mm in total length (Figure 5). All sites (except Mad River) were dominated by fish 260 to 270 mm in total length; Mad River was populated by smaller fish 220 to 240 mm in total length (Figure 5). Overall, mean total length of *A. rhodoterus* was not different across MPAs and reference sites [T_{30}=0.61, P=0.55] (Figure 6). On average, female fish were larger than males [$F_{1,880}$=7.53, P<0.01] (Figure 7). Not all sites had equally-sized fish [$F_{6,875}$=8.24, P<0.001] (Figure 8); Mad River had significantly smaller fish than Pyramid Point SMCA, Kellogg Beach, and Reading Rock, while Samoa SMCA has significantly smaller fish than Pyramid Point SMCA. While MPAs in general had larger fish than reference sites, MPAs and their nearby respective reference sites did not differ in *A. rhodoterus* length.

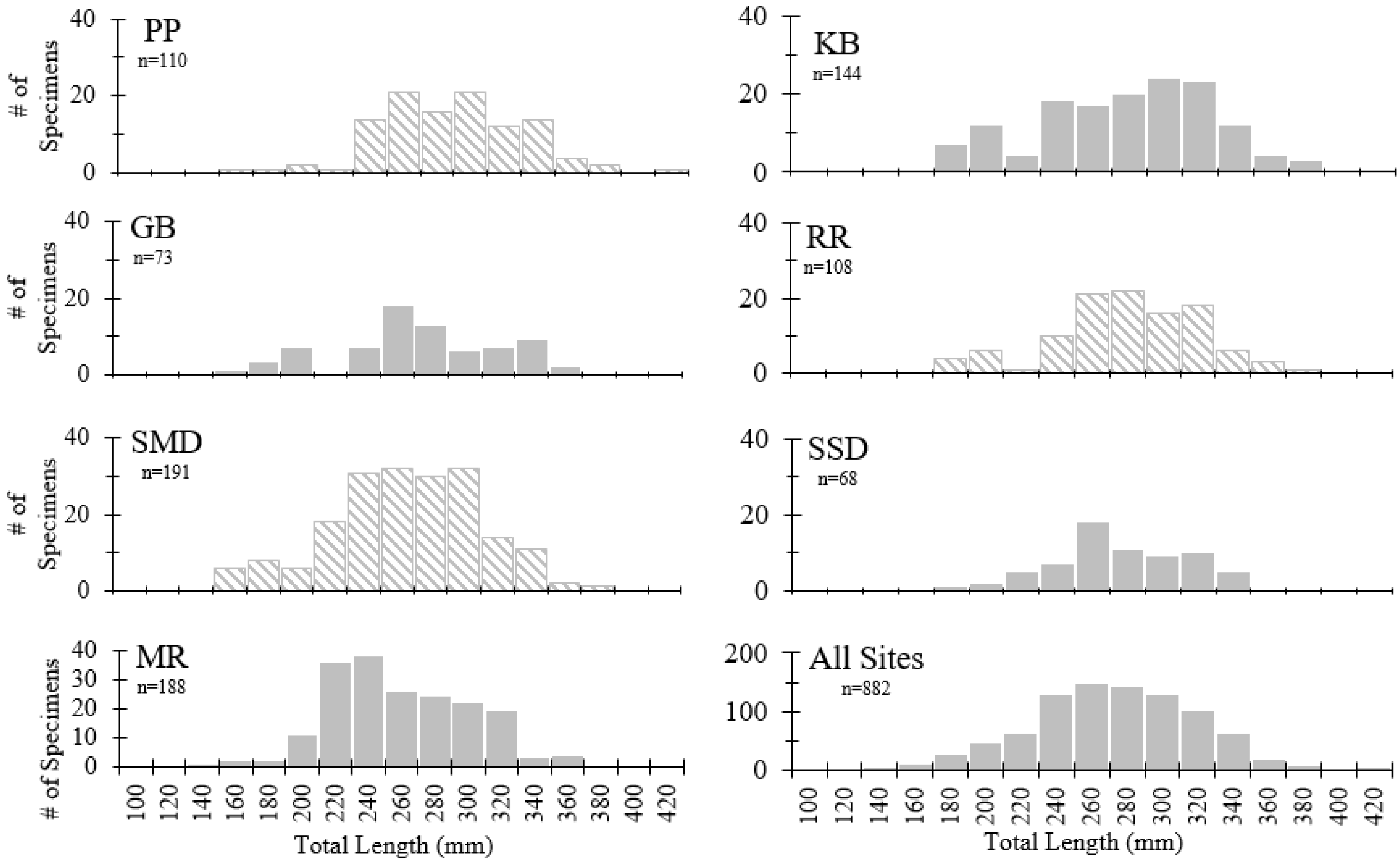


Figure 5. Length frequency histograms of *A. rhodoterus* total lengths (mm) sampled within the northern California MPA bioregion, 2014-2016. MPAs indicated by diagonal hatching. Site abbreviations: PP = Pyramid Point SMCA, KB = Kellogg Beach, GB= Gold Bluffs, RR= Reading Rock SMCA, MR= Mad River, SMD= Samoa SMCA, SSD= South Samoa Dunes.

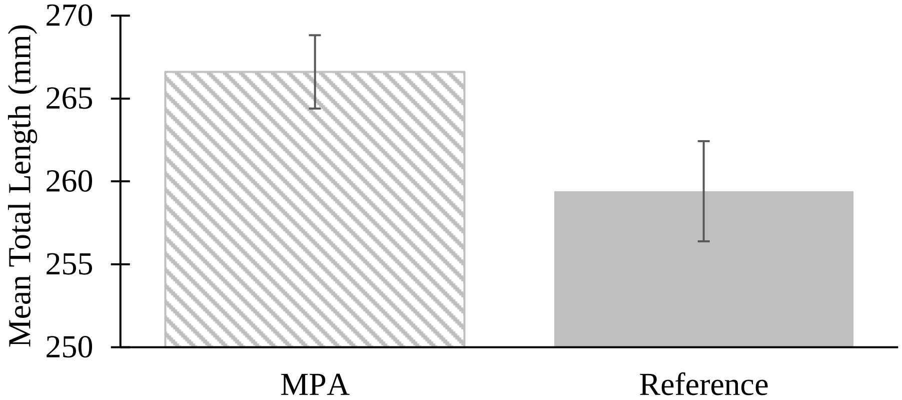


Figure 6. Mean total length (mm) of *A. rhodoterus* sampled at MPAs and reference sites in the northern California MPA bioregion, 2014-2016. All data are averages across all sites and years (±SE).

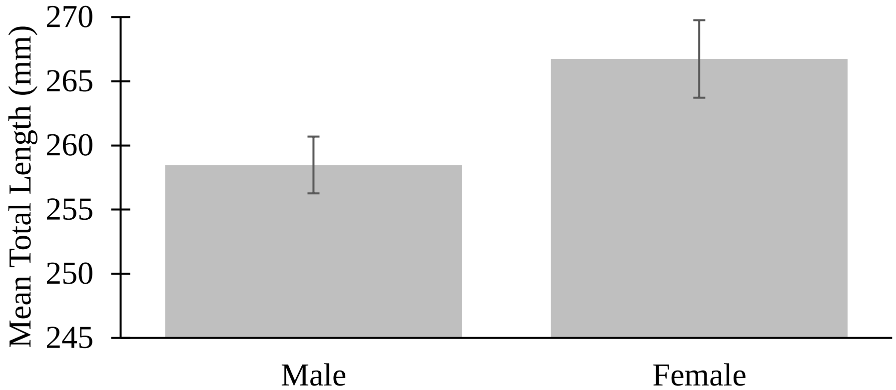


Figure 7. Mean total length (mm) of male and female *A. rhodoterus* sampled in the northern California MPA bioregion, 2014-2016. All data are averages across all sites and years (±SE). Female fish were larger than males [*P*<0.01].

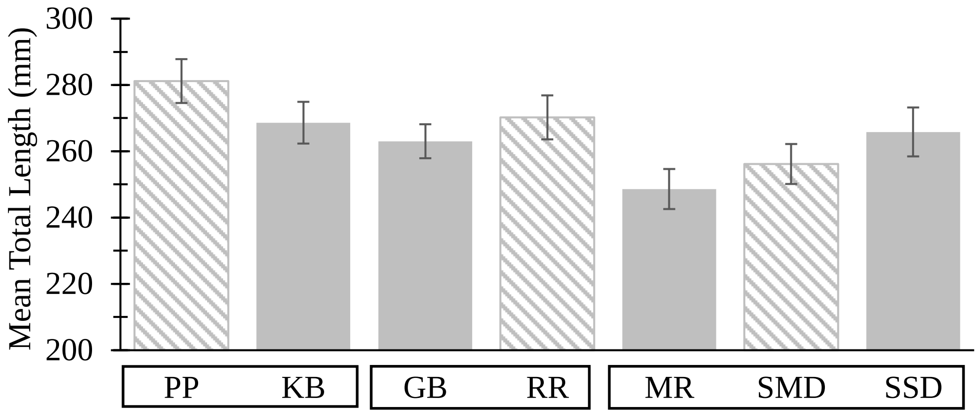


Figure 8. Mean total length (mm) of *A. rhodoterus* sampled in MPAs and reference sites within the northern California MPA bioregion, 2014-2016. All data are averages across all years (±SE). MPAs indicated by diagonal hatching. MPAs and associated reference sites are indicated by box around site abbreviations. Beaches are arranged from north to south along the horizontal axis. Site abbreviations: PP = Pyramid Point SMCA, KB = Kellogg Beach, GB= Gold Bluffs, RR= Reading Rock SMCA, MR= Mad River, SMD= Samoa SMCA, SSD= South Samoa Dunes. Mad River had significantly smaller fish than Pyramid Point SMCA, Kellogg Beach, and Reading Rock, while Samoa SMCA has significantly smaller fish than Pyramid Point SMCA [$P<0.001$].

Sex ratios of *A. rhodoterus* were not significantly different between MPAs and reference sites [T_8=-0.14, P=0.89] (Figure 9). Estimated sex ratios of *A. rhodoterus* populations indicate that differences in sex ratios occur across sites [$F_{6,10}$=3.36, P=0.04] (Figure 10). Although Tukeys post-hoc test could not detect any significant differences between pairs of sites, South Samoa Dunes had a greater percentage of males than Kellogg Beach, Mad River, and Reading Rock SMCA.

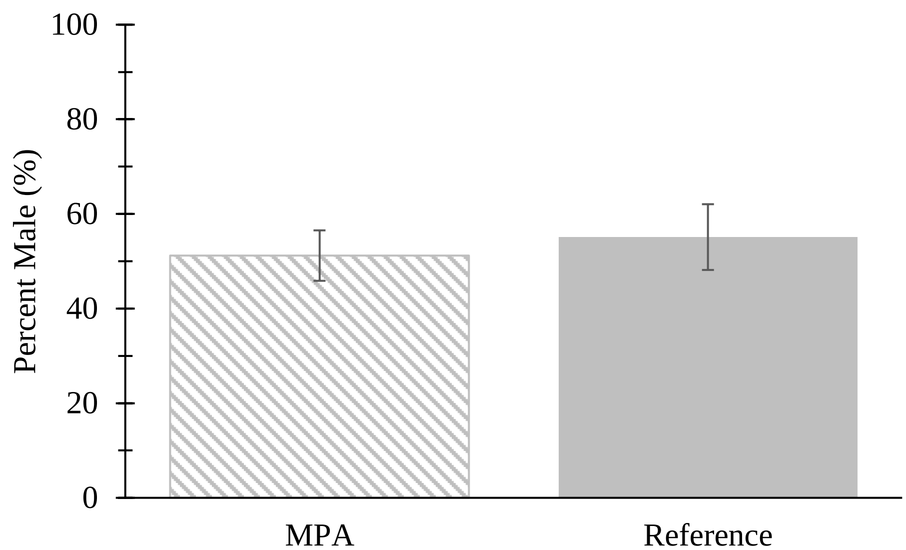


Figure 9. Sex ratios (shown as percent of sample that was male) of *A. rhodoterus* at MPAs and reference sites in the northern California MPA bioregion, 2014-2016. All data are averages across all sites and years (±SE).

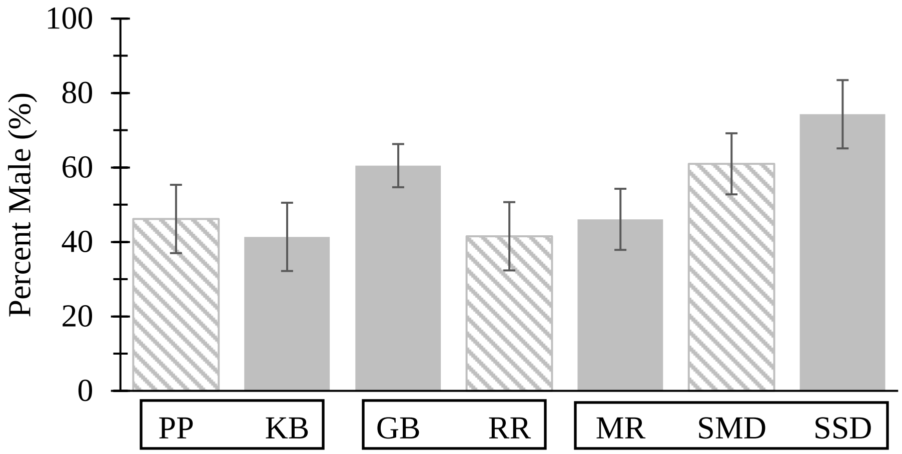


Figure 10. Sex ratios (shown as percent of sample that was male) of *A. rhodoterus* sampled at the MPAs and reference sites within the northern California MPA bioregion, 2014-2016. All data are averages across all years (±SE). MPAs indicated by diagonal hatching. MPAs and associated reference sites are indicated by box around site abbreviations. Beaches are arranged from north to south along the horizontal axis. Site abbreviations: PP = Pyramid Point SMCA, KB = Kellogg Beach, GB= Gold Bluffs, RR= Reading Rock SMCA, MR= Mad River, SMD= Samoa SMCA, SSD= South Samoa Dunes. Differences in sex ratios occur across sites [p=0.04], although Tukeys post-hoc test could not detect any significant differences between pairs of sites.

Condition of *A. rhodoterus* showed a north to south trend, with fish from southern sites in better condition than fish from northern sites [$F_{3,264}$=3.02, P<0.05] (Figure 11). Condition factors were calculated for 158 males and 161 females, from all reference sites within the north Coast MPA region. Condition for both sexes ranged from 2.39 to 4.53, with a mean condition of 3.73. Neither sex had greater condition than the other over for the duration of the study, with the condition of both sexes fluctuating simultaneously over time [$F_{1,266}$<0.01, P=0.99] (Figure 12).

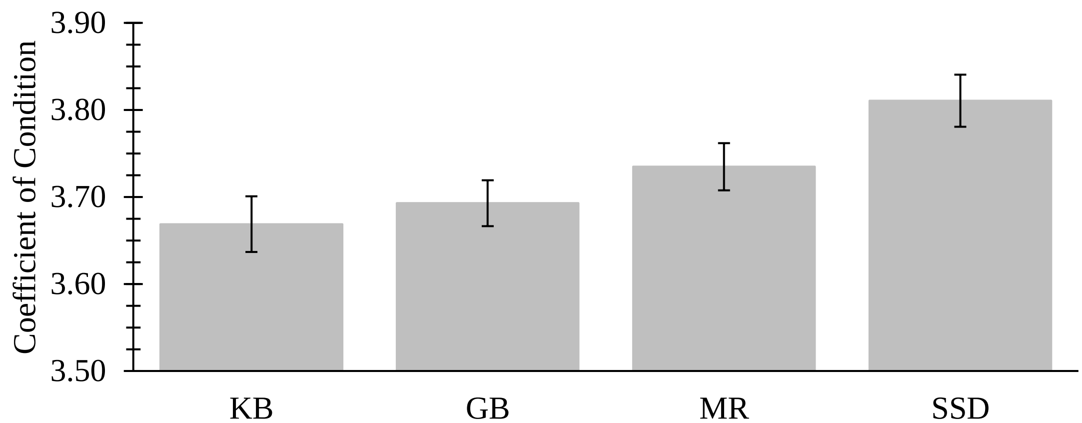


Figure 11. Mean coefficient of condition for *A. rhodoterus* collected in the northern California MPA bioregion, 2014-2016. All data are averages across all years (±SE). Beaches are arranged from north to south along the horizontal axis. Site abbreviations:KB = Kellogg Beach, GB= Gold Bluffs, MR= Mad River, SSD= South Samoa Dunes. Fish from SSD were in better condition than fish from GB ans KB [P<0.05].

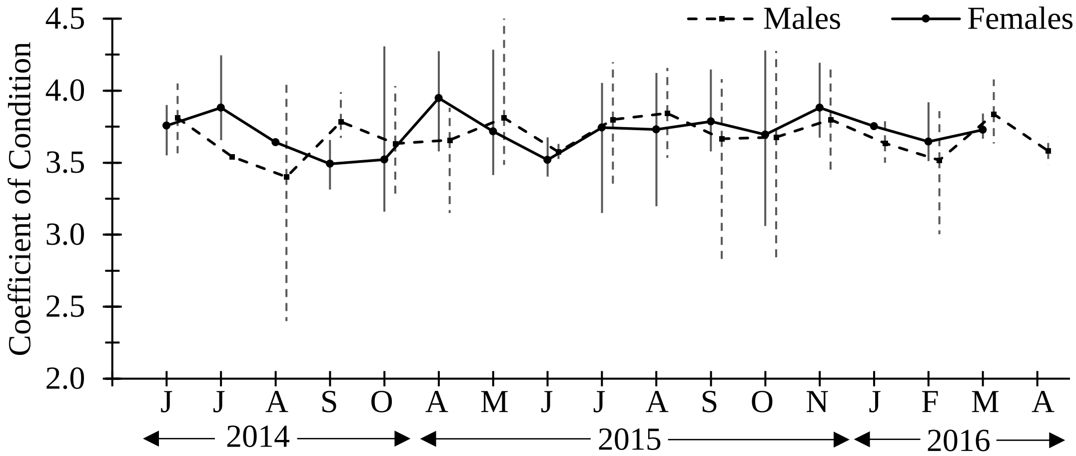


Figure 12. Mean coefficient of condition, by month, for male and female *A. rhodoterus* collected in the northern California MPA bioregion, 2014-2016. All data are averages across all sites, vertical lines show ranges.

Of the 884 *A. rhodoterus* individuals sampled, 497 were tagged, yielding a return of five tags by local recreational anglers (Table 2). Two of the returned tags were deployed at Pyramid Point SMCA and captured at the mouth of the Smith River, a distance of three km, after 13 and 14 days at liberty. One of the returned tags was deployed at Reading Rock SMCA and captured again at Gold Bluffs after 311 days at liberty, approximately eight km away. The two remaining tag returns were deployed at Samoa SMCA and captured after 30 and 316 days at liberty, at distances of approximately 12 and 18 km, at the North Jetty entrance to Humboldt Bay and Hilfiker Beach within Humboldt Bay, respectively.

Table 2. Deployment site of tags, date tagged, days at liberty, and distance of recaptured *A. rhodoterus* tagged with T-bar tags within the northern California MPA bioregion, 2014-2016. Distance travelled is estimated as shortest distance in marine water between site where the fish were tagged and the location of recapture.

Site of Tagging	**Date Tagged**	**Days at Liberty**	**Distance Travelled**
Pyramid Point SMCA	15 August 2014	13	3 km
Pyramid Point SMCA	17 September 2015	14	3 km
Reading Rock SMCA	24 July 2015	311	8 km
Samoa SMCA	2 July 2014	30	12 km
Samoa SMCA	23 July 2014	316	18 km

Emerita analoga population characteristics

Sampling for *E. analoga* was restricted to the swash zone of the beach, therefore all estimates for *E. analoga* populations only represent *E. analoga* within the swash zone of each beach. Sampling year did not significantly affect *E. analoga* relative abundance estimates [$F_{1,31}$=2.50, P=0.12], therefore, analyses were performed on the combined data for both years. Relative abundance of *E. analoga* did not differ across MPAs and reference sites [T_{14}=-0.10, P=0.93] (Figure 13). When examined as individual sites, relative abundance of *E. analoga* at South Samoa Dunes was significantly lower than at Gold Bluffs [$F_{3,29}$=3.45, P=0.03] (Figure 14). By comparing relative abundance of *E. analoga* to water quality and beach morphology measurements, it was determined that relative abundance of *E. analoga* within the swash zone is unaffected by beach slope [$F_{1,23}$=0.20, P=0.66] (Figure 15B). Although abundance of *E. analoga* increased with increasing water temperature [$F_{1,17}$=4.39, P=0.051] and salinity [$F_{1,23}$=3.51, P=0.07] (Figure 15C), these trends were not statistically significant.

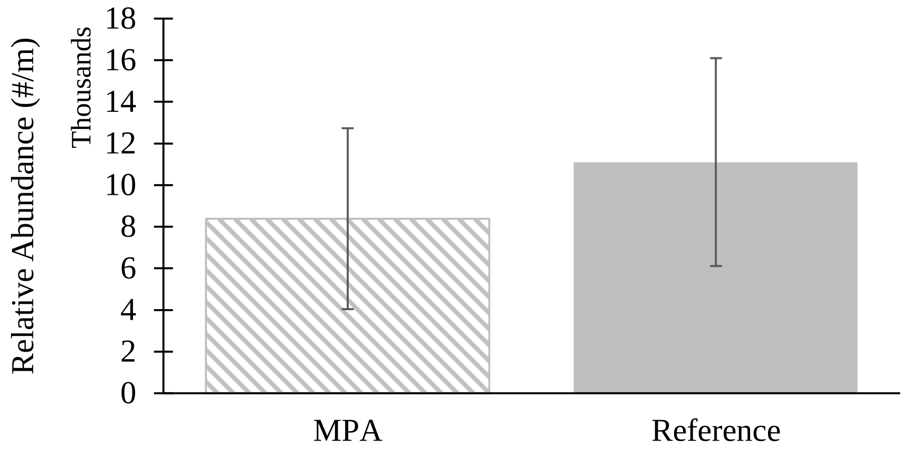


Figure 13. Relative abundance (#/meter) of *E. analoga* sampled at MPAs and reference sites within the northern California MPA bioregion, 2015-2016. All data are averages across all sites and years (±SE).

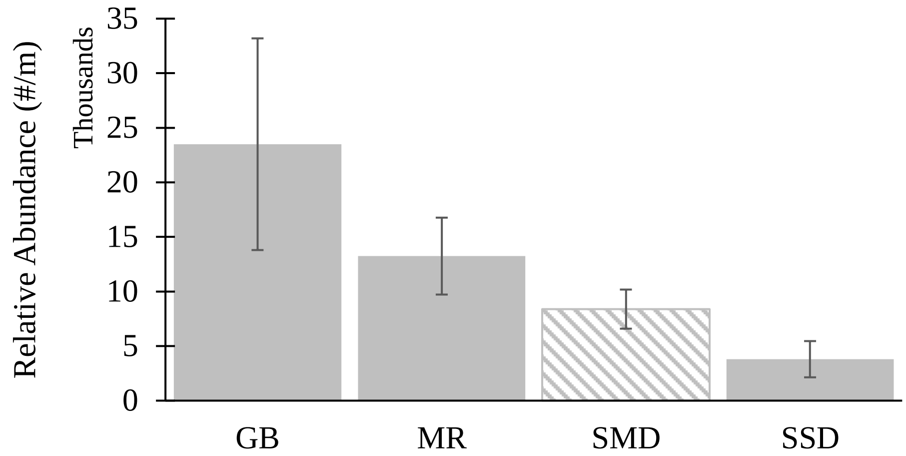


Figure 14. Relative abundance (#/meter) of *E. analoga* sampled in MPAs and reference sites within the northern California MPA bioregion, 2015-2016. All data are averages across all years (±SE). MPAs indicated by diagonal hatching. Beaches are arranged from north to south along the horizontal axis. Site abbreviations: GB= Gold Bluffs, MR= Mad River, SMD= Samoa SMCA, SSD= South Samoa Dunes. Relative abundance was significantly lower at South Samoa Dunes than Gold Bluffs [*P*=0.03].

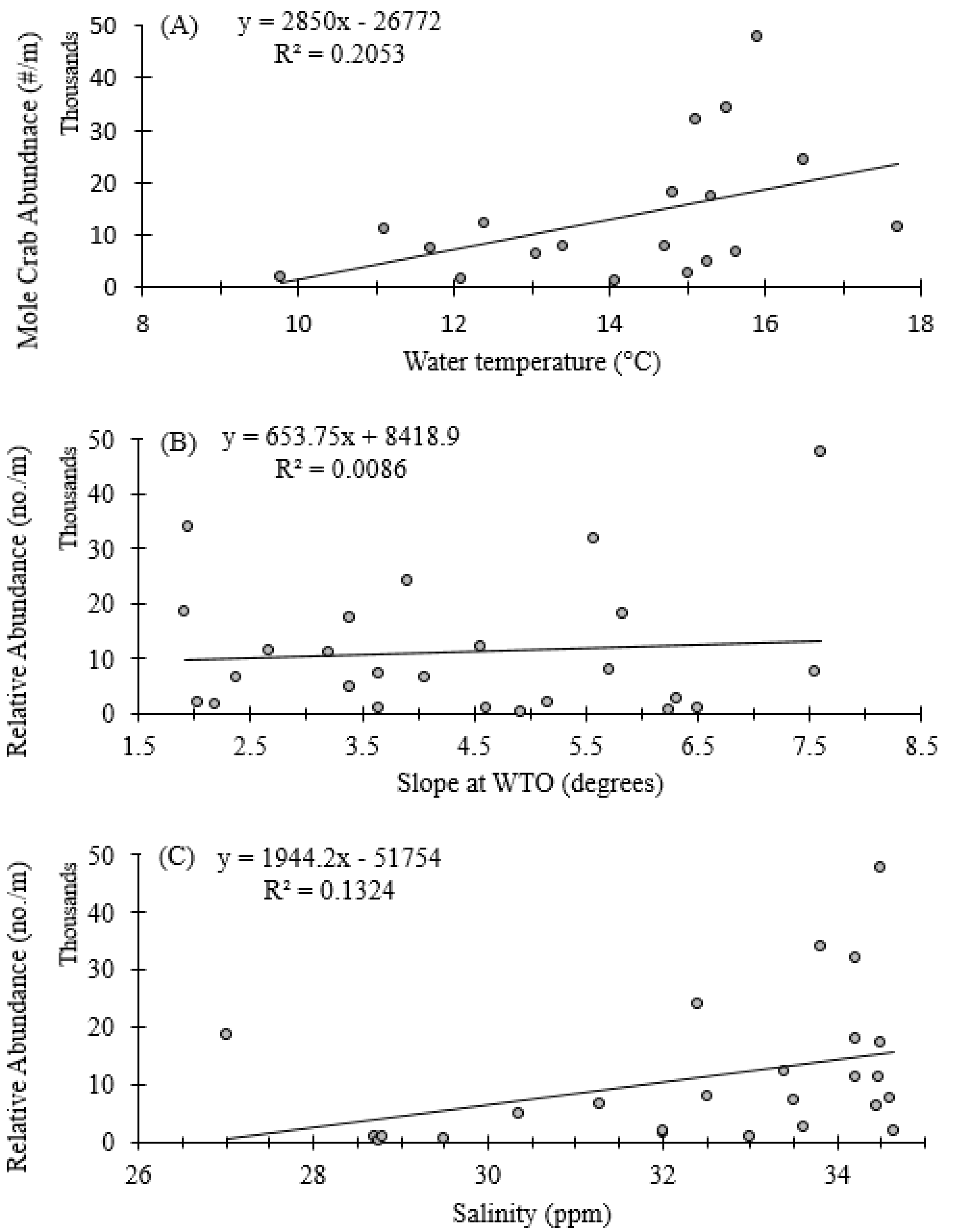


Figure 15. The effect of A) water temperature, B) beach slope at the water table outcrop, and C) salinity on the relative abundance (#/meter) of *E. analoga* sampled in the northern California MPA bioregion.

All sampled *E. analoga* individuals were placed into size categories (small <10 mm; medium 10 mm to <15 mm; large ≥15mm) to compare the size frequency distribution at Samoa SMCA and reference sites. Overall, sites were dominated by small crabs (Figure 16); only Mad River had a greater abundance of medium sized crabs than small crabs. All sites had very few large crabs present (Figure 16). Mean carapace length at Mad River was significantly larger than both Gold Bluffs and South Samoa Dunes, while *E. analoga* at Gold Bluffs and South Samoa Dunes were the same size [$F_{2,11398}$=264.10, P<0.001] (Figure 17). To determine the timing of recruitment and reproduction of *E. analoga* within the northern California region, the mean abundance of different size categories across all sites was examined for the duration of the survey (Figure 18). In 2015, there was a 53-fold increase in the mean number of small-sized crabs from June to July, as well as a two-fold increase in the mean number of medium-sized crabs from July to August. From August to September in 2015, there was a 4-fold decrease in the mean number of small-sized crabs, followed by a three-fold decrease in the mean number of medium-sized crabs between September and October. In March 2016, there was a slight pulse of medium and large-sized crabs, both size classes increasing nearly eight-fold. Other than the slight increase of large crabs in March 2016, large-size crabs remained infrequent throughout the duration of the study.

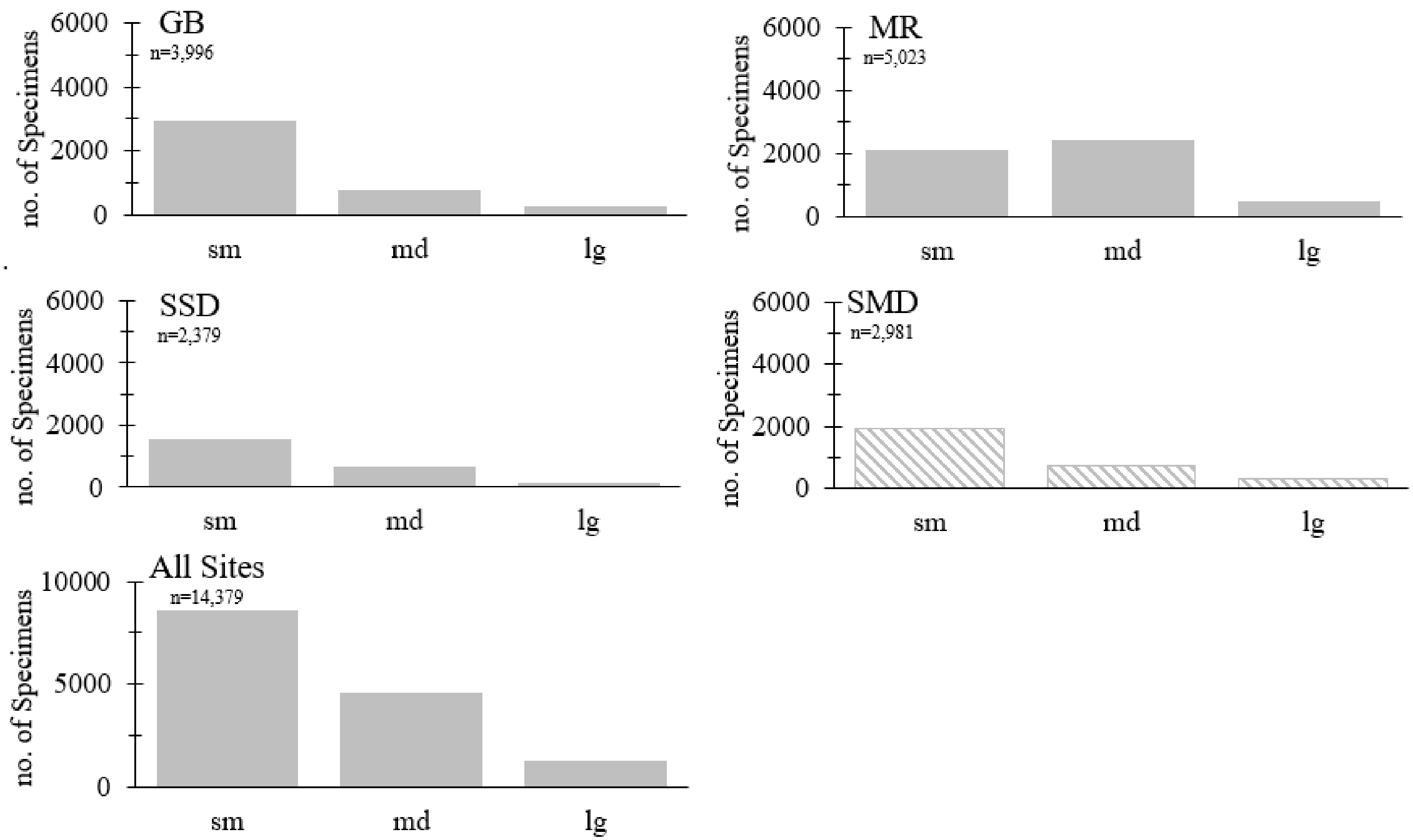


Figure 16. Frequency of occurrence of *E. analoga* size categories (<small <10 mm; medium 10 mm to <15 mm; large ≥15mm) sampled within in the northern California MPA bioregion, 2015-2016. MPAs indicated by diagonal hatching. Site abbreviations: GB= Gold Bluffs, MR= Mad River, SMD= Samoa SMCA, SSD= South Samoa Dunes.

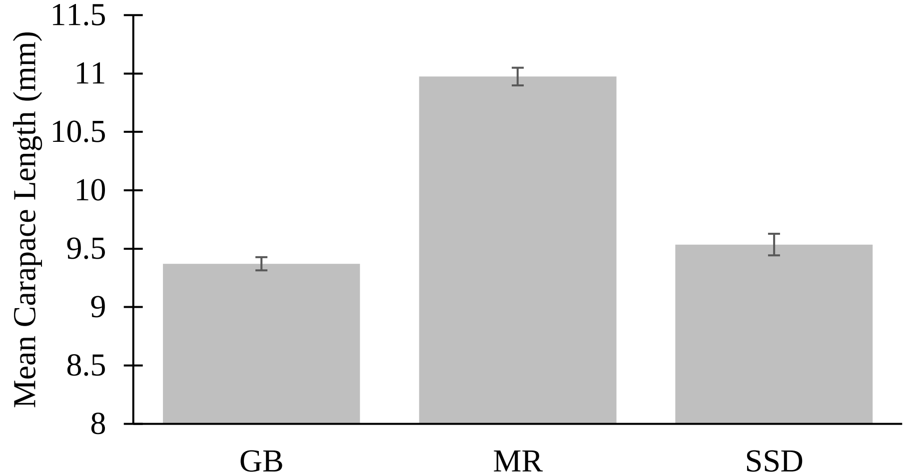


Figure 17. Mean carapace length (mm) of *E. analoga* sampled at reference sites within the northern California MPA bioregion, 2015-2016. All data are averages across all years (±SE). Beaches are arranged from north to south along the horizontal axis. Site abbreviations: GB= Gold Bluffs, MR= Mad River, SSD= South Samoa Dunes. Mean carapace length at Mad River was significantly larger than both Gold Bluffs and South Samoa Dunes [P<0.001].

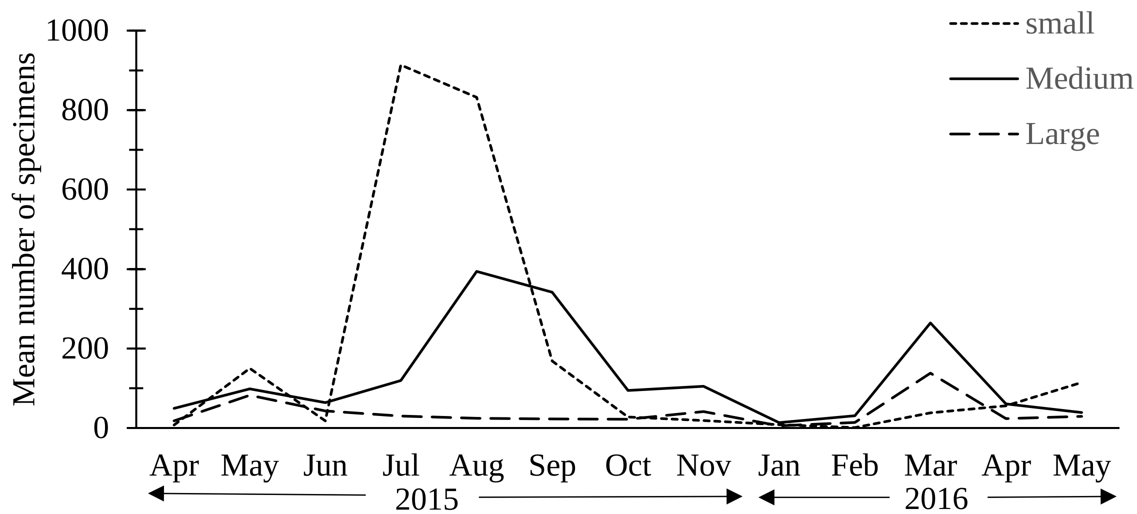


Figure 18. Mean number of *E. analoga* sampled across all sites within the northern California MPA bioregion, 2015-2016. All individuals were placed in size categories small <10 mm; medium 10 mm to <15 mm; large ≥15mm).

To estimate the biomass of *E. analoga*, within the swash zone at reference sites, a weight-length relationship was determined (Figure 19). Estimated mean biomass was different across sites [$F_{2,22}$=4.77, *P*=0.02], with South Samoa Dunes having a significantly lower biomass of *E. analoga* than Gold Bluffs (Figure 20). The estimated mean biomass of *E. analoga* combined for all sites was examined over time for the duration of the survey (Figure 21). Similar to the mean number of *E. analoga* individuals in figure 18, there is an increase in *E. analoga* biomass in August 2015, followed by a decrease in October 2015 (Figure 21). There is a general decrease in *E.* analoga swash zone biomass over the winter months, followed by a sudden increase in mean biomass in March 2016 that quickly decreases again by April 2016.

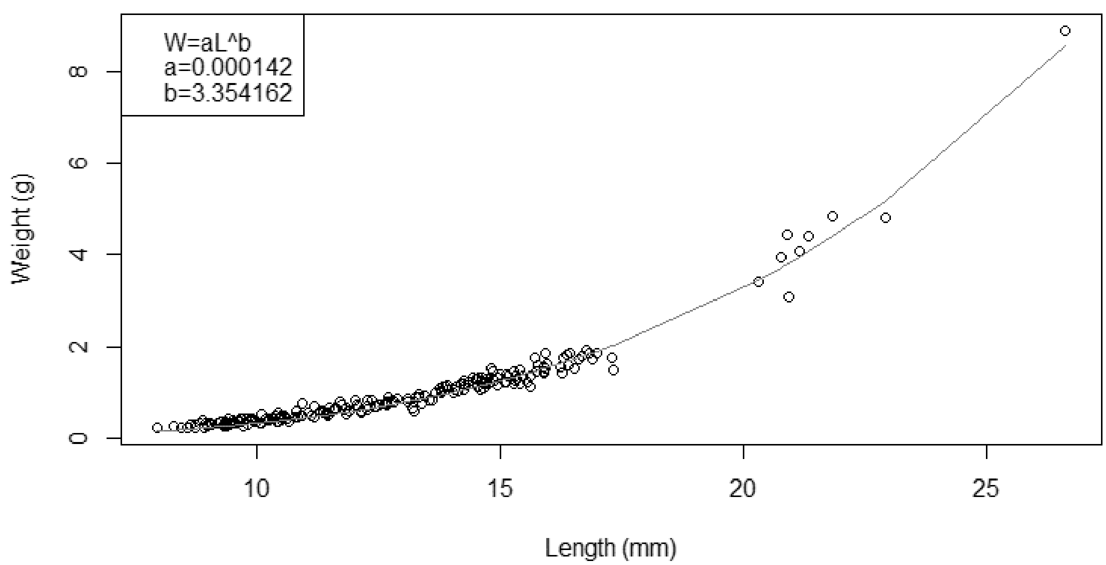


Figure 19. Weight-length relationship of *E. analoga* sampled in the northern California MPA bioregion, 2015-2016. A subset of 230 individuals were measured and weighed to generate the model.

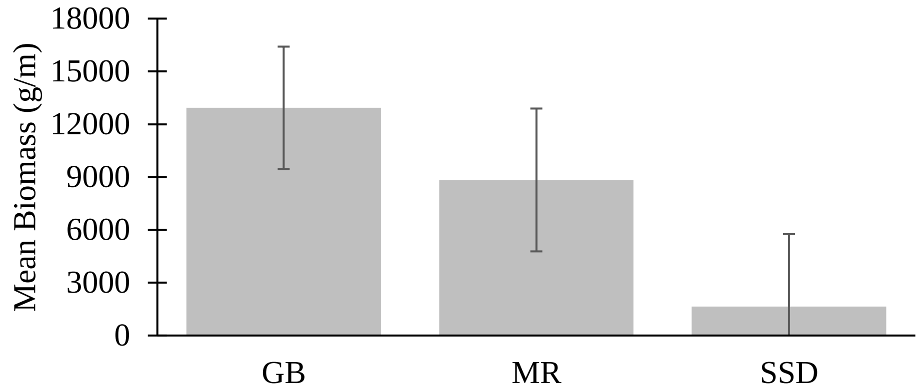


Figure 20. Estimated mean biomass (g/m) of *E. analoga* at reference sites within the northern California MPA bioregion, 2015-2016. All data are averages across all years (±SE). Beaches are arranged from north to south along the horizontal axis. Site abbreviations: GB= Gold Bluffs, MR= Mad River, SSD= South Samoa Dunes. South Samoa Dunes had a significantly lower biomass of *E. analoga* than Gold Bluffs [*P*=0.02].

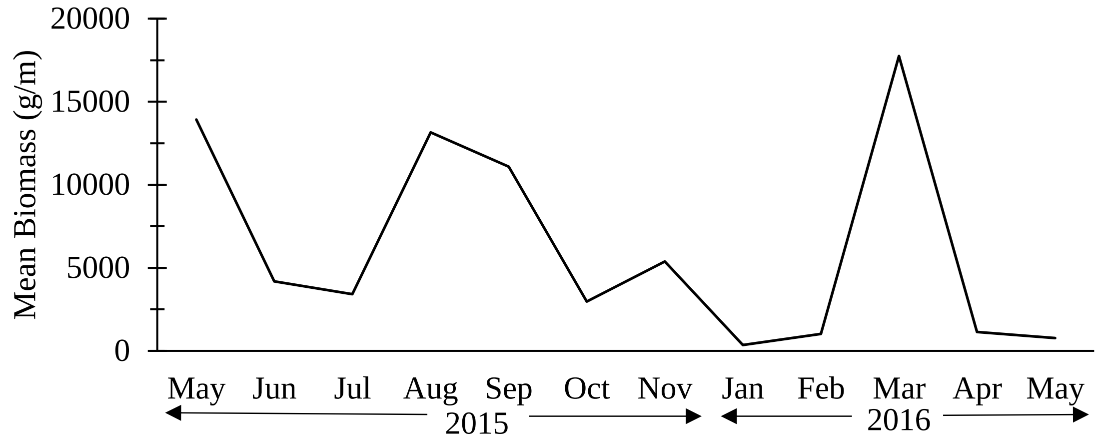


Figure 21. Estimated mean biomass (g/m) of *E. analoga* across all sites sampled within the northern California MPA bioregion, 2015-2016.

DISCUSSION

Amphistichus rhodoterus Population Characteristics

No significant difference was detected in the relative abundance of *A. rhodoterus* across all sites sampled within the California north coast MPA region between the years 2014 to 2017 (Figure 3). Relative abundance of *A. rhodoterus* decreased with decreasing salinity, though this trend was not quite significant statistically (P=0.055) (Figure 4). The response of *A. rhodoterus* to salinity may be due to decreases in prey resource availability near areas of freshwater input. There is freshwater discharge at each sampling site in this study: Smith River near Pyramid Point SMCA and Kellogg Beach, Redwood Creek near Reading Rock SMCA and Gold Bluffs, and Mad River near Samoa SMCA, Mad River (beach), and South Samoa Dunes. Defeo & de Alava (1995) and Lercari & Defeo (1999) have shown that freshwater discharge, and the resulting decrease in salinity, can lead to a decline in the abundance of sandy beach invertebrates, and consequently, prey resources for surf zone fishes.

Mean total length of *A. rhodoterus* differed across sampling sites, however, overall, reference sites were not significantly different from their respective MPAs (Figure 8). Female *A. rhodoterus* were larger than males throughout the northern California MPA bioregion (Figure 7), a trend likely due to differential growth rates of the sexes. Bennett and Wydoski (1977) determined that the differences in the lengths of *A. rhodoterus* increases progressively after sexual maturity, a trend that occurs in white

(*Phanerodon furcatus)*, shiner (*Cymatogaster aggregata*), walleye (*Hyperprosopon argenteum*), and pile (*Rhacochilus vacca*) surfperch species as well (Anderson and Bryan 1970, Wares 1971).

Condition of *A. rhodoterus* increased along a north to south trend; fish in South Samoa Dunes had a mean condition of 3.8, and were in better condition than fish in Kellogg Beach, that had a mean condition of 3.68 (Figure 11). In order to compare the condition of our specimens to *A. rhodoterus* sampled in Oregon (Bennett and Wydoski 1977), our condition calculations (using gut-free weight and standard length) were converted to match the condition calculation used in that study (overall weight and total length). After the transformation, it was determined that *A. rhodoterus* sampled in northern California were in better condition than those sampled in Oregon (mean conditions of 1.87 and 1.6 for California and Oregon, respectively). It is unclear whether these differences in condition are a function of sampling year (Bennett and Wydoski sampled from 1967 to 1969), a continuation of the north to south trend in condition exhibited in this study, or due to biological or oceanographic conditions. A positive sea surface temperature anomaly developed in the NE Pacific Ocean during the winter of 2013 to 2014 (commonly known as "the blob"), with warm temperatures persisting through spring 2015 (Bond et al. 2015). Although the effects of the blob are not yet completely understood, effects to the phytoplankton communities within the region have been detected (Gómez-Ocampo et al. 2017). Changes to these oceanic producers will likely lead to changes within higher trophic levels. These biological and oceanographic changes may have altered the available food for *A. rhodoterus*, and their condition.

Additional condition analyses from a longer proportion of the species' range may shed light on this trend.

Despite deployment of more than 500 tags, only five tags were returned by recreational anglers (Table 2). Low numbers of tag returns could be due to multiple factors: poor tag retention, fish death, and/or possible lack of angler participation in reporting recovered tags. In addition, large stretches of inaccessible sandy beach habitat, to anglers, may have limited the number of tag returns. A tag retention study that tested plastic T-bar anchor tags like those used in our study, determined that *A. rhodoterus* health was unaffected by these tags (Pruden 2000). Based on their findings, it is unlikely that premature death due to tagging or poor tag retention were causes of low tag returns.

Although limited, our tagging effort may indicate that *A. rhodoterus,* in northern California, remain relatively local, as tag returns showed less than 20 kilometers of movement (Table 2). In contrast, a similar tagging study in southern Oregon showed that *A. rhodoterus* move considerable distances along the open coastline, but may be limited by barriers that obstruct natural movement (Pruden 2000). Increased future tagging will be required to confirm these initial findings for the northern California region.

Emerita analoga Population Characteristics

Overall, relative swash zone abundance of *E. analoga* was the same across MPAs and reference sites (Figure 13). Among sites, however, only South Samoa Dunes had a significantly lower abundance (Figure 14). While it is possible that disturbance from off-highway vehicles (OHV) impacted *E. analoga* abundance at South Samoa Dunes (the only site where OHV driving is permitted), other populations of *E. analoga* have been shown to be unaffected by OHV beach-driving (Jaramillo et al. 1996). Furthermore, commercial anglers at Gold Bluffs, where abundance of *E. analoga* was greatest, drive on the beach with small trucks while searching for surf zone fish, making disturbance from any kind of beach-driving an unlikely cause for low abundance.

Veas et al. (2013) determined that *E. analoga* populations differ in abundance across beaches with varying morphodynamics (reflective versus dissipative beaches), allowing beaches to serve as either source or sink habitats. Beaches with milder conditions (dissipative beaches) tended to have greater densities of adults and recruits and were able to serve as source habitats. More information would need to be collected on the morphodynamics of beaches within the northern California MPA bioregion to determine if beach morphodynamics affects the abundance of *E. analoga* in this region.

Variability in swash zone abundance of *E. analoga* was not correlated to any environmental conditions measured. However, swash zone abundance increased with increasing temperature and salinity, though these trends were not quite significant (P=0.051 and P=0.07, respectively) (Figure 15). Large inputs of fresh water from rivers and streams, especially during winter months (when heavy rain in the northern California region leads to a large inflow of fresh water), likely decrease *E. analoga* abundances, a trend observed for other sandy beach invertebrates (Defeo & de Alava 1995, Lercari & Defeo 1999). Furthermore, concurrent decreases in surface water temperatures during winter months may be adding to the overall decrease in *E. analoga* abundances during certain times of the year. Our results show an overall drop in abundance and biomass of

E. analoga during the winter sampling (Figures 18 and 21), however, further study is required to parse out these two confounding effects.

The swash zone of most sites was dominated by small-sized *E. analoga* (Figure 16). Mean carapace length was greater at Mad River than at Gold Bluffs or South Samoa Dunes due to a greater proportion of medium-sized crabs (Figure 17). All sites had relatively few large-sized crabs present within the swash zone (Figure 16). Populations of *E. analoga* have been shown to distribute by size along the vertical intertidal gradient, with small size classes being further up shore than large size classes (Efford 1965). A greater abundance of large-sized crabs was possibly present at each sampling site, but these were out of range for swash zone core-sampling and could not be included in any swash zone estimates.

Abundances of different size classes of *E. analoga* differed throughout the duration of the study, giving insight into the reproductive cycle of northern California populations. Recruitment of *E. analoga* to beaches occurred from July to August 2015, noted by a large influx in small-sized crabs during that time (Figure 18). From August to September 2015, an increase in medium-sized crabs, coupled with a decrease in small-sized crabs, marked the growth of recently-recruited crabs (Figure 18). Spawning in *E. analoga* occurs from spring to late summer (MacGinitie 1938), which was detected as a pulse in medium and large crabs in March 2016 (Figure 18).

Estimated biomass of *E. analoga* reflected the abundance of various size classes present across the duration of the study. Estimated biomass and relative abundances were greatest at Gold Bluffs and lowest at South Samoa Dunes (Figure 20). Peak *E. analoga* biomass occurred in March 2016 during an increase in abundance of medium and large-sized crabs, presumably during a spawning event (Figure 21). A lesser peak in biomass, despite the greatest abundance of crabs present, occurred in August and September 2016, due to the arrival of small recruits onto northern California beaches (Figure 21).

Future Monitoring

Comprehensive surveys of sandy beaches can be informative regarding ecosystem condition, however, methods can be labor and time intensive. Instead, focusing on a select few indicator species, that only require simple tools to measure, can be invaluable to future monitoring efforts. In the north coast MPA region, *E. analoga* and *A. rhodoterus* were observed at every site and only required simple methods to measure. *Amphistichus rhodoterus* are easily sampled with catch and release fishing methods, and when studied with these simple methods, can provide valuable information on their population status. Relative abundances across sites indicated that *A. rhodoterus* populations are relatively similar along north coast sandy beaches at this time. Coupled with the fact that northern California populations may show relatively limited movements, these results make *A. rhodoterus* a good candidate for long-term monitoring.

Emerita analoga populations serve as important prey sources for birds and surf zone fishes, making them a valuable indicator of resource availability for sandy beach predators. However, variability in population abundance throughout the span of a year should be considered when identifying the best time to sample in the northern California region. Based on our results, sampling should occur in late spring through early summer to measure mature populations of *E. analoga*, with additional sampling in late summer through early fall to characterize recruitment. Continued sampling to better understand seasonal and interannual variation will better inform a long-term monitoring and management strategy.

Appropriate reference site selection is crucial in future MPA monitoring efforts. It is important to ensure that reference sites reflect the ecological conditions of recently-established MPAs so that any sampling that cannot be conducted in MPAs (e.g. diet analyses which require destructive sampling) may be conducted within reference sites with the results inferred to MPAs. Multiple indices of *A. rhodoterus* and *E. analoga* population characteristics within MPAs were comparable to their associated reference sites within the north coast region. These similarities suggest our reference sites were appropriate and may be used to assess any future change post-MPA establishment.

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CHAPTER 2 ABSTRACT

TROPHIC INTERACTIONS BETWEEN PACIFIC MOLE CRABS AND REDTAIL SURFPERCH ON NORTHERN CALIFORNIA SANDY BEACHES

Michelle Succow

Amphistichus rhodoterus and *Emerita analoga* are residents of sandy beaches in northern California. As inhabitants of the swash zone, *E. analoga* is known to be preyed upon by surf zone fishes. However, the importance of this species to the diet of *A. rhodoterus* has not been previously examined. We studied the diet of *A. rhodoterus*, and the importance of *E. analoga* to the diet of *A. rhodoterus* across the northern California bioregion. In addition, the mean size of *E. analoga* consumed by variously-sized *A. rhodoterus* was examined. Lastly, the sizes of *E. analoga* in the stomachs of *A. rhodoterus* was compared to the sizes of *E. analoga* available in the swash zone to determine if *A. rhodoterus* show size-based feeding selectivity. The diet of *A. rhodoterus* was opportunistic and *E. analoga* was the most important prey resource for *A. rhodoterus* at all sites examined. Over 80% of *A. rhodoterus* specimens had *E. analoga* in their stomachs. On average, smaller-sized *A. rhodoterus* fed on smaller-sized *E. analoga* relative to medium and large-sized fish. Large-sized *E. analoga* were selectively fed on by medium and large-sized *A. rhodoterus*, despite their relative infrequency in the northern California surf zone during the time of this study. The importance of *E. analoga*

to the diet of *A. rhodoterus* is an example of a trophic interaction that links sandy beach resources to fish populations in intertidal waters.

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INTRODUCTION

Ecosystems are interconnected through a variety of ecological processes, shaping the communities that reside within them. One such process is the trophic connectivity of populations via allochthonous inputs, or resource transfer across habitat boundaries. Allochthonous inputs take many forms (e.g. movement of prey species into a predator-occupied habitat) and have the potential to increase productivity in habitats that otherwise have low productivity (Polis et al. 1996). Allochthonous inputs leading to trophic connections between sandy beaches and adjacent coastal ecosystems have been previously documented. Subsidies of wrack (detached kelp, surfgrasses, and seagrasses that are deposited on the beach), arriving from nearby kelp forests, rocky intertidal areas, estuaries, and wetlands, provide essential food and cover for sandy beach invertebrates (e.g. Griffiths and Stenton-Dozey 1981, Lavoie 1985, Dugan et al. 2000, Dugan et al. 2003, Heck et al. 2008) that in turn serve as prey for surf zone fishes and birds (De Martini 1969, Bennett and Wydoski 1977, Bradley and Bradley 1993, Kirkman and Kendrick 1997, Takahashi et al. 1999, Dugan et al. 2003, Lercari et al. 2010).

One method of examining trophic connectivity is to investigate prey selection by a predator. Selection is the process in which an organism chooses to utilize a resource despite the resource's disproportionate availability (Manly et al. 2002); it is commonly assumed through optimal foraging theory that selected resources will best satisfy survival requirements. A resource is considered chosen when it is utilized by an organism in some manner, such as space that becomes occupied, or a prey item that becomes consumed.

Furthermore, a resource is considered available for selection only if it is accessible to the organism/predator at the time of utilization (Manly et al. 2002). In selectivity analyses, such as Ivlev's electivity index, utilized resources are compared to available resources to draw conclusions regarding resource selectivity.

Amphistichus rhodoterus (redtail surfperch) is an abundant surfperch in Northern California that feeds within sandy beach surf zones. The diet of *A. rhodoterus* has been previously described as diverse, including polychaetes, molluscs, isopods, amphipods, decapods, and other fishes (De Martini 1969, Bennett and Wydoski 1977, Miller et al. 1980), though there is disagreement on which prey sources are the most important. Furthermore, *A. rhodoterus* is known to feed on *Emerita analoga* (pacific mole crabs), though to what extent has not been determined. Despite the turbid environment in which they feed, *A. rhodoterus* are believed to depend on sight in their search for prey (Bennett and Wydoski 1977). Although prey species selection may be opportunistic, it is possible that *A. rhodoterus* use sight to selectively feed on specific sizes of prey. Whether *A. rhodoterus* selects for particular sizes of *E. analoga* has not been previously examined.

Our gut analysis examined the prevalence and sizes of *E. analoga* in the diet of *A. rhodoterus*. Dip net field surveys of *E. analoga,* assessing sizes available in the field, were compared to sizes of *E. analoga* in the stomachs of *A. rhodoterus* to determine if *A. rhodoterus* show size-based feeding selectivity for *E. analoga*. This study sought to gain a better understanding of the trophic links that connect *A. rhodoterus* and *E. analoga,* thereby increasing the understanding of connectivity between coastal ocean and beach habitats which drives community structure in northern California.

METHODS

Amphistichus rhodoterus Gut Analysis

Gut Analysis

Dissections were performed on sacrificed *A. rhodoterus* collected from reference sites (Kellogg Beach, Gold Bluffs, Mad River, and South Samoa Dunes; see *Description of Study Sites* in Chapter 1) during both 2015 and 2016 sampling seasons. All fish were dissected within 24 hours of capture to ensure *A. rhodoterus* specimens and gut contents did not begin to degrade. Before dissection, the weight, standard body length, and sex of each fish were recorded. Standard length measurements of *A. rhodoterus* were used to place individuals into size length classes (small <170 mm; 170 mm <medium ≤220 mm; large >220 mm). Each gut was severed posteriorly at the anus and anteriorly at the esophagus where it crosses the transverse septum.

Dietary Analysis

The stomach contents were analyzed by Department of Fisheries Biology researchers, at the Telonicher Marine Laboratory. The embiotocid dietary analysis is part of long-term dietary studies involving marine and freshwater fishes of the Pacific Northwest. Gut contents were analyzed and identified to the lowest possible taxon. All specimens classified were enumerated, with every individual prey counted. Blotted wet weights were taken for each taxonomic grouping, with weights less than 0.0001 g recorded as 0.0001 g. No gut contents were excluded from the dietary analysis based on quantity.

Selectivity Analysis

Any *E. analoga* found in the gut were set aside to determine the sizes of individual *E. analoga* consumed. Carapace lengths of consumed *E. analoga* could not be directly measured because of their condition after being eaten by *A. rhodoterus.* Instead, consumed *E. analoga* individuals were identified and enumerated by measuring (to the nearest hundredth of a mm) each *E. analoga* telson found within the gut contents. The lengths of each telson obtained from the guts were used to estimate each carapace length using the linear regression line calculated from dip net surveys (see *Emerita analoga* Dip Net Surveys, below).

Data Analyses

The following calculations were made for each prey group classification. These measures were then used to calculate the Index of Relative Importance (IRI) for each prey type found within the stomachs of *A. rhodoterus* from each site:

- Percent Number = [number of items of a given classification/total number of items] *100
- Percent Weight = [weight of items of a given classification/total weight of items] *100
- Percent Frequency of Occurrence = [number of stomachs containing items of a particular classification/total number of stomachs] *100
- IRI= [percent number + percent weight] * [percent frequency of occurrence]

Analysis of Variance (ANOVA), followed by a Tukeys post-hoc test, compared sizes of *E. analoga* consumed by different size classes of *A. rhodoterus*.

Emerita analoga Dip Net Surveys

<u>Survey Design</u>

To estimate the availability of *E. analoga* as a prey source for *A. rhodoterus*, dip net surveys within the swash zone were completed on the same dates as *A. rhodoterus* population surveys (see Chapter 1: *Amphistichus rhodoterus* Population Surveys). It was assumed that all *E. analoga* collected in the dip net are representative of what is available to *A. rhodoterus* while feeding in the surf zone. For each sampling area where *A. rhodoterus* abundance was estimated using hook-and-line fishing methods, three randomly-spaced transects were sampled within the swash zone, perpendicular to the beach face. Transects began five meters beyond the lower end of the swash zone (surf conditions permitting) and were sampled by dipping a 40 cm by 22 cm D-frame dip net (3 mm mesh) for 30 seconds while walking back towards the beach until the high point of the swash zone was reached. All *E. analoga* obtained were retained and placed in Ziploc bags, chilled on ice, and processed at the Telonicher Marine Lab in Trinidad, California.

<u>Data Analyses.</u>

A linear regression analysis was performed for all mole crabs collected in the surf zone, to examine the relationship between the carapace and telson lengths of individual crabs. The resulting linear regression was used to estimate the sizes of *E. analoga* consumed by *A. rhodoterus* (see *Amphistichus rhodoterus* Gut Analysis, above) by calculating the total carapace length of an individual *E. analoga* associated with a given telson length. The mean size of *E. analoga* at each sampling site was compared to the size of *E. analoga* found in the gut contents of dissected *A. rhodoterus*, using Ivlev's electivity index. This index values determine if *A. rhodoterus* selectively fed on *E. analoga* based on size. Values of this index range from negative one to positive one, where positive one indicates full selection, and negative one indicates complete avoidance, while zero values indicate that prey are chosen at the same proportion as are available in the environment (e.g. no selectivity).

RESULTS

A total of 252 *A. rhodoterus* were dissected and gut contents examined from Kellogg Beach, Gold Bluffs, Mad River, and South Samoa Dunes from both 2015 and 2016. The diet of *A.* rhodoterus was diverse and included many taxonomic groups, including decapods, polychaetes, amphipods, isopods, cirripeds, and echinoderms (Tables 1-4). The most important prey source for all sites, however, was *E. analoga*. After *E. analoga*, the next most important prey items varied by site. In the northern sites, Kellogg Beach and Gold Bluffs, the second and third most important prey items were fish eggs and shrimp, respectively (Tables 1 and 2). The second and third most important prey items differed at the southern sites. At Mad River, the second and third most important prey items were invertebrate eggs and amphipods, respectively (Table 3). At South Samoa Dunes, the second and third most important prey items were worms and shrimp, respectively (Table 4). *Emerita analoga* was found in 82% of all guts sampled (Table 5). A smaller percentage of fish from northern sites (Kellogg Beach and Gold Bluffs) had *E. analoga* in their guts than fish from the more southern sites (Mad River and South Samoa Dunes) (Table 5). Furthermore, a greater percentage of small *A. rhodoterus* consumed *E. analoga* relative to medium or large *A. rhodoterus* (Table 6). Male and Female fish did not differ in the percentage that consumed *E. analoga* (Table 7).

Table 3. Percent number, percent weight, and index of relative importance (IRI) of prey items consumed by 46 *A. rhodoterus*, at Kellogg Beach, sampled within the northern California MPA bioregion, 2015-2016. Data came from dietary study.

Prey Item	**Percent Number**	**Percent Weight**	**IRI**
Fish egg	83.23	2.55	2424.19
E. analoga	14.31	65.87	5926.61
Shrimp	0.65	13.54	493.51
Unidentified	0.39	1.69	13.55
Worm	0.36	0.53	11.51
Amphipod	0.36	0.02	3.26
Crus. exoskeleton	0.23	2.52	41.76
Echinoderm	0.19	6.42	86.22
Fish	0.13	6.00	53.32
Microcrustacea	0.06	0.00	0.29
Crab	0.03	0.77	1.75
Acorn barnacle	0.03	0.09	0.26
Isopod	0.03	0.01	0.08

Table 4. Percent number, percent weight, and index of relative importance (IRI) of prey items consumed by 55 *A. rhodoterus*, at Gold Bluffs, sampled within the northern California MPA bioregion, 2015-2016. Data came from dietary study.

Prey Item	**Percent Number**	**Percent Weight**	**IRI**
Fish Egg	67.60	0.56	867.56
E. analoga	20.58	60.73	6357.15
Stalked barnacle	3.15	1.09	46.18
Acorn barnacle	2.64	2.01	25.35
Shrimp	2.38	12.09	473.49
Amphipod	1.19	0.01	10.96
Fish	0.94	21.63	328.22
Crus. exoskeleton	0.60	0.47	11.62
Crab	0.26	0.99	6.78
Worm	0.26	0.20	2.51
Unidentified	0.26	0.20	2.49
Mussel	0.09	0.01	0.17
Nematode	0.09	0.00	0.16

Table 5. Percent number, percent weight, and index of relative importance (IRI) of prey items consumed by 88 *A. rhodoterus*, at Mad River, sampled within the northern California MPA bioregion, 2015-2016. Data came from dietary study.

Prey Item	**Percent Number**	**Percent Weight**	**IRI**
E. analoga	60.65	91.89	14213.67
Invertebrate egg	25.13	0.69	88.02
Amphipod	7.83	0.10	45.06
Worm	2.07	0.58	15.05
Crus. exoskeleton	2.07	0.57	44.88
Shrimp	0.75	2.84	32.70
Unidentified	0.38	0.51	5.03
Salp	0.31	0.89	2.74
Crab	0.25	1.64	8.61
Isopod	0.25	0.01	1.19
Echinoderm	0.19	0.27	1.05
Microcrustacea	0.06	0.00	0.07
Nematode	0.06	0.00	0.07

Table 6. Percent number, percent weight, and index of relative importance (IRI) of prey items consumed by 63 *A. rhodoterus*, at South Samoa Dunes, sampled within the northern California MPA bioregion, 2015-2016. Data came from dietary study.

Prey Item	**Percent Number**	**Percent Weight**	**IRI**
E. analoga	74.14	91.04	15993.69
Worm	19.75	2.29	384.74
Shrimp	1.78	3.63	94.56
Amphipod	1.15	0.05	11.35
Fish	1.02	1.35	18.77
Crus. exoskeleton	0.76	1.00	14.01
Acorn barnacle	0.38	0.03	0.66
Isopod	0.38	0.02	1.28
Echinoderm	0.13	0.23	0.57
Salp	0.13	0.17	0.47
Crab	0.13	0.09	0.35
Unidentified	0.13	0.07	0.31
Mollusc	0.13	0.04	0.26

Table 7. Percent of *A. rhodoterus* examined with *E. analoga* found in their gut across sites sampled within the northern California MPA bioregion, 2015-2016. Data came from dietary study.

Site Name	**No. sampled**	**% with *E. analoga* in gut**
Kellogg Beach	51	67
Gold Bluffs	61	70
Mad River	90	91
South Samoa Dunes	66	92
Total	268	82

Table 8. Percent of small, medium, and large-sized *A. rhodoterus* examined with *E. analoga* found in their guts, pooled across sites sampled within the northern California MPA bioregion, 2015-2016. Data came from dietary study.

Fish Size Class	**No. sampled**	**% with *E. analoga* in gut**
Small	45	96
Medium	137	78
Large	86	81

Table 9. Percent of male and female *A. rhodoterus* examined with *E. analoga* found in their gut, pooled across sites sampled within the northern California MPA bioregion, 2015-2016. Data came from dietary study.

Fish Sex	**No. sampled**	**% with *E. analoga* in gut**
Male	136	82
Female	132	83

Regression analysis indicated that telson length could be used to estimate carapace length of consumed *E. analoga* (Figure 1). Sizes of consumed *E. analoga* ranged from 2.1 to 25.68 mm, estimated carapace length; the most abundant size consumed was around 10 to 12 mm carapace length (Figure 2). Small-sized (<170 mm) *A. rhodoterus* consumed smaller *E. analoga* when compared to both medium (>170 mm, < 220 mm) and large (> 220 mm) fish, while medium and large fish did not differ in the sizes of crabs consumed (Figure 3) [$F_{2,174}$=6.01, P<0.01].

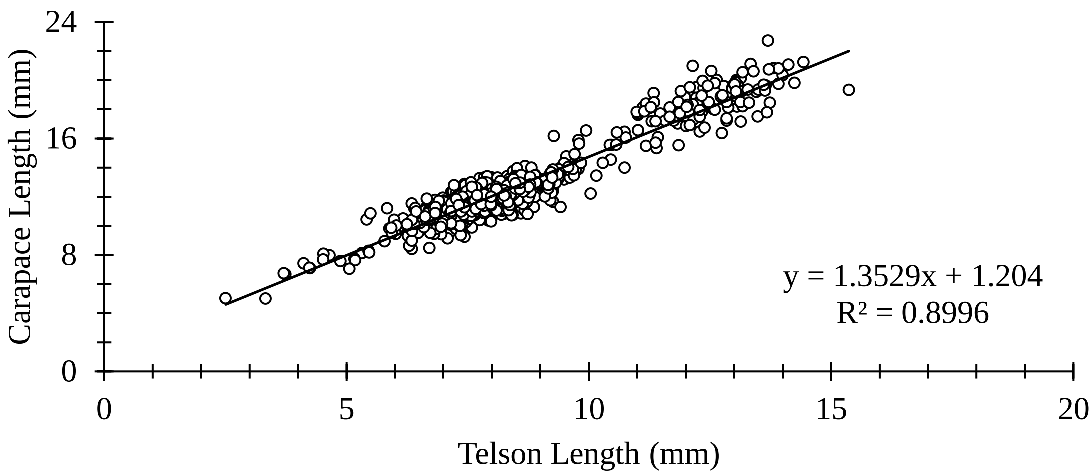

Figure 1. Regression analysis comparing carapace and telson lengths of *E. analoga* sampled across reference sites (Gold Bluffs, Mad River, South Samoa Dunes) within the northern California MPA bioregion, 2015-2016.

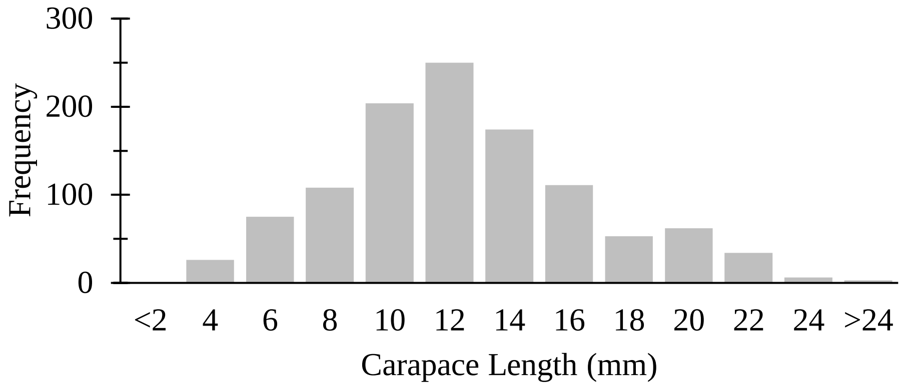

Figure 2. Frequency of occurrence of *E. analoga* carapace lengths (mm) consumed by *A. rhodoterus*, sampled within the northern California MPA bioregion, 2015-2016.

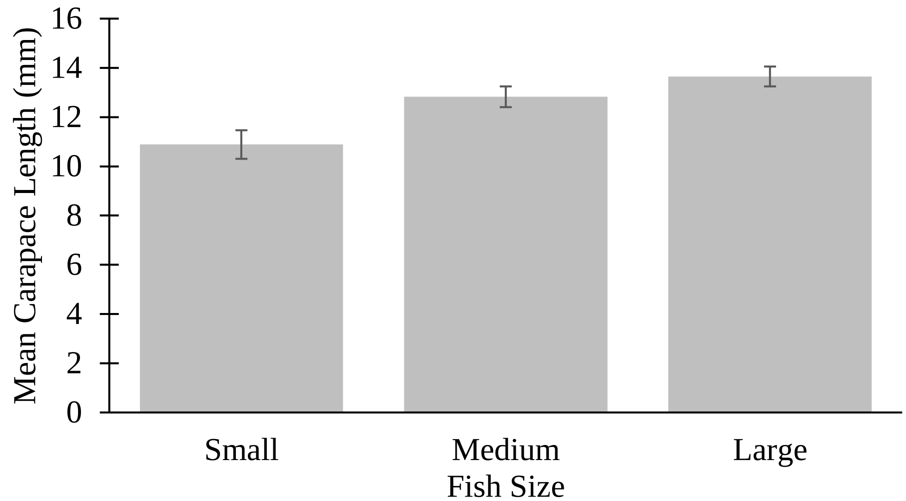

Figure 3. Mean carapace length (mm) of *E. analoga* consumed by small, medium, and large *A. rhodoterus* sampled within the northern California MPA bioregion, 2015-2016. All data are averages across sites and years (+SE). Small-sized *A. rhodoterus* consumed smaller crabs when compared to both medium and large fish [P<0.01].

To determine if *A. rhodoterus* were selectively feeding on a particular size class of *E. analoga*, sizes of *E. analoga* consumed were compared to sizes available within the swash zone using a Ivlev's electivity index. Because the actual feeding locations of these fish were unknown, and sampling areas were similarly populated by *E. analoga*, we pooled the gut content data from all sites within each month for the selectivity analysis. *Amphistichus rhodoterus* that fed on *E. analoga* showed strong selectivity for particular sizes of mole crabs (values above 0.5) during certain times of the year (Figure 4). Medium and large *A. rhodoterus* were selective for small-sized *E. analoga* during May 2015 and March through April 2016, but were otherwise not selecting for small crabs throughout the study (Figure 4A). Small fish selected for small *E. analoga* as prey during July 2015 (Figure 4A), when small crabs were most abundant in the environment (Figure 4D). None of the three different size classes of *A. rhodoterus* selectively fed on medium-sized *E. analoga* over the duration of the study (Figure 4B), even though medium-sized crabs peaked in abundance from August to September of 2015 and March of 2016 (Figure 4D). Medium and large *A. rhodoterus* selectively fed on large-sized crabs for almost the entire duration of the study (Figure 4C), despite their low availability (Figure 4D). Furthermore, small *A. rhodoterus* did not avoid feeding on large-sized *E. analoga* during the duration of the study (figure 4C).

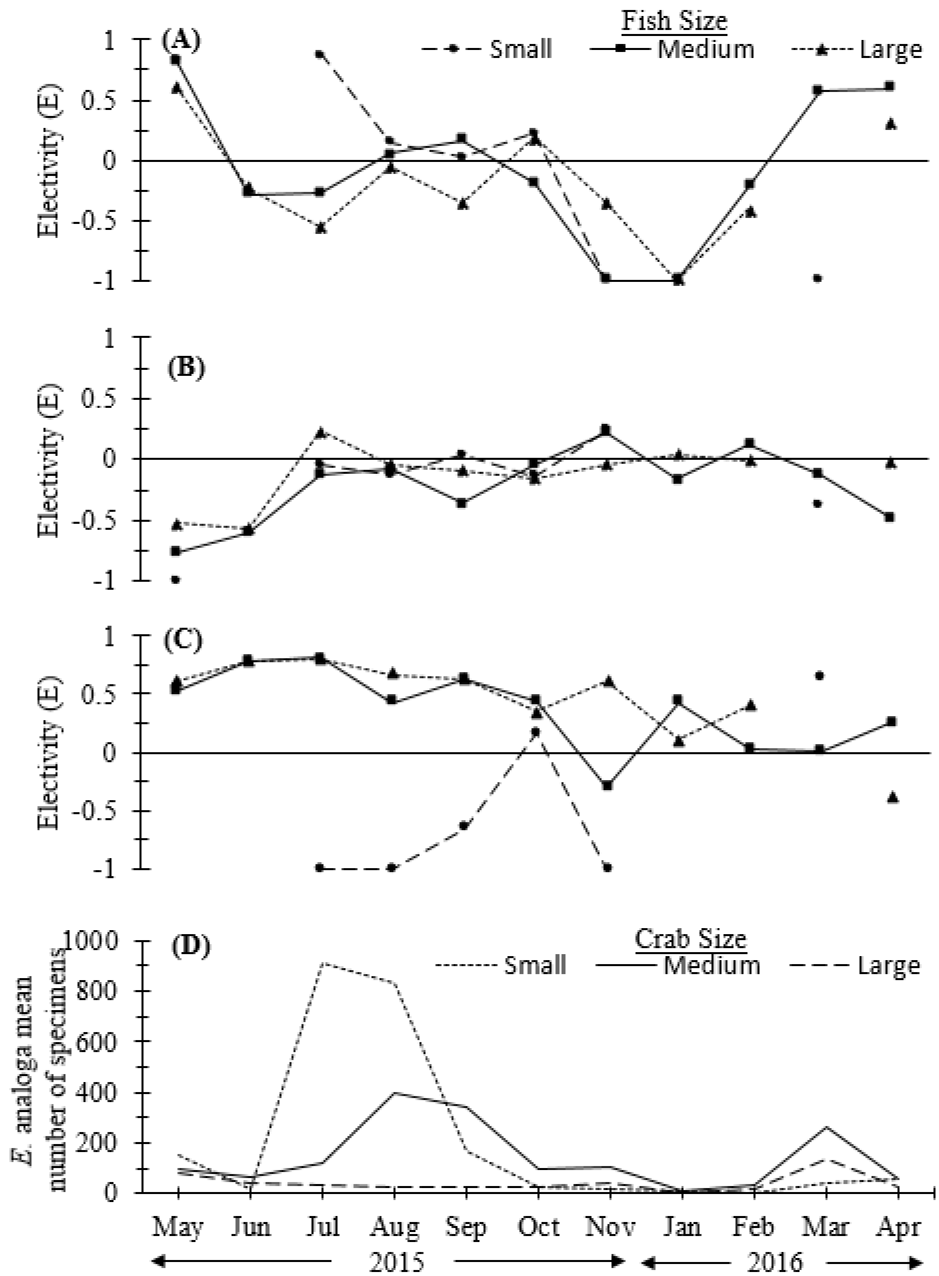

Figure 4. Selectivity (E) by different sizes of *A. rhodoterus* upon A) small, B) medium, and C) large-sized *E. analoga* compared to D) mean number of *E. analoga* sampled across all sites within the northern California MPA bioregion, 2015-2016.

DISCUSSION

The diet of *A. rhodoterus* contained a variety of prey species, originating from both sandy beach and rocky intertidal zones. In the northern sites, Kellogg Beach and Gold Bluffs, where rocky intertidal zones are interspersed throughout the stretches of sandy beach found there, the diet of *A. rhodoterus* contained species from both rocky intertidal (barnacles and mussels) and sandy beach habitats (amphipods and shrimp) (Tables 1 and 2). In contrast, fish sampled from an uninterrupted sandy beach (i.e. Mad River), preyed predominantly on sandy beach organisms (Table 3). Guts from the most southern site, South Samoa Dunes, consisted of prey from both rocky intertidal and sandy shores (Table 3). This may be due to the proximity of this site to the rocky jetties at the entrance of Humboldt Bay. Overall, the diversity of prey consumed suggests that *A. rhodoterus* are opportunistic feeders.

Previous feeding studies on *A. rhodoterus* generally agree with our results. However, there is some disagreement on which prey items may be most important. De Martini (1969) reported that *A. rhodoterus* mainly fed on molluscs, small fish and amphipods, with limited feeding on shrimp and *E. analoga*. These results, however, were from a limited sample of 11 specimens, and did not specify how prey items were ranked in importance. Bennett and Wydoski (1977) examined the stomachs of 335 *A. rhodoterus*. They reported the diets to consist of crustaceans, fishes, molluscs, and polychaetes, in decreasing order of importance, and failed to separate out *E. analoga* from other decapods. The results from this study may be misleading because importance of prey was ranked solely on frequency of occurrence, which does not accurately portray relative importance (e.g. a few large prey items are found less important than many small prey items due to low numbers). Our IRI results indicate that *E. analoga* were the most important prey resource over sandy beaches sampled within the northern California bioregion (Tables 1-4). More than 80% of *A. rhodoterus* had *E. analoga* in their guts (Table 5). This result appears especially true for small-sized (<170 mm standard length) *A. rhodoterus*, in which 96% of the fish contained *E. analoga* in their diet (Table 6). The importance of *E. analoga* in the diet of *A. rhodoterus* may be a function of its generalist foraging behavior, as *E. analoga* is one of the most common prey available in northern California sandy beaches.

Sizes of *E. analoga* were selected by *A. rhodoterus* at proportions different from their availability in the habitat. Small-sized *E. analoga* were rarely selected for, except during early spring to late summer by small-sized fish, when large numbers of recruits were settling on northern California beaches (Figure 4). *Amphistichus rhodoterus* never selected for medium crabs, even when their availability increased after recruitment and spawning events (Figure 4). In contrast, large-sized *E. analoga* were highly selected for by medium and large *A. rhodoterus* throughout most of the sampling period, despite their low availability (Figure 4). The fact that medium and large-sized *A. rhodoterus* preyed on larger sizes of *E. analoga* is consistent with optimal foraging theory, where predators select for the largest and most profitable prey.

To conclude whether *A. rhodoterus* were actively selecting specific sizes of *E. analoga*, the detectability of prey and the effect of turbidity must be considered.

Detectability of prey increases with increasing prey size (Werner and Hall 1974), impacting the rate at which fish encounter and react to prey of different sizes. Because of this, small-sized prey are generally not detected as frequently as large-sized prey. In highly turbid waters, however, the proportion of prey sizes, perceived by fish, has been shown to be equal to the true distribution available for consumption (Vinyard and O'Brien 1976, Gardner 1981). As inhabitants of the highly turbid surf zone, the perception of *E. analoga* by *A. rhodoterus* should be equal to their available distribution. However, *A. rhodoterus* demonstrated size-based selectivity, where medium and large-sized fish selectively fed on large-sized *E. analoga* despite their low abundance.

In conclusion, *A. rhodoterus* in the northern California bioregion, are opportunistic feeders reflecting the beach near where they were caught; fish caught at beaches near rocky intertidal areas had rocky intertidal invertebrates in their guts as well as *E. analoga*. Overall, *E. analoga* serve as the most important prey resource for *A. rhodoterus* in the northern California MPA bioregion. Additionally, medium and large *A. rhodoterus* selectively feed on larger *E. analoga,* although they occur in fewer numbers than much smaller crabs.

The results from this study can be used to better understand the important trophic link between *A. rhodoterus* and *E. analoga* within northern California. Furthermore, our study has management implications for *A. rhodoterus* populations in northern California, on which important commercial and recreational fisheries exist. As the most important prey resource for *A. rhodoterus,* fluctuations in the abundance and size distributions of *E. analoga* populations have the potential to impact *A. rhodoterus* populations. Abundance and size structure of *E. analoga* populations within northern California sandy beaches should continue to be monitored to predict potential impacts upon *A. rhodoterus* populations.

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