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Functional Ecology and metabolics of the California moray (Gymnothorax mordax)

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FUNCTIONAL ECOLOGY AND METABOLICS OF THE CALIFORNIA MORAY (*Gymnothorax mordax*)

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in

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by

Benjamin A. Higgins

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The Dissertation of Benjamin A. Higgins is approved:

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Abstract

FUNCTIONAL ECOLOGY AND METABOLICS OF THE CALIFORNIA MORAY (*GYMNOTHORAX MORDAX*)

Benjamin A. Higgins

Consistent pressures from overfishing and extirpation have led to the study and conservation of many of the apex consumers within kelp forest ecosystems. Among kelp forests, those of Southern California have been described as the most diverse in the world. Yet, despite the large body of data on species interactions within these ecosystems, information on the ecology for many of the top predators is lacking. This paucity of information may be because of predator declines (e.g., giant sea bass) or simply the elusiveness of some species. One example of a large elusive predator about which little is known is the California moray (*Gymnothorax mordax*). The combination of a cryptic lifestyle and lack of a commercial fishery has enabled morays, in general, to have remained virtually undetected in standard species surveys. Moreover, basic biological information on morays is scarce. I use field methods, laboratory measurements, and metabolic experiments, to investigate the functional ecology of the California moray to answer questions pertaining to its dispersal, habitat preference, diet, and physiology. Data from my studies reveal that California moray dispersal is primarily driven by changes in oceanic currents caused by El Niño events. Larvae then settle to shallow Santa Catalina Island habitats consisting mainly of boulder and cobble substrates in densities ≤100x greater than previously estimated.

The California moray is a piscivorous predator, consuming kelp bass, but also preying upon a wide range of fish and invertebrate species. Lastly, I discovered that the California moray has a relatively low standard metabolic rate (SMR) compared to non-anguilliform fish taxa of similar mass and that the SMRs of larger individuals do not respond to chronic changes in temperature as strongly as smaller individuals. The California moray has a subcutaneous adipose layer that increases in thickness as morays increase in mass. The adipose layer may be a physiological mechanism underlying the lower response in SMR of larger individuals at decreasing temperatures. Cumulatively, the results of this research suggest that the California moray is an apex consumer, with the potential to influence Southern California kelp forest community structure similar to patterns observed of morays in tropical communities.

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I would like to extend my deepest gratitude to my mentor and friend, Dr. Rita S. Mehta, for her incredible support, guidance, and knowledge throughout my six years at the University of California, Santa Cruz. Rita has been an incredible steward of both my academic and personal goals, providing the space and flexibility for a creative approach to science, as well as the firm boundaries for keeping me on track. I would also like to thank my committee members Dr. Mark Carr, Dr. Terrie Williams, Dr. Jim Estes, and Dr. Jan Freiwald. The input and support I received during the meetings and emails I shared with them were some of the highlights of my time in the program. Having such amazing minds all in the same room at the same time focusing on my work was a genuinely special feeling, and I am both humbled and extremely grateful for having them on my dissertation committee.

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Statement of Contribution

The text of this dissertation includes reprints of the following previously published material:

Chapter 1:
Higgins, B. A., Pearson, D. and Mehta, R. S. 2017. El Niño episodes coincide with California moray Gymnothorax mordax settlement around Santa Catalina Island, California. Journal of Fish Biology 90, 1570-1583.

For this chapter, I was responsible for the majority of laboratory work, data analysis, manuscript preparation, and submission. The second co-author listed in this publication, D. Pearson, assisted in otolith ageing techniques, provided age data validation, and revisions to the manuscript prior to submission. The additional co-author listed in this publication, Rita Mehta, directed and supervised the research which forms the basis for the dissertation. A signed statement of permission from D. Pearson is available in the Appendix (section A.1).

Chapter 2:
Higgins, B. A. and Mehta, R. S. 2018. Distribution and habitat associations of the California moray (Gymnothorax mordax) within Two Harbors, Santa Catalina Island, California. Environmental Biology of Fishes 101, 95-108.

In Higgins and Mehta (2018), I was responsible for the majority of the data collection, data analysis, manuscript preparation and submission. The co-author listed in this publication, Rita Mehta, directed and supervised the research which forms the basis for the dissertation.

Introduction

Kelp forests are structurally complex, highly productive and incredibly diverse ecosystems (Mann, 1973; Steneck et al., 2002; Christie, 2003). Off the coast of California, the stability of these ecosystems rely primarily on the health and abundance of predator populations (Estes and Palmisano, 1974; Watson and Estes, 2011). However, the increased diversity and functional redundancies among apex predators in Southern California kelp forest fish communities are hypothesized to have kept these systems from urchin overgrazing and resultant deforestation (Steneck et al., 2002). Thus, studying the functional roles of the apex predators within the Southern California kelp forest ecosystems is important to understanding community structure and species interactions. However, the functional roles of certain apex predators remain unknown (Allen et al., 2006; Carr and Reed, 2016).

The waters off the coast of California are oceanographically complex and generally recognized to support an impressive diversity of species (Horn and Allen, 1978; Steneck et al., 2002). Biogeographical boundaries along the California shore have been shown to guide species distributions, as they influence both oceanic currents and temperatures (Horn and Allen, 1978; Dawson et al., 2006). One such boundary is Pt. Conception, a headland located in southwestern Santa Barbara County (roughly 34.4^{o} N, 120.5^{o}W) along the California coast. Studies have shown that Pt. Conception limits gene flow between northern and central marine populations (Chabot et al., 2015) and has significant effects on species distributions (Horn and Allen, 1978; Allen et al., 2006). Pt. Conception also serves as the northern boundary of the Southern California Bight (SCB), which extends south to San Diego (Hickey, 1979; Shanks and Eckert, 2005). Within the SCB, the faunal communities are susceptible to intense, yet intermittent pulses of recruits, some of which have been found to be solely driven by large-scale oceanic events, such as El Niño. For example, the California sheephead (*Semicossyphus pulcher*) is only able to settle to northern edges of its range (northern Channel Islands) during El Niño events, and, during these years, no recruits settle in the southern reaches of its range (Cowen, 1985). Furthermore, El Niño events allow certain fish species (e.g., spotted sand bass; *Paralabrax maculatofasciatus*) to reach locations that would otherwise not be accessible (Allen et al., 1995). Thus, the varying temperatures and dynamic currents to the north and south of Pt. Conception have altered community structures (Allen et al., 2006). For example, kelp forest communities to the north of Pt. Conception lack many species that are considered "common" in similar Southern California habitat (Larson et al., 1984; Carr and Reed, 2016). In fact, some of these species such as California sheephead (*Semicosyphus pulcher*), swell sharks (*Cephaloscyllim ventriosum*), California hornshark (*Heterodontus francisci*), white seabass (*Atractoscion nobilis*), and giant sea bass (*Stereolepis gigas*) are large, carnivorous fishes that have been described as important predators within the system (Graham, 2004; Allen et al., 2006; Hamilton and Caselle, 2014).

Despite the large body of literature on the life history and ecology of the icthyofauna found within the coastal waters of Southern California (Allen et al., 2006), data on the more sessile and cryptic fishes within the Southern California kelp forest ecosystem are lacking (Willis and Anderson 2003; Graham, 2004; Sandoval, 2005). Moreover, it has been shown that the cryptic vertebrate species have a disproportionate influence on kelp forest community structure due to their highly underestimated densities (Allen et al., 1992). One large elusive predator about which little is known is the California moray eel (*Gymnothorax mordax*). The limited information that exists for *G. mordax* suggests that, like *S. pulcher,* the northern limit of its range is also determined by Pt. Conception, and extends southward to Santa Maria Bay in Baja California (Fitch and Lavenberg, 1971). This predatory species has been hypothesized to reside in shallow waters and can be found in large densities around offshore islands within the SCB, such as Santa Catalina Island (Fitch and Lavenberg, 1971; McCleneghan, 1973). Additional intriguing hypotheses were proposed during the early 1970s, suggesting that waters are too cold, or not warm long enough to permit complete gametogenesis (McCleneghan, 1973) and that propagules are carried up from the southern reaches of their range during oceanic flow reversals caused by large scale climatic events (e.g., El Niño). Therefore, the California moray eel population residing around Santa Catalina Island may be a sink population, persisting only as much as immigration to the island by propagules is possible. The combination of a cryptic lifestyle and lack of a commercial fishery has enabled morays, in general, to have remained virtually undetected in standard species surveys (Gilbert et al., 2005), and excluded the species as the focus of any scientific studies until the past few years (see Page et al., 2013). In this dissertation, I utilize a combination of field and laboratory - based methodologies to provide novel insights into the functional role of this previously unstudied predatory fish.

My first chapter investigates how California moray settlement varies in response to El Niño events in Two Harbors, Santa Catalina Island, a location towards the northern edge of the moray's range. With the guidance of Don Pearson at the Southwest Fisheries Science Center, I conduct an ageing study to determine the relationship between moray standard length and otolith annuli. Using these ages, I back-calculated settlement dates and cross-referenced them with The National Weather Service's Oceanic Niño Index (ONI) to determine the relationship between El Niño events and the transport of moray larvae to Santa Catalina Island.

In my second chapter, I examine the density and abundance patterns of the juveniles and adults of California moray. I collected moray eels and conducted habitat surveys in various coves in Two Harbors, Santa Catalina Island. In this chapter I focus on identifying habitat associations by quantifying eel density across depths and the geomorphological features of the rocky reef. Traps were deployed in six different coves and a series of underwater transects co-located with each trap were used to correlate catch and demographic variables with substrate type and depth. Using these data, I ran principal component analyses to determine how well the measured habitat variables explain spatial variation in moray densities in Two Harbors.

My third chapter utilized a multi-year dataset to characterize the diet of the California moray. Using a linier selectivity index (Strauss, 1979) moray stomach content data were cross-referenced with prey availability and abundance counts collected by Reef Check California to understand the predatory habits of G. *mordax*.

Size data were also collected on consumed prey items to determine the relationship between prey size and moray size with ontogenesis. *In vivo* bite force analyses were also measured to quantify the feeding performance of morays with ontogenesis.

In my fourth chapter, I employ a physiological approach to better understand rates of predation (i.e. frequency of predation) for the California moray. In this chapter, I use closed-system respirometry and phase fluorometry to measure mass specific metabolic rates of an ontogenetic series of morays, tested at typical summer and winter temperatures. This final chapter sets the groundwork for future studies examining the metabolic ecology of the moray population in Two Harbors, Santa Catalina Island.

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Chapter 1

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El Niño episodes coincide with California moray *Gymnothorax mordax* settlement around Santa Catalina Island, California

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The hypothesis that El Niño events influence the settlement patterns of the California moray *Gymnothorax mordax* is tested. The pelagic larval duration (PLD) of larval *G. mordax* is unknown, but studies on leptocephalus of related species suggest that larvae are long-lived, up to 2 years. *Gymnothorax mordax*, an elusive predatory species and the only muraenid off the coast of California, is considered abundant in the waters around Catalina Island. Thirty-three individuals were collected from Two Harbors, Catalina Island, and otoliths were taken to provide estimates of their age. Settlement year for each individual was backcalculated using estimated age from otolith measurements. These ages were then cross referenced with the Oceanic Niño Index (ONI) developed by the National Oceanographic and Atmospheric Administration (NOAA) to correlate estimated age of settlement with known El Niño years. Of the 33 individuals collected, 30 settled at Catalina Island during El Niño years. The oldest individual in the data-set was 22 years old, placing *G. mordax* as one of the longer-lived predatory fishes in the system. The present study represents the first account of wild *G. mordax* ages and suggests that El Niño events have an important role in driving the settlement of recruits towards the northern edge of their range.

Key words: currents; Muraenidae; otolith; pelagic larval duration.

INTRODUCTION

Considerable effort has focused on identifying the factors that influence larval transport and dispersal throughout the fluid marine environment (Lubchenko *et al.*, 2003; Leis, 2006; Cowen & Sponaugle, 2009; Calò *et al.*, 2016). While some marine species can disperse during the juvenile and adult phases (*e.g.* whales, tunas and squid), most coastal marine fishes and invertebrates disperse during the larval stage of their life cycle, in which case the pelagic larval duration (PLD) often becomes an important variable in modelling or estimating dispersal ability (Victor & Wellington, 2000; Kinlin & Gaines, 2003; Shanks *et al.*, 2003; Palumbi, 2004; Iacchei *et al.*, 2016). Pelagic larval duration in fishes varies from 0 days in live bearers (*e.g.* Embiotocidae) to a few months in marine eels (Anguilliformes) (Lester & Ruttenberg, 2005; Leis *et al.*, 2013).

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A variety of factors affect the dispersal ability of larvae, such as larval behaviour and distribution (Leis, 1991), larval swimming speeds and orientation abilities (Stobutzki & Bellwood, 1994, 1997; Leis & Carson-Ewart, 1997). Thus, the more time propagules spend in the water column (*i.e.* increased PLD), the further they tend to be dispersed (Shanks *et al.*, 2003). Therefore, direction and speed of local currents can shape the range and connectivity of marine species (Shanks & Eckert, 2005; Pineda *et al.*, 2007; Cowen & Sponaugle, 2009).

Average current flow tends to be unidirectional for long periods of time along the coastline (Tchernia, 1980). This pattern holds true for the California Current (CC), which carries cold, nutrient-rich sub-Arctic waters throughout the Californian Channel Islands for the majority of the year (Shanks & Eckert, 2005). The CC roughly originates off the coast of southern British Columbia, driving waters south along the west coast of North America. Upon reaching Point Conception, this equatorial direction of water helps shape the Southern California Eddy (SCE) within the Southern California Bite (SCB), which extends from Point Conception to San Diego. The strength and direction of flow in the SCE, particularly in the Santa Barbara Channel, is heavily dependent upon the season and its associated predominant wind direction (Shanks & Eckert, 2005). Towards the southern edge of the SCE (roughly San Diego, CA), water is transported in a counter-clockwise direction along the California coast from south to north until it passes through the Santa Barbara Channel, where it merges again with the predominant CC and again flows south (Cowen, 1985). Therefore, depending on the time of year, there is potential for the northern Channel Islands to receive warmer waters, as well as any larval recruits drifting within.

In addition to seasonal variability in local current directionality, larval recruitment patterns are also affected by larger scale current variation caused by oceanic anomalies, such as episodic El Niño Southern Oscillation (ENSO) events (Davis, 2000). The distribution of white seabass *Atractoscion nobilis* (Ayres 1860) is largely influenced by the occurrences of El Niño episodes, as all age classes in southern California waters become more abundant during El Niño years (Dayton *et al.*, 1998). This increase in *A. nobilis* population is also thought to be partly attributable to the enhanced northward transport of larvae (Williams *et al.*, 2007). In Brazil's Patos Lagoon estuary, fish population dynamics and assemblages shifted dramatically during the 1997–1998 El Niño event, mainly attributed to drastic changes in salinity levels, current velocities and vertical mixing of the water column (Garcia *et al.*, 2003). This pattern was also detected at the same time along the coast of San Diego, California, where El Niño caused rapid and significant changes in fish assemblages of local tide pools (Davis, 2000). These abrupt changes in fish communities quickly returned to their pre-El Niño state, highlighting the intermittent nature of the effects. Furthermore, an extensive study examining the ichthyofauna at four different sites of San Diego Bay between 1994 and 1999 found that during the 1997–1998 El Niño, there was a noticeable change in fish assemblages. As the abundance of common schooling, planktivorous species declined, other species, typically those only associated with southern, more tropical waters became more common, five of which were encountered only during the El Niño event (Allen *et al.*, 2002). This episodic pulse of warm water propagated by El Niño is responsible for major recruitment events of California sheephead *Semicossyphus pulcher* (Ayres 1854), a reasonably large, long-lived (20–25 years) southern California kelp-forest predatory fish with a PLD of *c.* 2 months (Cowen, 1985). Major recruitment pulses to the northern portion of the *S. pulcher* range (northern Channel Islands) were also attributed to

El Niño events, as no recruits were observed in field sites towards the southern edge of their range during those years (Cowen, 1985).

The California moray eel *Gymnothorax mordax* (Ayres 1859), an elusive predatory species is considered abundant in the waters around Catalina Island (Fitch & Lavenberg, 1971; McCleneghan, 1973). *Gymnothorax mordax* is the only muraenid found off the coast of California. The elusive nature of this species and the lack of a regulated commercial fishery further underlie the paucity of biological and ecological information for *G. mordax*. The limited sources describing the natural history of *G. mordax* suggests that this shallow-water predatory fish is found in large densities around offshore islands reaching lengths of over 1·5 m and weighing as much as 6·5 kg (Fitch & Lavenberg, 1971). The distribution of *G. mordax* extends from just north of Santa Barbara to Santa Maria Bay in Baja California (Fitch & Lavenberg, 1971; Eschmeyer *et al.*, 1983). The literature describes the life expectancy of *G. mordax* to be upwards of 26 years, but this estimate is solely based on a single captive individual (Fitch & Lavenberg, 1971). Therefore, neither the maximum age of *G. mordax*, nor the age–size relationships are known for this species. Furthermore, no data currently exist on the recruitment patterns of *G. mordax*. As the age of a fish can provide some insight into recruitment time, the goal of the present study was to determine whether *G. mordax* recruitment events are associated with El Niño episodes, an evident pattern in the sympatric *S. pulcher*. The hypothesis that El Niño events are a major factor contributing to the dispersal and subsequent recruitment of *G. mordax* to the northern reaches of their range was initially proposed by McCleneghan (1973), but has yet to be tested. Additionally, the aim of the present study was to age a sample of individuals from a population of *G. mordax* from the western side of Santa Catalina Island, providing the first account of age structure for this southern California kelp-forest resident.

MATERIALS AND METHODS

SPECIMEN COLLECTION

Gymnothorax mordax were collected using custom-built, dual-chambered wire mesh traps (91 × 28 × 23) during the late summer months (July to September) of 2013–2015 at Two Harbors, Santa Catalina Island, CA (33° 26′ 45·4″ N; 118° 29′ 31·3″ W; Fig. S1, Supporting Information). Traps were set between 1800 and 1900 hours each night and baited with frozen anchovies *Engraulis mordax* Girard 1854, which were contained in plastic bottles. Trap retrieval occurred the following morning (0700–0800 hours), resulting in a soak time of *c.* 12 h. The majority of specimens analysed in this study were dead or injured upon trap retrieval due to aggressive encounters with other morays. Therefore, the data reported represents a random sampling of the *G. mordax* population within Two Harbors. Dead fish were placed in a −18° C freezer until moved to an ice-filled cooler to transport to the Long Marine Laboratory in Santa Cruz, California, where they were again stored in a −22° C freezer until otoliths were removed.

AGEING USING OTOLITHS

Prior to otolith removal, fish were thawed and measured (total length, L_T; body length, L_B; head length, $L_{H;}$ mass, M). The combination of a heavily fused skull and the lack of a true opercular opening leave standard otolith removal methods unsuitable for *G. mordax*. Therefore, otolith removal required severing the neurocranium from the first vertebrae. Lateral incisions were made along the foramen magnum, resulting in the removal of the ventral portion of the neurocranium containing both otoliths. Otoliths were then placed in a freshwater bath for 24 h to loosen the saccular vestibule. The left otolith of each specimen was cleaned and embedded in a 1 cm thick layer of clear resin (TAP Plastics; www.tapplastics.com). Embedded otoliths were thin-sectioned to a thickness of 500 μ on a Buehler Isomet low speed saw (www.buehler.com), equipped with parallel diamond-edged rotary blades. Thin-sections were polished with 1000 and 2000 grit wet–dry sandpaper, respectively. Polished otolith thin-sections were brushed with immersion oil and then mounted on a glass slide. Ageing took place on a compound microscope fixed with polarized transmitted light. Otoliths were aged independently by two readers to account for potential error in age estimates.

ANNULI VALIDATION

Identification of otolith presumed annuli were based on outer-edge growth relative to the month of capture (Andrews *et al.*, 2005). A marginal increment analysis (MIA) was conducted on the last four translucent bands (presumed summer growth regions). Images of these last four bands were captured using a camera fixed atop a compound microscope using polarized transmitted light. The widths of these last four bands were measured using ImageJ 1.48s analysis software (www.imagej.nih.gov).

EL NIÑO EVENTS

The age estimates of *G. mordax* were cross-referenced with historical ENSO episodes. The Oceanic Niño Index (ONI) developed by the National Oceanographic and Atmospheric Administration (NOAA) was used as a reference frame for determining periods of above and below normal sea surface temperatures (SST), using a threshold of $\pm 0{\cdot}5^\circ$ C. Periods where ONI values remained above $+0{\cdot}5$ for a minimum of five consecutive months were considered El Niño events, whereas those periods where ONI values dropped below $-0{\cdot}5$ for five consecutive months were considered La Niñas.

STATISTICAL ANALYSES

Scaling relationships between L_T and L_H were analysed using standardized major axis (SMA) regression in the R package SMAtr (www.r-project.org; Warton *et al.*, 2012). A slope value of 1 was interpreted as geometric similarity, thus providing the null hypothesis (*i.e.* a slope value of, or approaching 1 would indicate an isometric relationship).

An exact binomial test carried out in R was used to test the hypothesis that the probability of *G. mordax* settlement to Catalina Island was greater during El Niño events between 1990 and 2007 (*i.e.* 16 years).

An ANOVA was conducted in R on the mean widths of the four bands used in the MIA. The ANOVA was followed by a Tukey's honest significant difference (HSD) test to compare differences between otolith bands. Band width was $\log_{10}$-transformed to pass Levene's test for equal variance.

RESULTS

Thirty-three *G. mordax* was analysed, representing an ontogenetic series (L_T range: 407–1105 mm; Fig. 1). This range represents the wide distribution of *G. mordax* sizes found at Two Harbors. This range is based on a sample of 904 individuals collected during the course of 4 years (R. S. Mehta & B. A. Higgins, unpubl. data). Observations using scuba support the idea that smaller *G. mordax* do reside in these trapping locations, but they were never collected in the traps. Throughout ontogeny, L_H exhibits positive allometry, growing disproportionately longer as *G. mordax* increased in L_T (SMA, $r^2 = 0{\cdot}96$; d.f. $= 40$, $F_{1,40}$, $P < 0{\cdot}001$; Fig. S2, Supporting Information).

FIG. 1. Relationship between total length (L_{T}) of *Gymnothorax mordax* and otolith size. Both *G. mordax* specimens scaled to 5 cm. Otolith 1 extracted from the small specimen (407 mm L_{T}). Otolith 2 extracted from the large specimen (1105 mm, L_{T}). ⬭, location of otoliths in fortified neurocranium.

The marginal increment analysis supports the interpretation of summer growth (*i.e.* translucent bands) as annuli in *G. mordax* otoliths. The mean width of the outermost translucent band was significantly thinner than that of the previous three (Tukey's HSD, d.f. = 3, $P < 0{\cdot}001$) (Fig. S3, Supporting Information). There was no significant difference in mean width among the inner three translucent bands (Tukey's HSD, d.f. = 3, $P > 0{\cdot}05$).

Presumed otolith annuli presented ages ranging from 8 to 22 years for *G. mordax* (Fig. 2). Based on settlement times backcalculated from the age estimates, *G. mordax* settled at the trapping sites between 1991 and 2007. During this 16 year period, ONI values indicate 12 El Niño and 9 La Niña events occurred. Only 1993 displayed normal conditions when neither of these events occurred. Backcalculated ages indicate that 30 of the 33 individuals (91%) in the present study were recruited to the kelp forests of Two Harbors during an El Niño episode (Fig. 3). Moreover, the probability that this sample of *G. mordax* successfully recruited to Catalina Island during an El Niño event was statistically significant relative to the number of El Niño events ($n = 12$) in the 16 years spanning the data-set (two-sided exact binomial test: $P < 0{\cdot}05$).

As anticipated, younger fish were smaller in L_{T} and L_{H}, but the data show a single extreme deviation from this trend. The oldest specimen (22 years) had an L_{H} of only 510 mm. This outlier did influence the already strong positive relationship between L_{H} and age (SMA, $r^2 = 0{\cdot}56$; d.f. = 40, $F_{1,40}$, $P < 0{\cdot}001$; Fig. 4). When this specimen was removed from the data set, the age to L_{H} relationship is strengthened ($r^2 = 0{\cdot}75$).

DISCUSSION

The only published account of age for *G. mordax* was based upon a single, captive individual (Fitch & Lavenberg, 1971) and how age was determined for that individual remains unknown. A previous attempt to examine the otoliths of *G. mordax* from Two

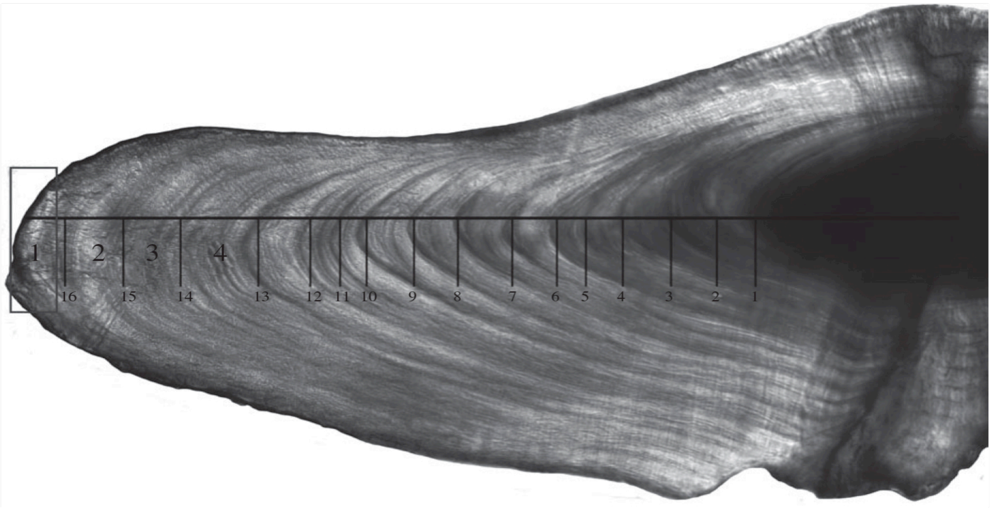

FIG. 2. Thin sectioned otolith of *Gymnothorax mordax* (810 mm total length, L_T) showing annuli (dark bands) counted to estimate ages. Note translucent edge of otolith highlighting (□) a summer (September) time of collection. The four outermost translucent zones (large numerals 1–4) were used in the marginal increment analysis to validate annuli (see Fig. S3, Supporting Information).

Harbors was inconclusive, as annuli were never verified (McCleneghan, 1973). The present study provides the first age estimates for individuals of *G. mordax* naturally occurring around Catalina Island.

With an upper age of *c.* 22 years, *G. mordax* appears to reach ages similar to the maximum ages of other southern California kelp-forest predators such as *S. pulcher* 25 years (Cowen, 1985), garibaldi *Hypsypops rubicundus* (Girard 1854) 20 years (Velte, 2004), barred sand bass *Paralabrax nebulifer* (Girard, 1854) 24 years (Love *et al.*, 1996) and treefish *Sebastes serriceps* (Jordan & Gilbert 1880) 25 years (Colton & Larson, 2007). Typically, kelp bass *Paralabrax clathratus* (Girard 1854) reach ages of around 16 years, but certain individuals have been reported to reach an age of 32 years (Young, 1963) and 33 years (Love *et al.*, 1996), while giant sea bass *Stereolepis gigas* Ayres 1859 may reach 76 years (Hawk & Allen, 2014). Other sympatric fishes such as opaleye *Girella nigricans* (Ayres 1860) maximum age 10 years (Bredvik *et al.*, 2011) and halfmoon *Medialuna californiensis* (Steindachner 1876) 8 years (Bredvik *et al.*, 2011) are much shorter lived.

In general, *G. mordax* head length was a fair predictor of age. The major outlier was one of the smallest individuals ($L_T = 510$ mm; $L_H = 63$ mm; $M = 0{\cdot}30$ kg) and yet was aged as the oldest moray (22 years). Individuals with comparable L_H (65 ± 10 mm) to this outlier ranged from 9 to 16 years. The next oldest individuals ($n = 4$, ages: 20–21 years) were at least double the length (964–1105 mm L_T; 123–155 mm L_H). There is no evidence to suggest that growth for *G. mordax* does not fit asymptotic patterns of growth as predicted by both von Bertalanffy and Gompertz growth models (Hawk & Allen, 2014). The outlier in the dataset suggests slow growth due to less than optimal behaviour or physiology due to the inability to acquire or assimilate resources (Fey, 2001). The only other study on *G. mordax* from the same population also observed

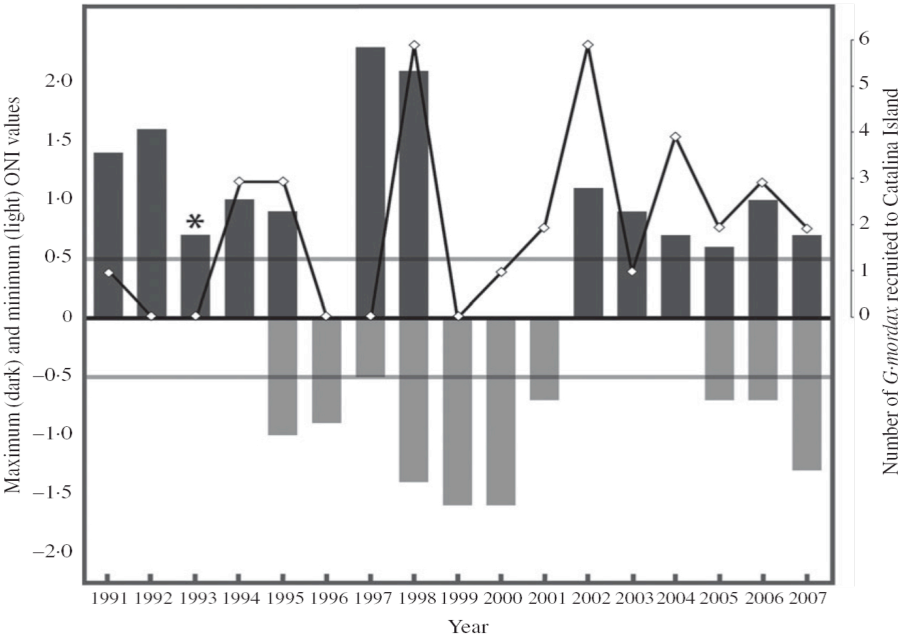

Fig. 3. Number of *Gymnothorax mordax* settled relative to the maximum (■) and minimum (▨) Oceanic Niño Index (ONI) values from 1991 to 2007. Years with ONI values exceeding +0·5 indicate an El Niño for that year, while years with ONI values below −0·5 indicate a La Niña for that year. *, The ONI value exceeded the +0·5 threshold, it did not do so for five consecutive months, therefore, 1993 is not considered to have contained an El Niño event.

that some older morays are shorter than younger individuals (McCleneghan, 1973). Additional, more robust validation methods were not applicable to this data set for numerous reasons. First, the smallest individuals did not recruit to the trapping gear and therefore eliminated the possibility of accurately validating annuli using daily ageing based on otolith microstructure (Campana, 2001), or using year 1 otoliths to calibrate the position of the first annulus (Allen & Andrews, 2012). Furthermore, all of the individuals analysed in the present study were collected during the same summer months and thus changes in otolith deposits throughout the year were not discernible. The results of the MIA, however, do suggest that all individuals collected in the present study were captured during their summer growth, as the outermost translucent band was significantly thinner compared with that of the previous three summers. The significantly smaller width (*i.e.* incomplete summer growth) of the outermost translucent band of all the otoliths analysed in the present study is likely to be explained by the interruption of summer growth due to the collection of specimens.

Based on historic ONI values, backcalculated ages of *G. mordax* reveal that for 30 of 33 individuals (91%), the year of larval recruitment coincided with an El Niño episode. These results suggest that *G. mordax* settlement to Santa Catalina Island appears to be mainly an episodic phenomenon. The absence of a continuum of ages in the data-set lends support to the long-standing hypothesis that southern California *G. mordax* populations do not reproduce (McCleneghan, 1973). Briefly, this hypothesis was

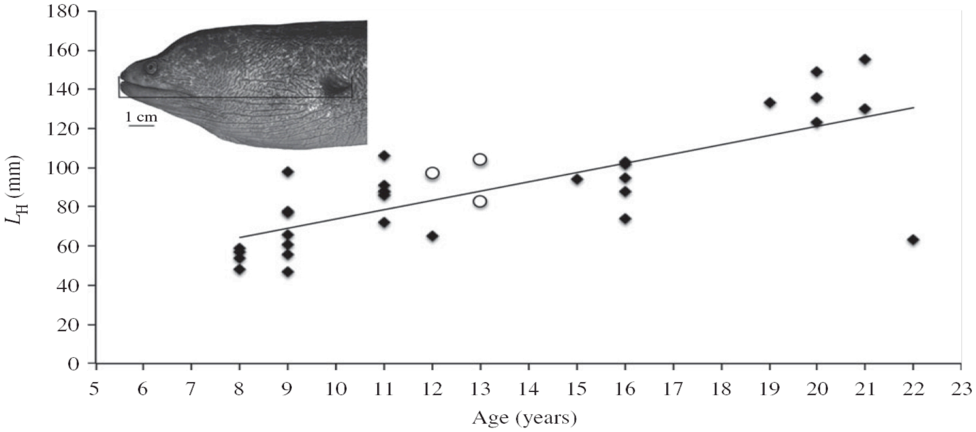

FIG. 4. Relationship between *Gymnothorax mordax* (head length, L_H) and number of annuli (age). ◆, El Niño period; ○, non El Niño period. The curve was fitted by: $y = 4{\cdot}73x + 26{\cdot}5$ ($r^2 = 0{\cdot}56$, $P < 0{\cdot}001$).

based on histological analysis of gonad tissues for both male and female *G. mordax* collected throughout the year. Females collected off the coast of southern California did not contain fully developed eggs within their ovaries while a specimen collected further south (Magdalena Bay, Baja California), contained larger, more developed eggs within its ovaries (McCleneghan, 1973). Thus, as was hypothesized by McCleneghan (1973), *G. mordax* populations towards the northern end of their range inhabit waters too cold, or not warm long enough to permit proper gametogenesis. This suggests that pulses of larval recruitment by El Niño events to northernmost areas of the range of *G. mordax,* such as Catalina Island, create sink populations.

As most nearshore marine fishes spend their early stages of development in the plankton as eggs or larvae, their dispersal is closely tied to the influence of currents (Johannes, 1978; Barlow, 1981; Cowen, 1985; Doherty *et al.*, 1985; Cowen & Sponaugle, 2009; Simons *et al.*, 2016). Predicting how these nearshore flows (*e.g.* California Current System, CCS) distribute propagules throughout their ranges can be difficult, as neritic currents tend to be more complex than those of the deep and coastal ocean, with many variable processes operating simultaneously, including surface waves, bottom topography, wind-forcing, large-amplitude internal waves, boundary-layer effects and, of course, climatic anomalies (Chelton *et al.*, 1982; Cowen, 1985; Pineda *et al.*, 2007).

One of the most prominent and dramatic climatic anomalies to affect the biology and distribution of nearshore biota is that of an El Niño event (Norris, 2006). The propagation of the El Niño oceanic signal across the Pacific basin is mainly transmitted by Kelvin waves (Das & Pan, 2016). These Kelvin waves permeate from west to east, as the westerly winds relax, permitting warmer waters to flow above colder waters, depressing the thermocline and altering the CCS dynamics on a large scale. Specifically, as the Kelvin waves reach the continental shelf, they deflect to the north and south, simultaneously pushing equatorial waters poleward and disrupting typical current patterns within the CCS (Norris, 2006). For example, studies conducted in CCS waters between 1997 and 1998 detected dramatic shifts in hydrological characteristics, such as sea surface temperatures, salinity levels, dissolved oxygen content and nutrient load (Lynn *et al.*, 1998; Chavez *et al.*, 2002). The changes in temperature, salinity and denitrification concentrations further resulted in overall changes in community composition, where the densities of warm temperate and tropical species increased, while those of typical northern cool-water species decreased (Marinovic *et al.*, 2002). The physical properties of the Kelvin wave, however, can result in the warm-water mass becoming quickly (*i.e.* within the same calendar year, *e.g.* 1998) displaced by the colder waters that are depressed below, resulting in La Niña conditions (Das & Pan, 2016).

During nominal conditions (*i.e.* non-El Niño periods), the circulation of the CCS is mainly influenced by wind. These winds along the coast are variable in the winter months, but during the spring and summer, the winds become more equatorward (Norris, 2006). The net result is the CC originating in the Pacific sub-Arctic, driving waters with high dissolved-oxygen, low salinity and low nutrient concentrations from north to south (Norris, 2006). When the CC reaches Point Conception, however, it helps to form the SCE, which rotates counter-clockwise within the SCB (Sverdrup & Fleming, 1941). Towards the southern edge of this eddy (roughly San Diego, California), warmer, tropical waters are drawn up from the south (Cowen, 1985; Norris, 2006). These waters continue to move poleward, through the Santa Barbara Channel, until being deflected back into the dominant equatorward waters of the CC at Point Conception (Browne, 1994). The net poleward eastern current of the SCE can act as a vector, distributing propagules that originate in warmer, southern waters further north. This pattern has been observed in the both the recruitment patterns (Cowen, 1985) and phylogeography (Poortvliet *et al.*, 2013) of *S. pulcher*.

Densities of *S. pulcher* are highest in sites associated with the southern and central portions of their range and lowest at the most north-western portions (Cowen, 1985). These distribution patterns have been attributed to both local (*e.g.* SCE) and larger-scale (*e.g.* El Niño) events (Cowen, 1985). For example, in the years of 1977–1978 and 1982–1983 (both El Niño periods based on historic ONI values), *S. pulcher* recruitment was anomalously high in the northern extent of their ranges (*e.g.* San Nicolas Island), whereas recruitment towards the southern end of their range was minimal. During non-El Niño periods (*i.e.* normal conditions), this pattern is exactly opposite, minimal to no recruitment at San Nicolas Island and consistent recruits settling at Islas San Benitos and Cabo Thurloe (Cowen, 1985). The changes in CCS dynamics during El Niño events and normal conditions are clearly observed in the stark contrasts between recruitment patterns of *S. pulcher* during these different periods. Therefore, the recruitment patterns observed for *S. pulcher* and *A. nobilis* may also describe a similar scenario of episodic northern *G. mordax* recruitment pulses to the northern extent of their range, mainly based upon the intensity and frequency of El Niño events. While still being indirectly affected by El Niño episodes, however, the recruitment patterns of the sympatric spotted sand bass *Paralabrax maculatofasciatus* (Steindachner 1868) are somewhat at odds with those of the aforementioned species. Allen *et al.* (1995) found that *P. maculatofasciatus* recruitment pulses were strongest in the years directly post El Niño events when mean summer SST were highest (*e.g.* 1984–1985 and 1998–1999). This discrepancy may be explained by elevated SST in years following El Niño events resulting in increased *P. maculatofasciatus* reproductive output, whereas the successful recruitment of *S. pulcher, A. nobilis* and *G. mordax* to southern California waters rests more heavily upon the current dynamics (*i.e.* not necessarily SST) during the El Niño events. While the currents may aid in larval transport, it is also possible that the elevated SST associated with El Niño may increase post-settlement survival rates, but this hypothesis was not tested in the current study.

In addition to the magnitude and periodicity of climatic anomalies, the PLD also probably influences how strong an effect these oceanic variables can have on the passive movement of species (Jones *et al.*, 2005; Taylor & Hellberg, 2005). The PLD of *G. mordax* is unknown, but studies on leptocephali of related species suggest that larvae can live in a pelagic environment for up to 2 years (Mochioka & Iwamizu, 1996; Bishop & Torres, 1999; Ishikawa *et al.*, 2001). Further evidence demonstrating the extended PLDs for the genus *Gymnothorax* Bloch 1795 is supported by the wide genetic continuity of the undulated moray *Gymnothorax undulatus* (Lacépède 1803) and the yellow-edged moray *Gymnothorax flavimarginatus* (Rüppell 1830), which span the entire Indo-Pacific (Reece *et al.*, 2010). The potential for *G. mordax* to remain in pelagic waters circulating the SCB for an extended period of time may explain why three of the individuals aged in the present study recruited to Santa Catalina Island during non-El Niño years. Further research is needed to determine if *G. mordax* does indeed share a PLD similar to those of its *Gymnothorax* relatives, as it would predict little to no genetic differentiation in the phylogeography of the *G. mordax* metapopulation.

Data on the natural history of *G. mordax* are largely absent from the scientific literature. The present study provides the first account of *G. mordax* age, but the addition of more specimens covering the extremes in size (very small to approaching maximum size for the species) and collected at different times of the year would help in validation of the ages. Given the small sample size (33 individuals) and the lack of larger specimens, it is likely that the maximum age of *G. mordax* is greater than the 22 years observed in this study. Regardless, the ages of *G. mordax* provide support for the hypothesis that recruitment to the northern portion of their range is mainly driven by El Niño events. With climate models predicting an increase in the frequency of extreme El Niño events (Cai *et al.*, 2014), however, it would be expected that the frequency of *G. mordax* recruitment episodes would also increase. Another possible outcome of more frequent and extreme El Niño events is a poleward range expansion of *G. mordax* into waters that have been presumed to be too cold to sustain this predatory fish. The thermal tolerance of the predatory *G. mordax* should be assessed in the future to better understand the potential effects of settled individuals on coastal communities north of Point Conception.

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Supporting Information

Supporting Information may be found in the online version of this paper:

FIG. S1. Map of field site showing coves where traps were deployed (in bold). Insert shows position of Catalina Island relative to Southern California coast. – – –, border of the Blue Cavern Onshore State Marine Conservation Area. The Wrigley Institute of Environmental Science field station of the University of Southern California (USC) is located in Big Fisherman Cove.

FIG. S2. Relationship between *Gymnothorax mordax* total length (L_T) and head length (L_H). ■, 95% C.I., ($y = 0{\cdot}14x$; $r^2 = 0{\cdot}97$).

FIG. S3. Mean ± S.D. widths of the last four bands of each otolith used in marginal increment analysis (MIA) to validate annuli. Band 4 represents the fourth to last summer (*i.e.* closest to otolith centrum), while band 1 represents the summer of the collection year (*i.e.* outermost translucent edge). Different lower-case letter indicate statistically significance difference ($P < 0{\cdot}05$).

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Supporting Information (Figures) for El Niño episodes coincide with California moray *Gymnothorax mordax* settlement around Santa Catalina Island, California

Benjamin A. Higgins, Don Pearson, & Rita S. Mehta

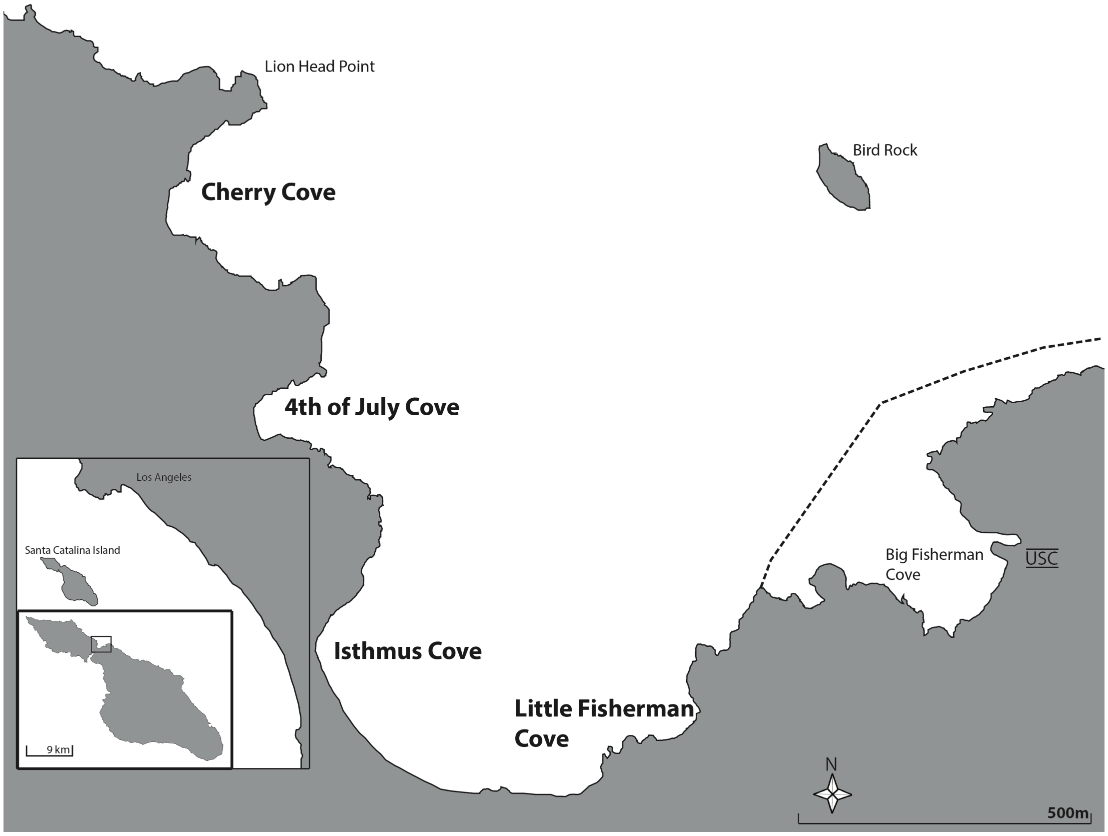

Fig. S1.1: Map of field site showing coves where traps were deployed (in bold). Insert shows position of Catalina Island relative to Southern California coast. ….., border of the Blue Cavern Onshore State Marine Conservation Area. The Wrigley Institute of Environmental Science field station of the University of Southern California (USC) is located in Big Fisherman Cove.

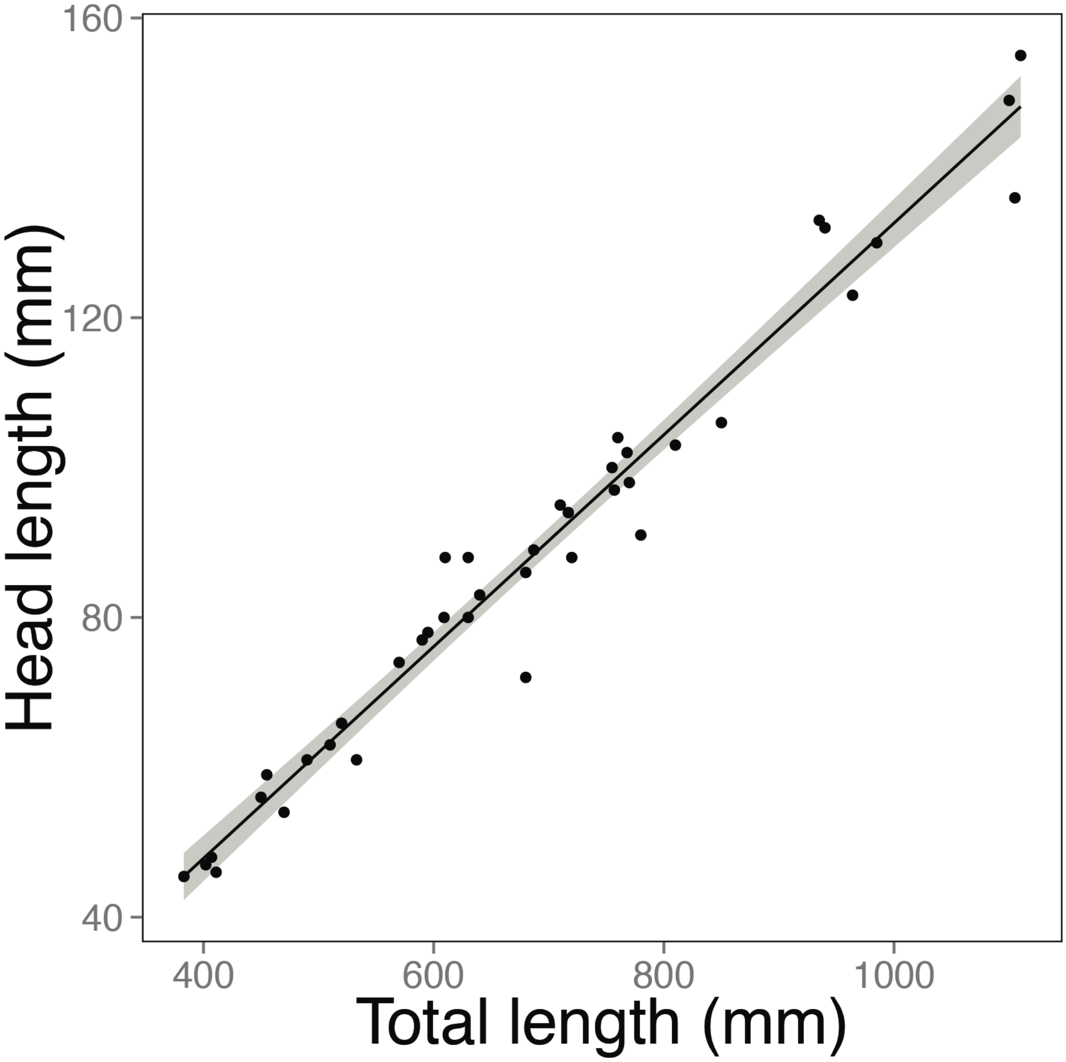

Fig. S1.2: Relationship between *Gymnothorax mordax* total length (L_T) and head length (L_H). , 95% c.i., ($y = 0{\cdot}14x$; $r^2 = 0{\cdot}97$).

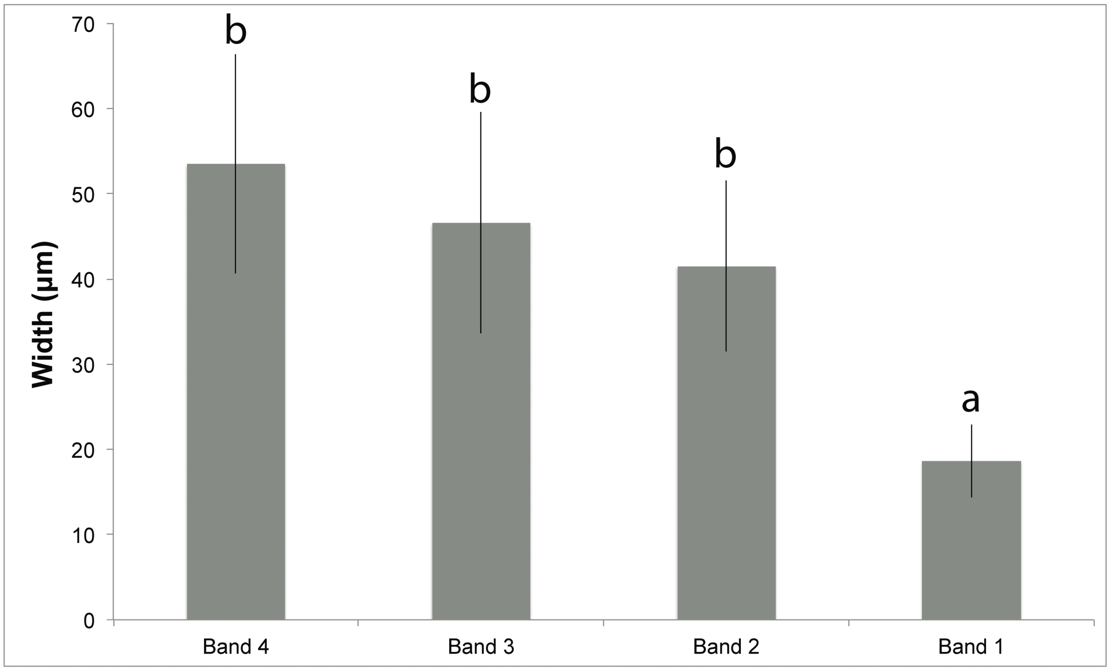

Fig. S1.3: Mean ± s.d. widths of the last four bands of each otolith used in marginal increment analysis (MIA) to validate annuli. Band 4 represents the fourth to last summer (*i.e.* closest to otolith centrum), while band 1 represents the summer of the collection year (*i.e. outermost translucent edge*). Different lower-case letter indicate statistically significance difference ($P < 0{\cdot}05$).

Chapter 2

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Distribution and habitat associations of the California moray (*Gymnothorax mordax*) within Two Harbors, Santa Catalina Island, California

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Abstract While kelp forests are some of the best-surveyed ecosystems in California, information on cryptic inhabitants and their role within the community are lacking. Kelp itself provides overall structure to the habitat; however the rocky reef to which the kelp attaches is known to provide additional structure for cryptic species. *Gymnothorax mordax,* the California moray, is an elusive predatory species that is considered abundant in the waters around Catalina Island. However, no life history data exists for this species. We examined habitat composition, relative abundance, size pattern distributions, and biomass of *G. mordax* within Two Harbors, Catalina Island. Habitats were sampled using a combination of baited trap collection and transect surveys using SCUBA. A total of 462 *G. mordax* were captured, primarily in shallow (< 10 m) waters. Individuals of *G. mordax* were associated with mostly boulder and cobble substrates. Measurements of relative abundance and density indicate that *G. mordax* is more prevalent than reported in previous studies. We also discovered that the 6 trapping sites from which all morays were collected, differed in size structuring and density while the relatively high biomass did not change across sites. In general, southern facing sites exhibited higher densities of morays, while northern facing sites showed more size structuring. We show how the structural complexity of the rocky reef habitat in an already diverse kelp forest ecosystem, can support a high biomass of a cryptic elongate predatory fish.

Keywords Catalina Island · CPUE · Muraenidae · Habitat · *Gymnothorax*

Introduction

Kelp forests are considered one of the most diverse and productive ecosystems in the marine environment (Mann 1973; Christie et al. 2003) having strong recreational and economic significance to society (Simenstad et al. 1978; Erlandson 2001; Steneck et al. 2002). Therefore, it is not surprising that some of the most well-studied marine communities are found within kelp forests (Steneck et al. 2002; Graham 2004; Allen et al. 2006). Despite the large body of literature on the life history of the icthyofauna and their associated habitats found within the neritic waters of coastal systems, data on the more sessile and cryptic vertebrate species within the kelp forest ecosystem are lacking and often influenced by more conspicuous species (Allen et al. 1992; Willis and Anderson 2003; Graham 2004; Sandoval 2005).

While the monitoring of kelp forest fish populations is important for ecosystem health, it presents numerous challenges (Harvey et al. 2004). Fish populations are frequently assessed using presence/absence data to understand overall abundance and diversity patterns. These data are

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typically collected using a variety of techniques, such as band transects, random point contacts, visual transects, and roving SCUBA diver counts (Davis et al. 1996; Stephens et al. 2006). Not surprisingly, these visual censuses are conducted during daylight hours and therefore abundance and density data is more commonly reported for diurnal fish populations (Ebeling and Bray 1976). Elusive and cryptic diurnal species such as burrowers and nocturnally active species are often excluded from such census data. For example, small cryptic diurnal species such as the blue-banded goby (*Lythrypnus dalli*) and spotted kelpfish (*Gibbonsia elegans*) were reported to be up to four times as dense as conspicuous fishes. Although their biomass may not be large, these species are thought to double the ichthyofaunal diversity in the system (Allen et al. 1992). As nocturnally active species often take refuge during daylight hours, the size of their populations and the resulting effects upon their community are unstudied (Helfman 1986). Furthermore, nocturnal communities tend to have a higher relative abundance of predatory species than diurnal communities (Helfman 1986; Hobson and Chess 1986), suggesting that crepuscular and nocturnal species may play an important role in shaping ecosystems, especially trophic dynamics.

The California moray eel (*Gymnothorax mordax*) is the only muraenid found off the coast of California. The distribution of *G. mordax* extends from just north of Santa Barbara to Santa Maria Bay in Baja California (Fitch and Lavenberg 1971; Eschmeyer et al. 1983). *Gymnothorax mordax* is an elusive predatory species considered abundant in the waters around Catalina Island (Fitch and Lavenberg 1971, b) but limited data exists on its natural history (Fitch and Lavenberg 1971). The combination of a cryptic lifestyle and the lack of a commercial fishery has enabled morays, in general, to remain virtually undetected in standard underwater visual surveys (Gilbert et al. 2005). However, Froeschke et al. (2006) included *G. mordax* in their dataset when examining the effects of a Marine Protected Area (MPA) on fish populations. Despite the presumed importance of cryptic predatory species, *G. mordax* has rarely been incorporated into Southern California kelp forest studies. In fact, no published study to date has focused on examining the distribution and relative abundance of *G. mordax* in the Southern California kelp forest ecosystem.

Similar to all members of the Anguilliformes, morays (Muraenidae), exhibit an elongate body plan (Böhlke et al. 1989). Anguilliform elongation in fishes is thought to promote a burrowing or crevice dwelling lifestyle (Smith 2012). Additionally, densities of tropical moray species were positively associated with structural complexity (Gilbert et al. 2005). Similarly, rocky bottom substrate was described as the ideal habitat for the Mediterranean moray eel (*Muaena helena*) (Matić-Skoko et al. 2011). Previous studies of *G. mordax* in Catalina suggest that the majority of their activity occurs during the night (McCleneghan 1973; BH & RSM pers. obs.). Therefore, because of their body shape and reduced activity during daytime hours, we hypothesize that habitat characteristics that promote structural complexity will strongly influence where individuals of *G. mordax* are found.

Roughly 10–15% of the Southern California coast is classified as rocky shoreline (Stephens et al. 2006). However, the habitat structure of the Southern California offshore islands (e.g., Catalina) consist largely of rocky shorelines, effectively doubling the amount of hard bottom rocky reef and kelp habitat off Southern California (Froeschke et al. 2006; Stephens et al. 2006). Thus, while the general habitat composition of the nearshore bathymetry around Catalina has been examined (see Seafloor Mapping Lab, California State University Monterey Bay), it lacks the detail necessary to understand moray habitat associations. Therefore, we know little about how habitat characteristics (e.g., rocky reef, sandy bottom, etc.) influence the distribution of *G. mordax.*

While habitat characteristics are important during and after settlement, the broad distribution of *G. mordax* around Catalina is likely influenced by the strength and directionality of the currents that are hypothesized to bring long-lived propagules from warmer, southern waters, primarily during El Niño events (McCleneghan 1973). We recently showed that El Niño events contribute to the dispersal and subsequent recruitment of individuals of *G. mordax* to Catalina Island (Higgins et al. 2017). Therefore, as current flow presumably influences larval settlement, we anticipate differences in adult size structuring among coves. As Catalina is well nested within the Southern California Eddy (SCE), the coves on the leeward side of the island are more likely bathed in waters moving from southwest to northeast (Cowen 1985; Hu and Liu 2002). Thus, we predict that the coves most exposed to westerly currents will host *G. mordax* populations with greater size structuring, as these are the sites first encountered by larvae.

To provide first-time data for a resident nocturnal predator, we organized our efforts to conduct a trapping study along the western side of Catalina Island. In doing so, we address the following questions: 1) Which characteristics within a kelp forest ecosystem is most associated with California moray eels?, 2) What are the relative abundances and density estimates for moray populations in Two Harbors?, and 3) Based on what we know about the exposure of leeward coves to incoming current flow, do we see size structuring of morays across coves?

Materials and methods

Trapping and location

Gymnothorax mordax were collected using custom-built, dual-chambered wire mesh traps ($N = 20$, 36″ × 11″ × 9″; Staten Island, NY) during the mid-late summer months (July–September) of 2014 and 2015 at Two Harbors, Catalina Island, CA (33°26′ 45.4″N, 118°29′31.3″W). We chose Catalina as the location for our study for several reasons: 1) there is excellent research infrastructure provided through the University of Southern California's Wrigley Institute for Environmental Study, 2) it contains near shore habitat that is representative of other Channel Islands (Stephens et al. 2006), and 3) populations of *G. mordax* were previously estimated in Two Harbors using standard underwater visual surveys conducted during daylight hours (Froeschke et al. 2006), which provided an opportunity for comparison.

Mesh traps were randomly thrown in shallow water (< 10 m) within six trapping sites spread across four coves in Two Harbors (Fig. 1). Because of the bathymetry of the near shore habitat in these various coves, sites that contained a wide range of habitat substrate types that resided in deeper (≥ 10 m) waters were not common, restricting our deep water trapping locations. Traps deployed in deeper waters were east of Lion's Head Point (33°27′10.58″N, 118°30′3.94″W), and the slopes between Cherry and Fourth of July Coves (33°26′ 56.74″N, 118°29′57.49″W), as well as Fourth of July and Isthmus coves (33°26′45.20″N, 118°29′52.44″W). Because we observed that depth had a strong negative effect on moray catch in 2014 (see Results), we focused our efforts on shallow water trapping in year 2015 to maximize our trapping efforts. Traps were set daily between 18:00–19:00 h and baited with frozen anchovies, which were placed into perforated plastic bottles allowing odor to serve as an attractant while prohibiting access to the bait.

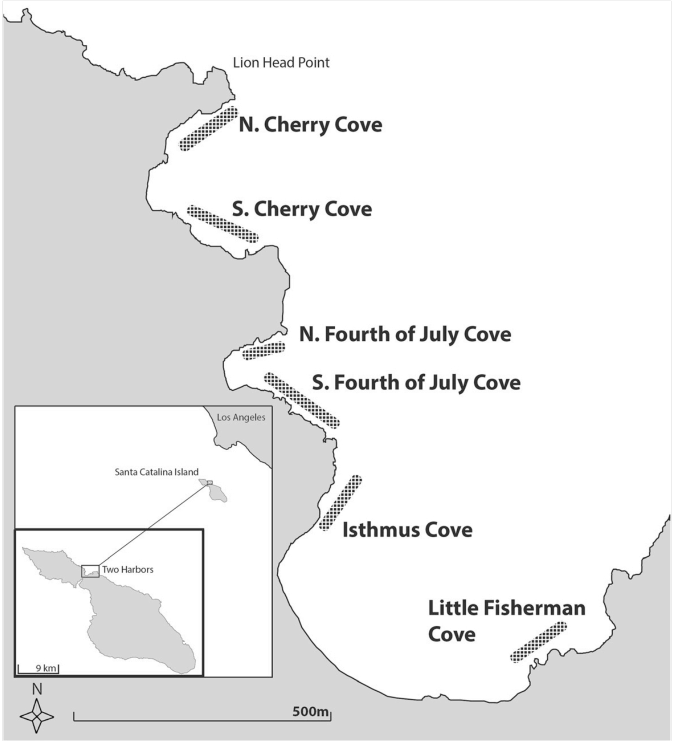
Habitat assessment

Within two hours of trap deployment, a team of SCUBA divers descended upon the traps to survey the adjacent habitat structure. Initial trap depth was recorded, after which the divers conducted four, 10 m transects per trap. Four transects were conducted along standard bearings from each trap (0°, 90°, 180°, and 270°). At every 0.5 m, the divers used a modified uniform point contact (UPC) method to record the depth and substrate characteristics of the habitat along the transect tape. Briefly, the UPC method is the preferred methodology used by Reef Check California, and focuses on the substrate under a point along the transect. This detailed method of categorization resulted in 80 measurements of substrate, and 81 measurements of depth associated with each trap. There are 81 measurements for trap depth rather than 80 because the trap itself was associated with a depth. The depth measurements were used to analyze changes in habitat slopes (i.e., depth profiles) along transects surrounding each trap. Substrate cover was categorized as % cover of boulder, cobble, sand or bedrock. Categorization of substrate cover was based upon the sampling protocols set by the Partnership of Interdisciplinary Studies of Coastal Oceans (PISCO; www.piscoweb.org). In brief, substrate cover was determined by particle diameter, such as sand, cobble (<10 cm diameter), boulder (10 cm – 1 m diameter) or bedrock (> 1 m diameter). These substrate and depth data were then cross-referenced with the *G. mordax* individuals trapped.

Measurements and tagging

Trap retrieval took place the morning after traps were initially deployed (07:00–08:00 h), resulting in a total soak time of ~12 h. Collected *G. mordax* were sedated using Tricaine Methanesulfonate (MS-222) buffered with sodium bicarbonate at roughly 90 mg/l of fresh seawater. Once sedated, total length to the 0.01 mm (tip of snout to posterior-most tip of tail; L_T) and mass (0.01 g) of each individual were recorded using

Fig. 1 Map of field site. Land is shaded gray. Specific regions where traps were deployed are represented by checkered rectangles. Insert shows relative position of Catalina Island to Southern California coast



analogue calipers and a digital pesola scale, respectively. From these measurements, we calculated Fulton's condition factor (K; Froese 2006), for individuals in each of the six trapping sites using the equation:

$$K = 100\frac{W}{L^3}$$

where W = whole body weight (grams), L_T (in cm). These values were then binned into 50 mm L_T groups to determine whether K, body condition, varied relative to size between trapping sites. Larger K values indicate thicker (i.e., healthier) individuals relative to a given length.

Passive integrated transponder (PIT) tags (BIOMARK© #BIO8.B.03v1) were implanted into the tail muscle of all captured individuals using a 16-gauge injector needle (BIOMARK© #N165). We then used a handheld reader (BIOMARK© #601) to identify and record the unique ten-digit tag number. PIT tags ensured that the relative abundance of *G. mordax* and population densities (see below) were not overestimated from recaptured individuals. Additionally, recaptured *G. mordax* provided some data on both movement and habitat preference. All trapping, release, and tagging of *G. mordax* were in accordance with California Department of Fish and Wildlife Permit #11366.

CPUE, relative abundance, and density

To account for daily sampling effort, total *G. mordax* catch per trapping site was divided by the number of traps deployed (i.e., catch per unit effort [CPUE]).

These CPUE values also provide an accurate measurement of the relative abundance of *G. mordax* (Stephens et al. 2006). In addition to relative abundance, we calculated moray density for each trap site by dividing the total morays collected by the total area of the respective trapping site. Previous unrelated trapping and tagging efforts showed that individuals did not move between or across coves, suggesting that trapping sites could be considered discrete units (BH & RSM, unpubl. Data). These sites were measured to the nearest 0.01 m using satellite images obtained from Google® Earth and

NIH ImageJ® analysis software. However, the total number of traps deployed at each trapping site was not consistent (N. Cherry: 20, S. Cherry: 57, N. Fourth: 16, S. Fourth: 57, Isthmus: 40, LFC: 18). To account for uneven sampling effort, we randomly subsampled 15 traps with replacement for each trap site using JMP® Pro v.13.0.0 (64-bit). This process was repeated 1000 times for each trap site to obtain a distribution curve and mean value for the total number of morays caught at each site. Densities across trap sites were standardized to the number of *G. mordax* individuals within 100 m^2.

Statistical analyses

To examine whether CPUE varied across sites, we first tested for equal variances in our data set using a Levene's test. To determine whether the number of captured morays varied across the two years sampled, we utilized an analysis of variance (ANOVA), followed by a Tukey's honest significance difference (HSD) test. The lack of significant difference between years enabled us to pool our data to determine whether CPUE varied across sites. The condition factor (K) of individuals within and across sites were also analyzed using an ANOVA and Tukey's HSD test.

Kernel density plots were used to visualize the size (L_T) distribution of morays trapped for each of the six sites. Size distributions were then compared using a Kolmogorov-Smirnov goodness of fit test in R© (v.0.98.1103–2009-2014 RStudio, Inc.). We also used a Hartigans' dip test (R© package "diptest" Maechler 2016) to determine whether size distributions were multimodal.

Densities of *G. mordax* populations data did not pass Levene's test for equal variance and transformed data also failed the test. Thus, these data were tested using a Kruskal-Wallis rank sum test in R© followed by a Nemenyi test with Tukey distribution proximation using "The pairwise multiple comparison of mean ranks (PMCMR)" package (Pohlert 2016).

We used JMP® Pro v.13.0.0 (64-bit) to run multiple stepwise general linear regression models to determine the effects of mean slope (defined as the average the change in depth from trap to end of transects), initial trap depth (defined as the depth of the trap itself), and % cover of boulder, cobble, sand, and bedrock on *G. mordax* catch. To account for differences in trapping location orientation (e.g., North vs. South Cherry coves), additional models were carried out with slope divided into two variables (North-South slope & East-West slope). Generalized linear models were also conducted in JMP to test if either depth or substrate type were good predictors of *G. mordax* size.

Principal components analyses (PCAs) were then run for each trap site to visualize the variation in trap depth and % cover for each site. Additionally, a Procrustes analysis of congruence test was conducted to assess the similarities in the habitat characteristics between different trapping site ordinations using the "Vegan" package (Oksanen et al. 2017) in R©. Briefly, this tests the non-randomness (i.e., significance) between the various ($N = 119$) configurations of PCA vectors across different trapping sites, where a significant correlation between a pair of trapping sites would suggest that the ordinations of their PCAs are the same. This test was run for every possible pair ($N = 27$) of trap site combinations.

Results

Catch by site and depth

A total of 462 *Gymnothorax mordax* were collected in 273 traps deployed during the summer months of 2014 and 2015. Of this total, 170 (~37%) were recaptured individuals. The mean daily catch per unit effort (CPUE) did not vary significantly across trapping years (d.f. = 8, $p > 0.081$), and were thus collapsed to examine CPUE across the six trapping sites (d.f. = 5, $p > 0.42$; Fig. 2). Trapping at deeper sites (> 10 m) in 2014 resulted in very few morays, even though substrate profiles within the habitats were similar (> 40% boulder; > 30% cobble; <10% bedrock and sand) to those in shallower waters. Thus, as CPUE varied based on trap depth with shallower (< 10 m) depths yielding significantly more *G. mordax* per trap (d.f. = 4, $p < 0.04$; Fig. 3), the majority of traps (208 of 273; ~76%) were deployed in water <10 m. These traps yielded 429 (~93%) of all *G. mordax* collected in the present study. Despite the high number of *G. mordax* captures in these deployments, 37% of the shallow-set traps ($N = 73$) were empty when retrieved.

Densities of *G. mordax* populations differed across all trap sites (Kruskal-Wallis rank sum test, d.f. = 5, $p < 0.0001$) with the exception of S. Cherry and Isthmus (Nemenyi test using Tukey distribution approximation, $p > 0.4$). The highest density of *G. mordax* was found in N. Fourth of July, with 2 individuals per 100 m^2. Both

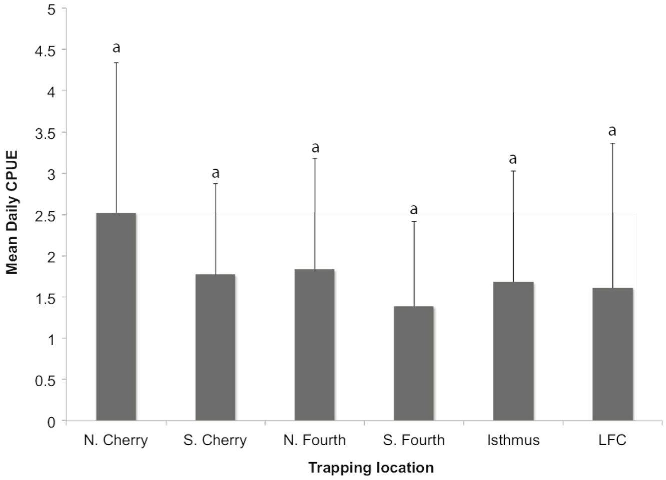


Fig. 2 Mean daily CPUE based on trapping location with years (2014 & 2015) combined. Error bars represent +1 standard deviation. Letters indicate significance groupings. Data is combined for 2014 & 2015 as no difference in mean daily CPUE was detected

N. Cherry and Isthmus coves contained the same densities at 1.48 individuals per 100 m^2. The remaining three trap sites contained slightly less than 1 individual per 100 m^2 (S. Cherry: 0.87, S. fourth, 0.79, and LFC: 0.71). In general, southern facing sites had higher densities.

Size distribution

Trapped individuals ranged from 400 to 1114 mm L_T across all sites. Size distribution did not vary significantly between trapping sites (two-sample Kolmogorov-Smirnov goodness of fit test, $p > 0.13$; Fig. 4). Additionally, there was no significant difference in biomass among the six trapping locations (Tukey's HSD test, d.f. = 5, $0.09 < p < 0.99$). The size distribution for all trapping locations was unimodal (Hartigans' dip test for unimodality, $p > 0.462$) with a mean size of 600–700 mm L_T for all sites.

Generalized linear models revealed that trap depth was a poor predictor of *G. mordax* size for all trapping locations with R^2 values ranging from a minimum of 0.00 in Isthmus and LFC, to a maximum of 0.32 in North Fourth of July Cove. Similarly, substrate type was a poor predictor of *G. mordax* size ($0.0001 < R^2 < 0.167$).

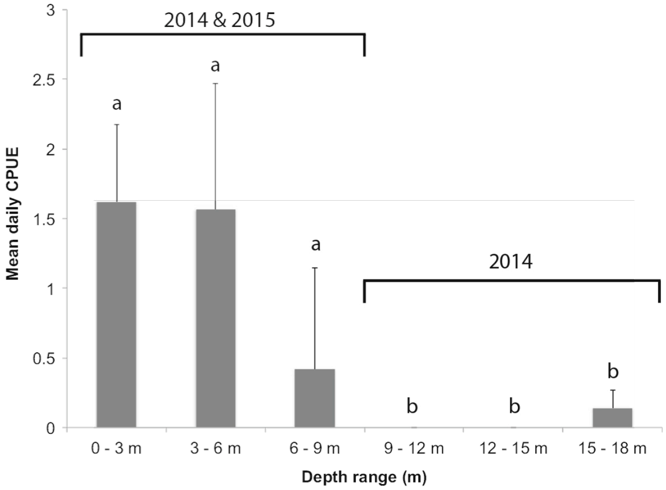


Fig. 3 Combined CPUE based on trap depth in 3 m bins. Error bars represent +1 standard deviation. Letters denote significance groupings. Data for 0–9 m ranges are combined for 2014 & 2015 as no difference in mean daily CPUE was detected

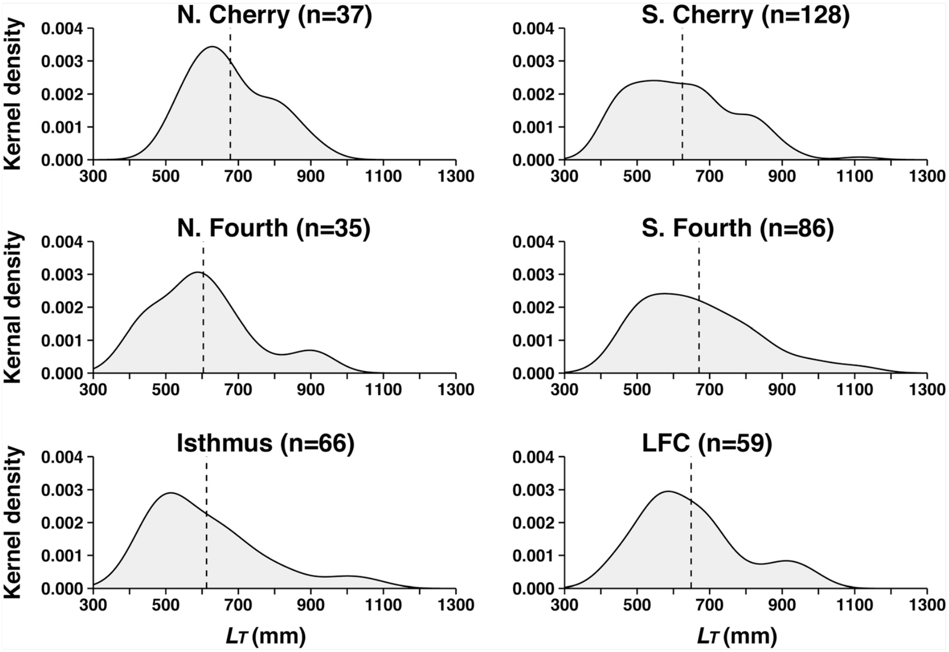


Fig. 4 Kernel density distribution plot of *G. mordax* size from the 6 trapping locations. Dashed vertical lines represent the mean size for each location with n = number of *G. mordax* collected. Hartigans' dip test results indicate that all distributions are unimodal

The condition factor (*K*) of *G. mordax* ranged from 0.15–0.24 across most size bins. Interestingly, the only size bin to show any significance between *K* values occurred in the smaller of the bins, 501–550 mm L_T size range (Tukey's HSD test, d.f. = 5, $0.001 < p < 0.01$; Fig. 5). In this bin, the skinniest individual, found in Cherry cove (K = 0.07; 555 mm L_T) was only 5 mm shorter than the thickest

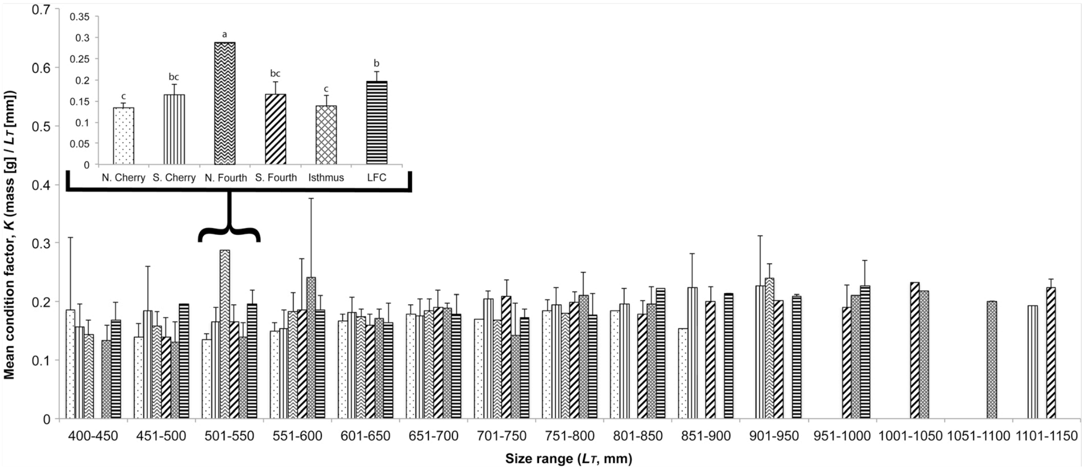


Fig. 5 Fulton's condition factor (K) for each trapping site binned in 50 mm (LT). Inserted graph highlights the only size group with a significant difference between sites. Letters above bars indicate significance groupings. Absent bars from size classes indicates no data available for the specific site in that size class. All error bars are +1 S.D.

individual 0.44 found in (Isthmus, 560 mm L_T). Statistical analysis could not be conducted on size bins greater than 901–950 mm L_T because too few individuals were collected ($N \leq 7$).

G. mordax Distribution and substrate associations

Based on the procrustes congruence tests, habitat characteristics varied significantly in their contribution along the different PC axes across the six trapping sites so that they could not be combined and were thus analyzed separately (Protest, $p > 0.05$; Fig. 6). Irrespective of trapping location, changes in mean, North-South, or East-West slopes were negligible (< 0.3 m) and loaded weakly in a preliminary PCA analyses. Therefore, all slope variables were omitted from further analyses. The PCA analyses using the variables trap depth, and % cover of boulder, cobble, sand, and bedrock, revealed that % boulder cover and cobble loaded strongly on the first two principal component axes for all six trapping sites (Table 1). This indicates that the number of *G. mordax* individuals caught was greater when traps were deployed in habitats with higher % cover of boulder and cobble, and lower % cover of sand and bedrock (Fig. 7). A complete loadings table is provided in Table S1.

When habitat composition was >40% sand or bedrock cover zero to few morays were collected. Roughly 14% of all traps thrown in locations with mainly boulder and cobble contained four or more individuals, with two cases containing as many as 10, and 12 individuals per trap. However, these patterns were not uniform throughout the depths sampled, as deeper sites that contained similar quantities of % boulder cover and cobble yielded few individuals compared to shallower sites.

Recaptured *G. mordax* were collected in habitats displaying an increase in % boulder and cobble, while decreasing in % cover of sand and bedrock. While this pattern held true between primary and secondary captures, as well as between secondary and tertiary captures, the change in habitat composition between captures were not statistically significant (Kruskal-Wallis rank sum test, $p > 0.2$).

Discussion

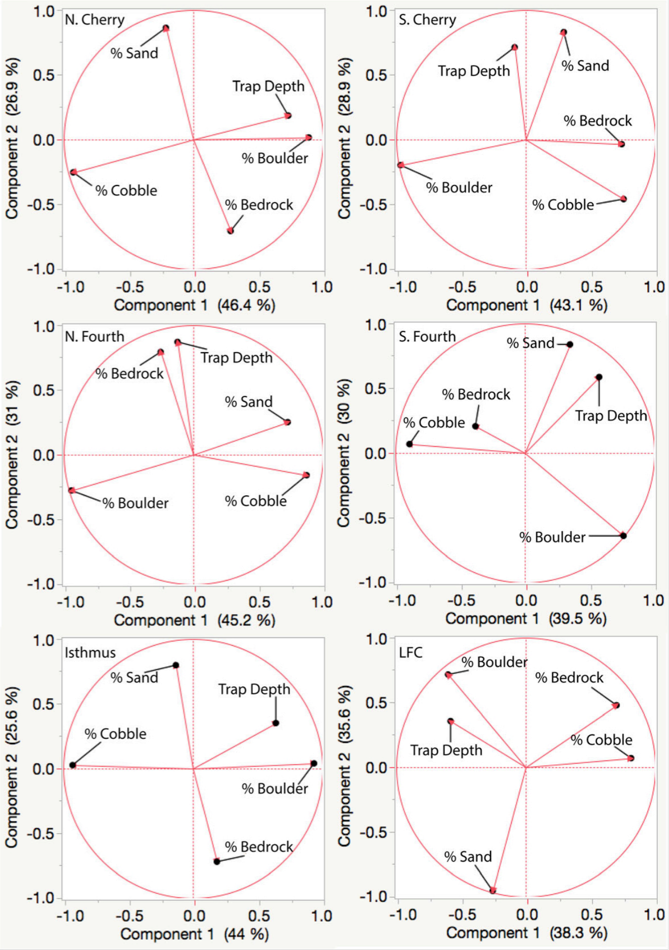
Our study provides the first description of *G. mordax* distribution based on associated habitat characteristics along a section of the leeward side of Catalina Island. We also report on the relative abundance, density and condition of individuals trapped. As predicted, our CPUEs increased with structural complexity; more morays were trapped in areas containing large proportions (50%+) of boulder cover and cobble. CPUE decreased as trapping area consisted of larger percentages of sand or bedrock. Furthermore, our results also suggest that *G. mordax* did not display signs of trap aversion, as mean daily CPUE did not decrease with repeatedly sampling the same trapping sites. Habitat transect slopes did not accurately predict *G. mordax* catch, suggesting that within the coves of Two Harbors, *G. mordax* distribution is primarily based upon shallow habitats covered with boulder (e.g., N. Fourth of July, S. Fourth of July, Isthmus, and LFC) or cobble (e.g., N. and S. Cherry).

Few published studies have incorporated data on *G. mordax* populations within Southern California waters. Graham (2004) surveyed both forested and deforested areas of kelp forests within the Channel Islands National Park, and found that *G. mordax* had the lowest frequency of occurrence compared to other kelp forest species. Additionally, Froeschke et al. (2006) found that *G. mordax* density averaged 0.01 ± 0.01 (SE) individuals per 100 m^2 within the Catalina Marine Science Center State Marine Reserve, and 0.02 ± 0.02 (SE) per 100 m^2 outside of the reserve, suggesting that *G. mordax* is one of the more rare carnivorous fishes within the system. However, these data were collected using standard fish population survey methodologies, such as diurnal, visual transects on SCUBA between 10:00 and 14:00 h (Froeschke et al. 2006). The density estimates based on our trapping results show that *G. mordax* is an abundant species within Two Harbors, occurring at densities of up to 100 times (e.g., N. Fourth) greater than previously reported.

Habitat complexity

Structurally complex habitats can promote species coexistence by providing more niche space, thus, reducing niche overlap and increasing overall system biodiversity (Levins 1979; Huston and DeAngelis 1994; Li et al. 2016). Strong relationships between habitat complexity and species distributions have been observed in both temperate and tropical marine ecosystems (Gray 1974; Jenkins et al. 1997; Beck 2000; Friedlander et al. 2003; Thrush et al. 2003; Anderson 2008; Graham and Nash 2013; Nash et al.

Fig. 6 Principal components analysis factors (unrotated) of all 6 trapping sites. For all sites, component PC1 accounted for no less than 39% of the variation whereas PC2 accounted for more than 21%



2013; Robinson 2015). Additionally, the complexities of rocky reef habitats have also been shown to impose strong effects on fish community structure (Sánchez-Caballero 2017). The high relative abundance of a relatively large marine predator, *G. mordax* in Two Harbors supports these ideas.

Structural complexity within habitat(s) not only serves to prevent resource overlap but may also play a role in providing refuge from predators especially smaller organisms that may be more vulnerable (Emson and Faller-Fritsch 1976; Crowder and Cooper 1982; Coull and Wells 1983; Diehl 1988; Safriel and Ben-Eliahu 1991; Hereu et al. 2005; Sandoval 2005; Smith et al. 2014). Therefore, habitat complexity serves multiple roles (Beck 2000). Another study found that different combinations of top predators (newts and salamanders) had variable effects on different habitat complexity treatments on intraguild predator survival (Anderson and Semlitsch 2016). Thus, the extent to which habitat complexity mitigates trophic interactions, by possibly reducing predation (i.e., increases predator free space) and competition may depend on various factors, such as shelter availability, behavioral attributes of interacting organisms, and the developmental stages of the predator/prey species at the time of the interaction (Almany 2004; Grabowski 2004). Therefore, the structural complexities of habitats have varying effects on different assemblages of species, and it confuses the study of habitat structure to combine them (Beck 2000). The discrepancies in relationships that different

Table 1 Abbreviated loadings for 5 variables used in PCA analyses. Numbers in parentheses indicate % variation explained by each component. A full list of PCA loadings can be found in the supplemental materials (Table S1)

North Cherry			South Cherry	
Parameter	Component 1 (46.4)	Component 2 (26.9)	Component 1 (43.1)	Component 2 (28.9)
Trap depth	0.73	0.19	−0.08	−0.71
% Boulder	0.89	0.02	−0.96	−0.19
% Cobble	−0.93	−0.26	0.75	−0.46
% Sand	−0.21	0.86	0.29	0.82
% Bedrock	0.29	−0.71	0.74	−0.03
North Fourth			South Fourth	
Parameter	Component 1 (45.2)	Component 2 (31)	Component 1 (39.5)	Component 2 (30)
Trap depth	−0.12	0.86	0.57	0.59
% Boulder	−0.94	−0.27	0.76	−0.64
% Cobble	0.87	−0.15	−0.89	0.07
% Sand	0.72	0.25	0.35	0.84
% Bedrock	−0.25	0.79	−0.38	0.20
Isthmus			LFC	
Parameter	Component 1 (44)	Component 2 (25.6)	Component 1 (38.3)	Component 2 (35.6)
Trap depth	0.64	0.35	−0.57	0.35
% Boulder	0.93	0.03	−0.59	0.71
% Cobble	−0.92	0.02	0.81	0.06
% Sand	−0.13	0.79	−0.25	−0.95
% Bedrock	0.18	−0.72	0.70	0.47

species have with similar degrees of habitat complexity will likely elicit a range of responses that are largely dependent upon the life history and ecology of the animals involved. For example, habitat characteristics that may provide refuge from predation for some species may simultaneously provide preferable foraging habitat for other predators in the system.

While temporal differences (i.e., day vs. night) were not tested in the present study, the combination of *G. mordax* preferring habitats with large % cover of

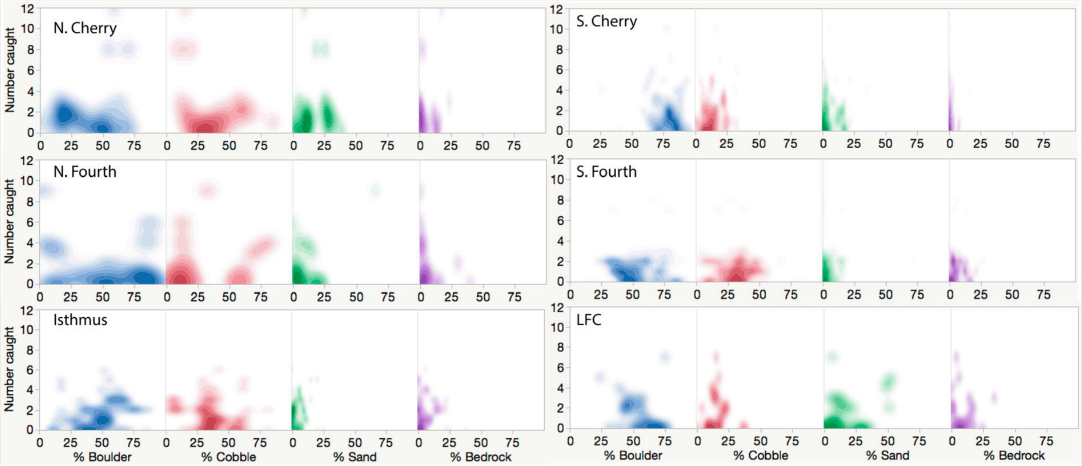


Fig. 7 Contour plots of all 6 trapping locations mapping number of *G. mordax* collected based on % cover of 4 substrate types

boulder and cobble and the striking temporal shifts documented in kelp forest community profiles potentially provide insights into which species morays may prey upon. During daylight hours, many large-mouthed generalized predators (e.g., kelp bass and olive rockfish), surfperches (e.g., black surfperch and striped surfperch), and small-mouthed grazing fishes (e.g., blacksmith, garibaldi, and halfmoon) remain within the water column within the kelp fronds above the reef (Ebeling and Bray 1976). However, at night, the large-mouthed predators and small-mouthed grazers take shelter within the cracks and crevices of the reef. As *G. mordax* has been described as an elusive species during daylight hours, it is considered a nocturnal hunter (Fitch and Lavenberg 1971). Therefore, the range of potential prey for *G. mordax* may be quite large as they forage in the same spaces between boulders and cobble as the diurnal species seeking shelter throughout the night. Research focused on the feeding ecology of *G. mordax* is necessary to understand the relationship between habitats and potential prey species.

We predicted that sites most exposed to the prevailing currents would reveal the most size structuring and have the highest densities of *G. mordax.* As predicted, moray populations with the highest degree of size structuring, were found at sites with more east/northeastern orientations. Individuals larger than 1100 mm L_T were captured only at South Cherry and South Fourth of July Coves. This discrepancy in size structuring across sites may be explained by current patterns and larval settlement. Circulation data obtained by QuikSCAT surface wind observations suggest that throughout the year, Two Harbors is continuously bathed in currents moving from the southwest to the northeast due to its placement within the Southern California Eddy (SCE) (Hu and Liu 2002). This effect is likely magnified during El Niño events, which is when *G. mordax* larvae are hypothesized to recruit to the island (McCleneghan 1973; Higgins et al. 2017). Therefore, sites that are more exposed to waters entering Two Harbors from the east may have a greater likelihood of being settled by *G. mordax* recruits. Furthermore, these sites may see enhanced settlement during weak recruitment years, as the probability of *G. mordax* settling to only these sites increases. However, while somewhat related to our hypotheses about settlement and the directionality of the currents, the possibility also exists that larger individuals are found within these coves because of more resources, such as prey size, and/or breadth of prey available. Additionally, the result that larger individuals were found only within the aforementioned coves may be due to variables related to habitat complexity that were not examined in our study. For example, crevice size may dictate resident moray size.

While our data support our prediction about size structuring, it did not support our data about densities. The largest densities were found in trap sites with south/southeast orientations (N. Cherry, N. Fourth, and Isthmus). This pattern may be explained by the fact that morays are generally solitary and tend to be cannibalistic (Hixon and Beets 1989, 1993; Fishelson 1997; Young and Winn 2003). We have also found conspecifics in the stomachs of larger (890–1100 mm L_T) *G. mordax* (Higgins and Mehta, unpubl. Data). Therefore, high density areas may exhibit less size structuring because of predation or intraspecific competition for den space – a behavior observed in tropical congeners (Lozano-Álvarez et al. 2010).

Allen et al. (1992) found that the average densities of cryptic species were up to four times as dense as more conspicuous fishes in shallow waters (<10 m) of Two Harbors. However, due to the small size, fast growth, and short life span of the cryptic species observed in their study, the authors suggested that such species accounted for only about 10% of the biomass of the conspicuous fishes. A recent ageing study of *G. mordax* suggest that California morays are a large, long-lived and slow growing species (Higgins et al. 2017), and likely to contribute far greater biomass to the system than cryptic species documented by Allen et al. (1992). In fact, we calculated *G. mordax* biomass to be 173.83 kg in the coves of Two Harbors during our trapping efforts (excluding recaptured individuals, ~37% of all captured individuals). We presume that a biomass of this magnitude would make a substantial contribution to the resident predator biomass within the kelp forest system, similar to what is suggested for tropical morays (Gilbert et al. 2005). Additionally, we suggest that there are likely more individuals inhabiting the crevices between the boulders and cobble than reported here, because smaller individuals did not recruit to the trapping gear deployed in this study. The smallest *G. mordax* we were able to collect was 400 mm L_T, either because smaller individuals did not enter the trap, or were able to escape through the wire mesh during trap soak time. Difficulties in capturing smaller individuals of fishes with similar elongate body shapes have been documented in other studies (morays: Matić-Skoko et al. 2011, conger eels: Hood et al. 1988; O'Sullivan et al. 2003).

Insights into moray movement

Throughout the course of our study, 35 *G. mordax* were recaptured in traps associated with habitat data across all six sites. Interestingly, all 35 of the recaptured individuals were captured in the same trapping site at which they were originally collected, suggesting very little movement, even across years. In addition to providing some data on the habitat composition of recaptured *G. mordax*, PIT tag data also indicated that both within and across years, individuals did not move between trapping locations, or cross even relatively narrow stretches of sandy bottom / rhodolith bed habitat present in North and South coves of Cherry (~197 m @ narrowest point) and Fourth of July (~72 m @ narrowest point). Moreover, even if suitable habitat and shallow depths was available, individuals were not observed to move between South Fourth of July and Isthmus trapping sites, which is separated by roughly only 86 m of coastline. Generally speaking, moray eels are thought to rarely leave their respective crevices, maintaining high site fidelity (Böhlke et al. 1989). Our results suggest that *G. mordax* not only exhibits cove fidelity but also may even exhibit small-scale site fidelity in Two Harbors, Catalina Island. Such small-scale site fidelity may result in ecological impacts similar to those found in tropical species in the Bahamas, where the density of morays inhabiting patch reefs greatly influenced both the local density and size structure of recently settled reef fishes (Carr and Hixon 1995).

Evidence from studies conducted in tropical waters suggest that moray eels are predatory fishes that can be found in densities (5.6 individuals per 125 m^2) similar to commercially important predatory fishes, such as sea-basses, groupers and snappers (Gilbert et al. 2005). Moreover, the presence of morays has been shown to alter future community structure by preying upon newly settled recruiting fishes on Caribbean patch reefs (Parrish et al. 1986; Carr and Hixon 1995; Young and Winn 2003). Stable isotope analyses of giant morays (*Gymnothorax javanicus*) in Indonesia, confirms that morays can be apex consumers predating upon fishes, lobsters and octopus (Page et al. 2013). Morays have also been called upper-level predators because they are less frequently preyed upon by other organisms (Young and Winn 2003).

Recent documentation of diverse prey manipulation behaviors (Diluzio et al. 2016) and the ability of large individuals to consume both small and large kelp bass (Harrison et al. 2017) suggest that *G. mordax* may have an important functional role in Southern California kelp forest ecosystems. Our reports of similar densities for the California moray compared to tropical moray species studied thus far reveal that future research focused on gathering baseline life history data as well predator-prey interactions are important (Dayton et al. 1998). This is especially true with the designation of new marine protected areas, or more specifically, State Marine Conservation Areas, in and around Two Harbors. Information on California moray predation rates and the composition of prey in their diet with respect to our commercially important fisheries (e.g., California spiny lobster, kelp bass) will further help inform our understanding of species distributions and kelp forest community structure.

Previous studies on the Southern California kelp forest ecosystem have focused on diurnal species and their associated distributions with some exceptions (Lin et al. 2016). In combination with behavioral traits such as its benthic, nocturnal, elusive lifestyle and its preferred habitat consisting of mainly boulder and cobble substrates, *G. mordax* likely possess a functional role that has the potential to shape overall species distributions and community composition.

Evidence from ecological studies of tropical moray eels suggests that *G. mordax* may have an important functional role, particularly when considering this predator's high site fidelity, density, and biomass contributions to the southern California kelp forest ecosystem. It is also worth noting that the present study was conducted on Catalina Island – one of eight islands comprising the Channel Islands archipelago. Future studies examining moray distribution and relative abundance on other islands are necessary to better understand the distribution of leptocephalus larvae by California currents.

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Supporting Information (Table) for
Distribution and habitat associations of the California moray (*Gymnothorax mordax*) within Two Harbors, Santa Catalina Island, California

Benjamin A. Higgins & Rita S. Mehta

Table S1: Complete loadings list of 5 variables used in PCA analyses.

North Cherry

Parameter	Component 1	Component 2	Component 3	Component 4	Component 5
Trap depth	0.73	0.19	0.49	0.44	-0.00
% Boulder	0.89	0.02	-0.45	-0.05	0.00
% Cobble	-0.93	-0.26	0.04	0.27	0.00
% Sand	-0.21	0.86	0.40	-0.23	0.00
% Bedrock	0.29	-0.71	0.59	-0.26	0.00
% *Variation*	46.4	26.9	19.0	7.76	0.00

South Cherry

Parameter	Component 1	Component 2	Component 3	Component 4	Component 5
Trap depth	-0.08	0.71	0.63	0.27	0.00
% Boulder	-0.96	-0.19	0.12	-0.10	0.01
% Cobble	0.75	-0.04	0.05	0.46	0.01
% Sand	0.29	0.82	-0.47	-0.03	0.01
% Bedrock	0.74	-0.03	0.36	-0.55	0.00
% *Variation*	43.1	28.9	15.7	12.3	0.01

North Fourth

Parameter	Component 1	Component 2	Component 3	Component 4	Component 5
Trap depth	-0.12	0.86	0.25	0.40	-0.00
% Boulder	-0.94	-0.27	0.18	0.04	0.02
% Cobble	0.87	-0.15	-0.38	0.24	0.01
% Sand	0.72	0.25	0.57	-0.26	0.01
% Bedrock	-0.25	0.79	-0.47	-0.29	0.00
% *Variation*	45.2	31	16	7.78	0.02

South Fourth

Parameter	Component 1	Component 2	Component 3	Component 4	Component 5
Trap depth	0.57	0.59	-0.04	0.57	-0.00
% Boulder	0.76	-0.64	0.07	0.04	0.03
% Cobble	-0.89	0.07	-0.40	0.21	0.03
% Sand	0.35	0.84	-0.11	-0.41	0.02
% Bedrock	-0.38	0.20	0.90	0.07	0.01
% *Variation*	39.5	30.0	19.7	10.8	0.05

Isthmus

Parameter	Component 1	Component 2	Component 3	Component 4	Component 5
Trap depth	0.64	0.35	0.29	0.61	-0.01
% Boulder	0.93	-0.72	0.66	-0.06	0.04
% Cobble	-0.92	0.02	-0.04	0.34	0.11
% Sand	-0.13	0.79	0.48	-0.33	0.03
% Bedrock	0.18	-0.72	-0.66	-0.06	0.04
% *Variation*	44	25.6	17.2	12.5	0.64

LFC

Parameter	Component 1	Component 2	Component 3	Component 4	Component 5
Trap depth	-0.57	0.35	0.70	0.21	0.00
% Boulder	-0.59	0.71	-0.27	-0.22	0.05
% Cobble	0.81	0.06	0.39	-0.42	0.03
% Sand	-0.25	-0.95	0.03	0.13	0.05
% Bedrock	0.70	0.47	-0.09	0.51	0.03
% *Variation*	38.3	35.6	14.6	11.2	0.16

Chapter 3

Eat Whole and Less Often: Ontogenetic shift reveals size specialization on kelp bass by the California moray, *Gymnothorax mordax*

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Abstract

Despite the importance of predation in many ecosystems, gaps remain in our understanding of nocturnal marine predators. Although the kelp forests of Southern California are some of the most well-studied ecosystems, California morays, *Gymnothorax mordax,* are predominately nocturnal predators that have remained largely unstudied and their predatory effects on the kelp forest ecosystem are unknown. We use a multiyear dataset to examine the dietary breadth of *G. mordax* and to determine the functional role of this predator. We also quantify bite force to examine the potential limitations of morays in exploiting prey. Stomach content analyses and Linear Selectivity Index values indicate that *G. mordax* specializes on kelp bass, *Paralabrax clathratus*. Average size of kelp bass consumed varies across years, suggesting that morays respond to fluctuations in prey size availability. The scaling relationship of kelp bass standard length and moray head length reveals an ontogenetic shift where maximum prey size increases with moray size and the minimum size class of prey is dropped from the diet of larger individuals. Stomach content analyses also revealed that morays consume other small fishes and invertebrate prey. Moray bite force exhibited strong positive allometry with moray head size, suggesting that larger morays exhibit greater bite forces for their head and body size. However, we found no relationship between prey size and bite force, suggesting that a disproportional increase in bite force does not facilitate the consumption of disproportionately larger prey. Our results indicate that while *G.*

mordax of Catalina Island is a dietary specialist it is capable of exhibiting functional shifts in prey size and species based on their abundance.

Key Words: bite force, dietary specialization, kelp bass, morays, predator-prey size relationships

INTRODUCTION

Predation dramatically affects the dynamics, relative abundance, and distribution of prey populations thereby influencing the pattern and direction of energy flow from lower to higher levels in food webs (Morin 2011). The effects predators have on their prey depends on the degree of prey specialization which is often dictated by a predator's morphology (Werner 1977; Persson et al. 1996; Wainwright and Richard 1995) and whether predators themselves respond to changes in prey availability and density (Redpath and Thirgood 1999). Classification of predators as specialists or generalists informs the functional role of predators and how they may respond to fluxes in prey density (Andersson and Erlinge 1977). Whereas specialists tend to respond to changes in prey densities by immigrating to a new prey patch, generalists can respond similarly to specialists or can respond functionally via prey switching (Murdoch 1969; Andersson and Erlinge 1977; Redpath and Thirgood 1999). Such frequency-dependent predation has shown to have a stabilizing influence on prey numbers (Redpath and Thirgood 1999) and maintain overall biodiversity in the ecosystem.

The terms 'specialist 'and 'generalist' also describes the breadth of the dietary niche. However, dietary niche is not only defined by the types of prey consumed but also by prey size. Prey size is particularly important when investigating how feeding behavior and diet may change over a species' lifetime. There are a myriad of reasons as to why predators may become more successful at larger body sizes (i.e. increased muscle mass, larger gape, increased endurance). Therefore, it is expected that changes in body size may result in a linear shift in prey size (Arnold 1983; Persson 1990; Juanes 1994; Mittelbach and Persson 1998; Jacobson et al. 2018). Scharf et al. (2000) discovered that while larger predators (>500 mm) tend to exhibit a narrowing in the breadth of relative prey sizes consumed over ontogeny (i.e. ontogenetic telescoping), asymmetric predator-prey size distributions appear to be a common pattern in aquatic communities. Therefore, the relative sizes of predators and their prey are important factors in determining predator-prey dynamics (Shurin et al. 2006) and are a critical component to understanding the mechanisms of the observed predator-prey relationships (Woodward et al. 2005; de Roos and Persson 2013).

Studying the ontogenetic changes to the underlying functional morphology of the feeding apparatus can also contribute insight into understanding predator-prey relationships. Functional measures of feeding performance such as bite force have potential to indicate resource use among the potential prey available (Osenberg and Mittelbach 1989; Pérez-Barberia and Gordon 1999; Marshall et al. 2012). Ontogenetic changes in bite force can facilitate specialization or generalization on different prey types and/or sizes and can therefore be used to elucidate asymmetries in resource use. For example, individuals that can exert greater bite forces can expand their dietary breadth by consuming larger or more robust food items (Verwaijen et al. 2002; Herrel et al. 2006; Bulté et al. 2008) and/or reducing handling times for both prey capture and consumption (Verwaijen et al. 2002; van der Meij and Bout 2006; Anderson et al. 2008). Thus, the maximum size of prey predators may be able to consume should change throughout ontogeny (Erickson et al. 2003; Sánchez-

Hernández et al. 2012). We expect that predator-prey relationships will be especially strong in piscivorous predators that consume prey whole.

In this study, we examine the dietary ecology of the California moray eel, *Gymnothorax mordax.* While previous studies have revealed that morays exhibit specialized morphology for both prey capture and transport (Mehta and Wainwright 2007), the head length and vertical gape distance in the California moray increase disproportionately over ontogeny (Harrison et al. 2017) suggesting that the moray feeding apparatus may be under strong selective forces to quickly increase gape size enabling larger individuals to consume larger prey items (Mittelbach 1981; Wainwright and Shaw 1999). Nevertheless, no study has recorded the diet of the California moray and examined predator-prey size relationships in any detail.

Although researchers have traditionally identified California morays as predators in Southern California kelp forests with diverse prey handling strategies (Diluzio et al. 2016), their prey breadth remains unknown. The paucity of dietary information stems from the fact that California morays were thought to be relatively rare (Graham 2004; Froeschke et al. 2006). Recent work, however, revealed that the larvae of these cryptic predators are brought to Catalina Island during episodic El Niño events (Higgins et al. 2017) resulting in an abundant and relatively large biomass (~173.83 kg) of *G. mordax* within the rocky reefs of Two Harbors, Catalina Island (Higgins and Mehta 2017). As El Niño events have been shown to greatly alter the distribution of larval fish and resultant fish assemblages (Cowen 1985; Allen et al. 2002), one would anticipate temporal variation in predator-prey relationships.

Assessing temporal changes would require dietary analyses over consecutive years and preferably incorporating an El Niño event.

Here, we used a multi-year data set to examine diet and to detect any size-based feeding habits of the California moray eel. Our objectives of this study were three-fold. First, we examined the dietary breadth of *G. mordax* and determined where the California moray fits on a continuum from generalist to specialist with respect to prey available in the environment. Second, we recorded *in vivo* bite force for a size range of morays to examine how feeding performance changes over ontogeny. Third, we use information on prey size and moray size to test whether average prey size increased over ontogeny. Through this multifaceted approach, we can better understand the trophic position and functional role of this elusive but abundant predator inhabiting the southern California kelp forest ecosystem.

MATERIALS AND METHODS

Trapping

Gymnothorax mordax were collected using custom-built, dual-chambered wire mesh traps (N=20, 36” x 11” x 9”; Staten Island, NY) during the mid-late summer months (July-September) from 2012 - 2016 around Two Harbors, Catalina Island, CA (33°26’45.4”N, 118°29’31.3”W). Traps were set daily between 1800-1900 hours and baited with frozen anchovies, which were placed into perforated plastic bottles allowing odor to serve as an attractant while prohibiting access to the bait. Mesh traps were randomly deployed within six trapping sites spread across four coves in Two Harbors (Fig. 1). Additional traps were set east of Lion’s Head Point (33°27'10.58"N, 118°30'3.94"W), and the slopes between Cherry and Fourth of July Coves (33°26'56.74"N, 118°29'57.49"), as well as Fourth of July and Isthmus coves (33°26'45.20"N, 118°29'52.44"W). These traps were used as the start/end points for prey availability and abundance transects. Traps were deployed around 1600 hrs and retrieved the following morning between 7:30-9:30 am.

Gut content analysis & morphological measurements

Trapped *G. mordax* were brought onboard a 6 m skiff. Individuals were placed in a lidded bucket filled with seawater and Tricaine Methanesulfonate (MS-222) buffered with sodium bicarbonate at roughly 90mg/liter. Once sedated, moray mass (g), total length (L_T, mm; defined as distance from anterior tip of snout to posterior tip of tail), head length (L_H, mm; defined as the linear distance between the anterior tip of the head and the posterior edge of the parabranchial opening), head width (L_w, mm; defined as the linear distance spanning the lateral sides of the A2 subdivision of the adductor mandibulae muscles) were all recorded. Following these morphometric measurements, morays were examined for gut contents. We obtained consumed items via manual palpation, an effective and non-invasive method for recovering recently ingested items that is commonly used to obtain gut contents from snakes, another predator that consumes prey whole (Mushinsky and Herbard 1977; Fitch 1987). Prey items within the gut were massaged anteriorly and carefully extracted from the mouth and teeth with forceps (Fig. 2). All dietary items recovered were identified to lowest taxomonic group, and maximum lengths (mm) for whole prey were recorded.

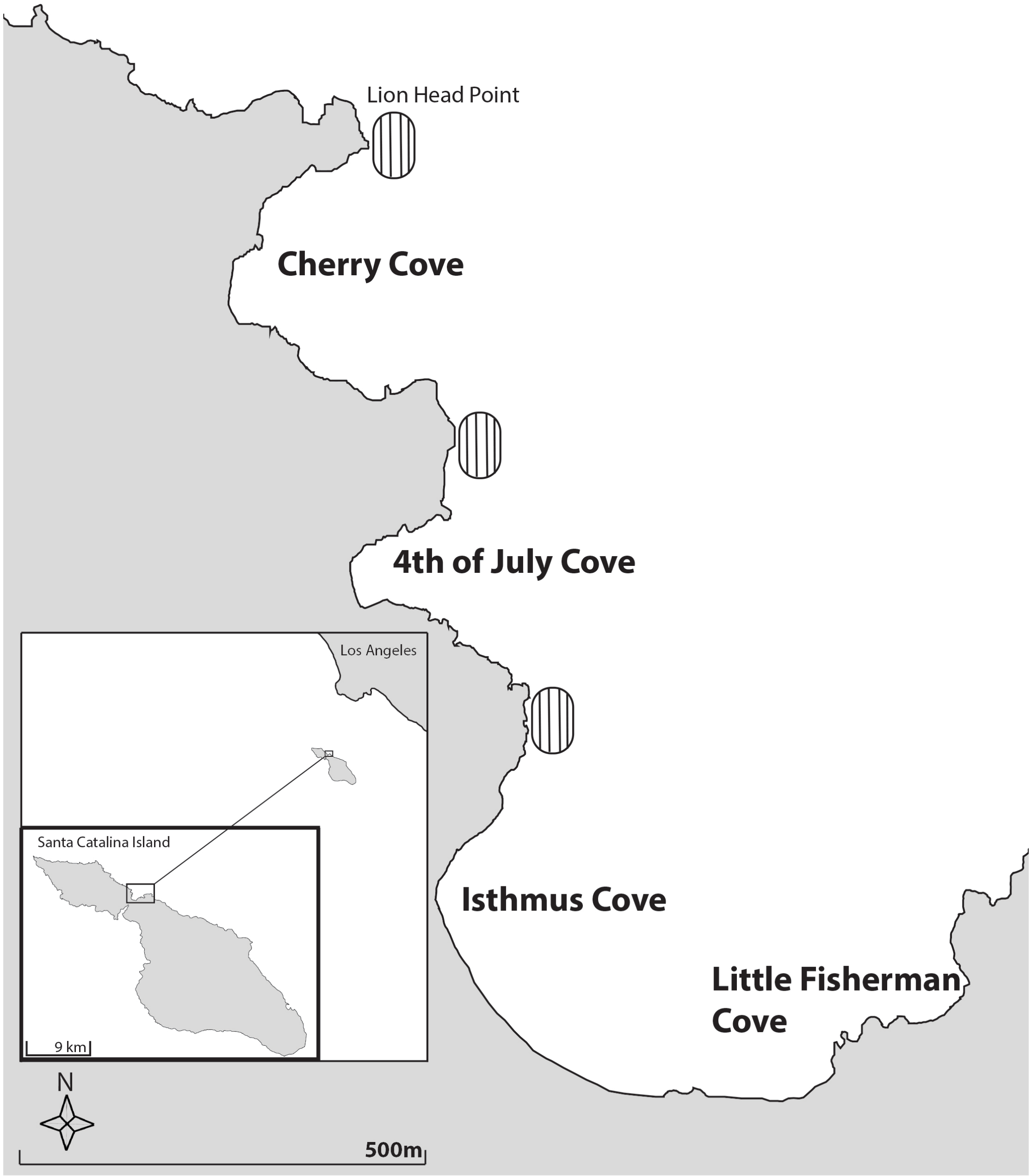

Figure 3.1: Map of Two Harbors, Catalina Island. Trapping locations are displayed in bold font. Ovals represent locations where prey availability and abundance transects were conducted in 2013.

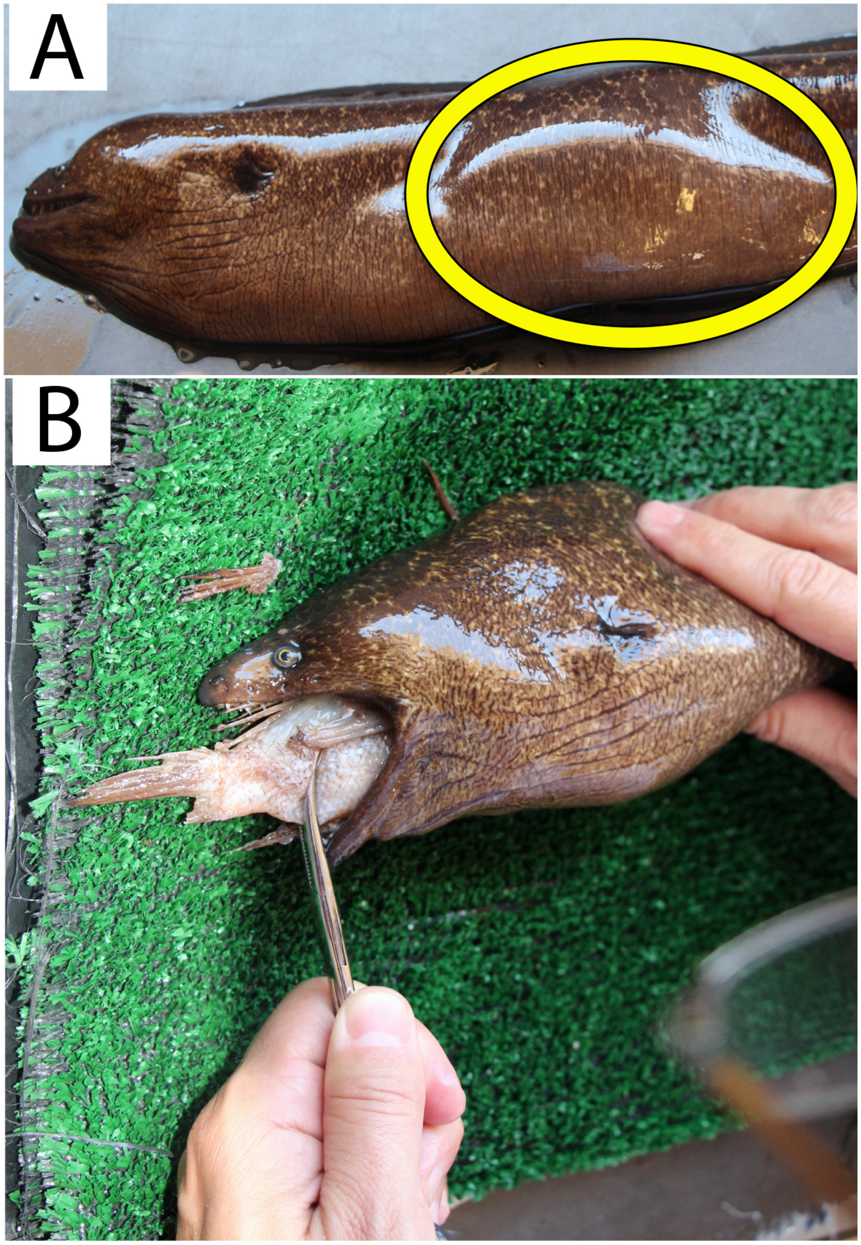

Figure 3.2: A) Prey bolus indicated by yellow circle on sedated *G. mordax.* B) Example of how we extract a prey item in this case, kelp bass, using forceps. The item was first massaged towards the oral jaws via manual palpation.

Prey availability and abundance

Observations of potential invertebrate and vertebrate prey were obtained from Reef Check California's online Global Reef Tracker database. These data enabled us to analyze prey availability and abundance for all years included in the present study (2012-2016). Reef Check California surveys the relative abundance and size distribution of species using a methodology based on the Department of Fish and Game's Cooperative Research and Assessment of Nearshore Ecosystems (CRANE) monitoring program. Transects are conducted in both onshore and inshore reefs with a maximum depth limit of 18 m, with a series of three transects spanning 30 m each. Transects are conducted annually at the same sites in which morays were collected. In 2013, we conducted our own prey availability and abundance transects to corroborate the Reef Check survey results and found strong correspondence (see supplemental materials).

To categorize morays as predators on a continuum from generalist to specialist, we used the linear selectivity index (*L*; Strauss 1979), which requires knowledge of both the prey items available in the environment and those found through gut content analyses. *L* selectivity is a unitless number and is the unweighted difference of the proportions of prey items found in the gut and the same item(s) recorded in the habitat. Thus, an *L* value of 0 would indicate that *G. mordax* is not specializing on any particular prey item(s) and is a generalist consumer whereas a value closer to 1 suggests that there is strong specialization for a particular prey, while negative *L* values indicate avoidance, or inaccessibility of prey.

Bite force

To quantify moray feeding performance over ontogeny, we measured *in vivo* bite force for as many of the trapped individuals as possible. We used a piezoelectric force transducer (Kistler Quartz Force Sensor type 9203) mounted between custom made steel cantilever beams and fitted with a handheld charge amplifier (Kistler type 5995A). Steel bite plates were fixed onto the cantilever beams and set 2.4 cm apart. Following recommendations from Lappin and Jones (2014), we covered the steel bite plates with leather to reduce stiffness of the bite plates and to avoid subjecting morays to possible tooth and jaw damage during biting trials. We recorded maximum bite forces from trapped individuals. An individual moray was placed in a 5 gallon bucket to constrain the body of the animal and the force transducer was positioned in front of the moray's mouth to elicit biting. All bite force data were recorded from anterior bites. Therefore morays presumably bit with the peripheral and median intermaxillary teeth and teeth along the anterior dentary of the oral jaws. We then sedated each individual to record the same suite of morphometric data (mass, total length, head length, and head width) as described above, and then released individuals to their original coves, once they recovered from anesthesia. These data were collected during the 2015 and 2016 summer months.

Statistical analyses

All statistics were carried out in R 3.4.1 (R Core Team, 2017). We tested whether prey distributions across all trapping sites varied between years using Kolmogrov

Smirnov tests. Differences in kelp bass sizes consumed across years was tested using an ANOVA followed by a Tukey's honest significant test (HSD). The variances of the annual kelp bass sizes were tested using Levene's test for equal variance. Repeated Hotelling's two-sample t-tests were used to determine if consumed prey proportions differed across years (R package "Hotelling"). For each year, we also presented the size distribution of morays with stomach contents.

We examined scaling relationships between moray size and bite force using standardized major axis (SMA) regressions in the R package smatr. Moray size measurements included the following morphometrics in mm: body mass, body length, head length, and head width. Scaling relationships were statistically compared using modified t-tests with null predictions of the isometric slopes: 1.0 for linear measurements, 2.0 for areas and forces, and 3.0 for masses based on Euclidean geometry (Hill, 1950; Schmidt-Nielsen, 1984). We observed whether the predicted slopes fell within or outside the 95% confidence intervals of the observed SMA regression slopes as a guide for positive or negative allometry, respectively. We adjusted all P values using a Benjamini-Hochberg correction to reduce the type I error probability across multiple comparisons (Benjamini and Hochberg 1995). This same statistical protocol was used to test the hypothesis that prey size varied with bite force. We tested whether the relationship between prey size and moray head length/bite force was significantly different from our isometric predictions to determine whether larger bite force facilitates access to larger prey and whether larger morays were consuming larger prey. To do this, we used the prey size data extracted from the stomachs of individuals that closely matched the sizes of morays from when we measured in vivo bite force.

We then tested the prediction that morays exhibit an ontogenetic shift in average prey size. Since morays exhibit morphological adaptations for consuming large prey, we wanted to establish the range of maximum and minimum prey sizes across moray ontogeny. To do this we adopted an approach by King (2002) which further uses regressions to examine the upper and lower bounds of prey. We first used ordinary least squares regression (OLS) of log-transformed moray head length and log transformed prey standard length to determine the relationship between the two variables. Then, we analyzed the variation in data surrounding the regression by examining only positive and then only negative residuals. We ran subsequent OLS regressions for data points falling above the regression line (points with positive residuals) and those data below the regression line (points with negative residuals) to determine whether the lines forming the upper and lower bounds of prey size were significantly different from a slope of 0. Slopes that were significantly different from 0 suggest that maximum and minimum prey size increases with moray size.

RESULTS

Gut contents

Between 2012 and 2016, we trapped 1338 moray eels across our six trapping sites (Fig. 1). From these morays, we isolated 169 distinguishable dietary items from the stomachs of 196 *G. mordax* (14.6%). The proportion of trapped morays with food in their stomachs varied little from 2013 to 2016 (16 - 17%). Ironically, in 2012, we trapped the most morays but retrieved the least amount of dietary items (8%).

During our five years of trapping, ~72% of the morays with stomach contents contained only a single dietary item in their gut. The most we recovered from a single moray was four kelp bass (*Paralabrax clathratus*). Moray diet consisted mainly of fish (range: 69% – 95%), with kelp bass as the most frequently consumed prey item (range: 63 - 297 mm, L_T; Fig. 3). On average, kelp bass composed ~64% of the dietary items recovered (range over the years: 40% – 93%). ANOVA revealed that the average size of consumed kelp bass varied across years ($p < 0.0001$; d.f. = 4; F = 12.75). A Tukey's post-hoc test showed the average size of kelp bass that morays consumed in 2015 (103 mm) was significantly smaller than those consumed in 2014 (140 mm; $p < 0.0001$), 2016 (135 mm; $p < 0.05$), and 2012 (172 mm; $p < 0.0001$). However, mean kelp bass size consumed in 2015 and 2013 wasinot significantly different ($p > 0.37$).

The second and third most frequently consumed items were red rock shrimp (*Lysmata californica)* and two-spotted octopus (*Octopus bimaculoides*), respectively (Supplementary Table 1). Harder prey items such as kelp crab (*Pugettia productus*) and California spiny lobster (*Panuliris interruptus*) were also retrieved from the stomachs; however, these items were typically on the smaller end of the size range for the species (< 100 mm) and infrequently consumed (8 times over five years; ~5% of all dietary items). Two mantis shrimp (*Hemisquilla ensigera*) were recovered from the stomachs of morays (in 2013 and 2016), and a single blind goby (*Typhlogobius* *californiensis*) was recorded in 2015. Other notable dietary items include juvenile garibaldi (*Hypsypops rubicundus*), blacksmith (*Chromis punctipinnis*), and conspecifics; cannibalism was only observed in 2015 and 2016 (Table S1). The number of prey items consumed did not vary across years (Kolmogrov Smirnov test, $0.09 < p < 0.7$). Similarly, no significant difference was detected between the proportions of prey items consumed across years (Kolmogrov Smirnov test, $0.09 < p < 0.94$).

We binned morays into four size categories to examine which moray sizes were consuming the range of kelp bass sizes within and across years (Fig. 4). While at least one individual from all size categories was represented across the five years, the most common size category for which we removed stomach contents was the 75mm-106mm L_H category. In 2015, stomach contents from multiple individuals from all four size categories were represented.

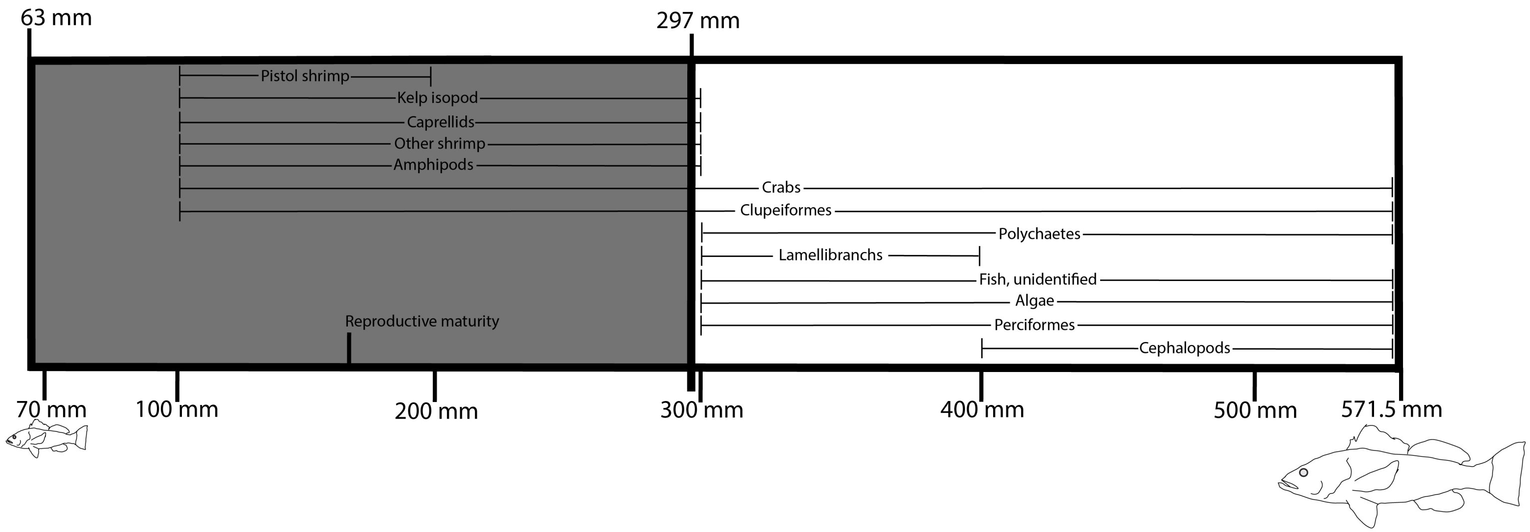

Figure 3.3: Size range of kelp bass consumed by *G. mordax* (shaded area) relative to reported size range of the species. Total size range of kelp bass was from data reported in Young, 1963. The reproductive maturity (178mm L_T) and most frequently consumed dietary items of kelp bass relative to size are overlaid (data from Quast, 1968).

Figure 3.4: Bars represent the contribution of five prey categories to the diet of *G. mordax*. Each bar reflects diet data for a single year. Kernel density plots are displayed on the right with mean size (vertical lines) of kelp bass consumption by L_H range (mm) and age class, in parentheses. L_H were converted to age class date following the regression line presented in Higgins et al. 2017.

Dietary habits: Specialist or Generalist

Although linear selectivity index values (*L*) varied across years (Fig. 5), kelp bass consistently exhibited the highest *L* relative to other items in the habitat in all years except 2013 *L* range = 0.84 – 0.17; *L* in 2013 = 0.17). Two-spotted octopus exhibited the highest *L* in 2013 (0.25). Red rock shrimp *L* range = 0.04 (2012) – 0.18 (2013) and two-spotted octopuses *L* range = 0.03 (2014) – 0.25 (2013) were the only other dietary items that displayed consistent positive *L* values across years. We found that morays did not consume the most commonly occurring species in the environment. Although blacksmith were the most dominant vertebrate species counted in transect surveys, these fish were infrequent in the stomachs of morays (*L* range = -0.50 – -0.44). Señorita (*Oxyjulis californica*) and California sheephead (*Semicossyphus pulcher*) were also commonly observed in the environment but neither of these species were ever recovered from moray stomach contents. Overall, these results suggest that *G. mordax* primarily specializes on kelp bass with invertebrates serving as supplementary prey.

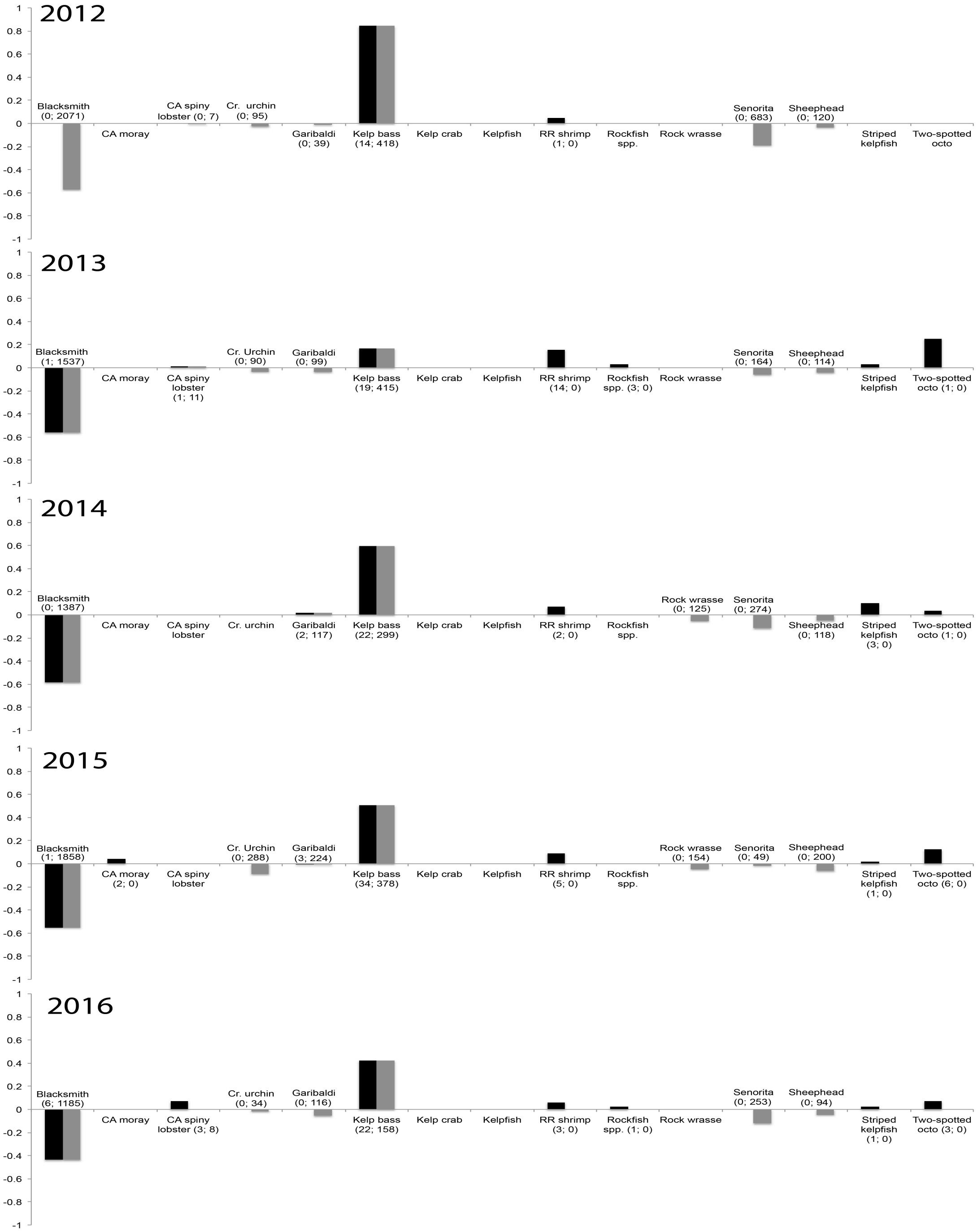

Figure 3.5: Paired linear selectivity index (*L*) values for the dietary items *G. mordax* consumed across years (black bars). Grey bars indicate *L* values for those items counted (if present) by Reef Check California survey transects. Numbers in parentheses indicate number of items morays consumed; number of individuals Reef Check California counted.

Bite Force

We collected bite force measurements on 49 *G. mordax* (range: 567 – 1192 mm L_T; mean: 804 mm L_T) during the 2015 and 2016 trapping seasons. Bite forces ranged from 32.69 to 467.69 N and scaled with strong positive allometry with most morphological measurements (mass: $R^2 = 0.43$, slope = 0.73; L_T : $R^2 = 0.46$, slope = 2.65); and L_H : $R^2 = 0.46$, slope = 2.4; both $p < 0.0001$). Head width (L_w) was the only morphological feature that showed a negative allometric relationship with bite force ($R^2 = 0.42$, slope = 1.71, $p < 0.0001$; Fig. 6). Based on the strong allometry between bite force and head length, we tested the relationship between prey size (SL_{mm}) and bite force. We found no relationship between prey size and bite force in each of our prey categories (kelp bass, $p > 0.383$); mixed fishes, $p > 0.684$; and invertebrates, $p > 0.665$) suggesting that an increase in bite force does not facilitate morays consuming larger kelp bass, larger mixed fishes or invertebrate prey.

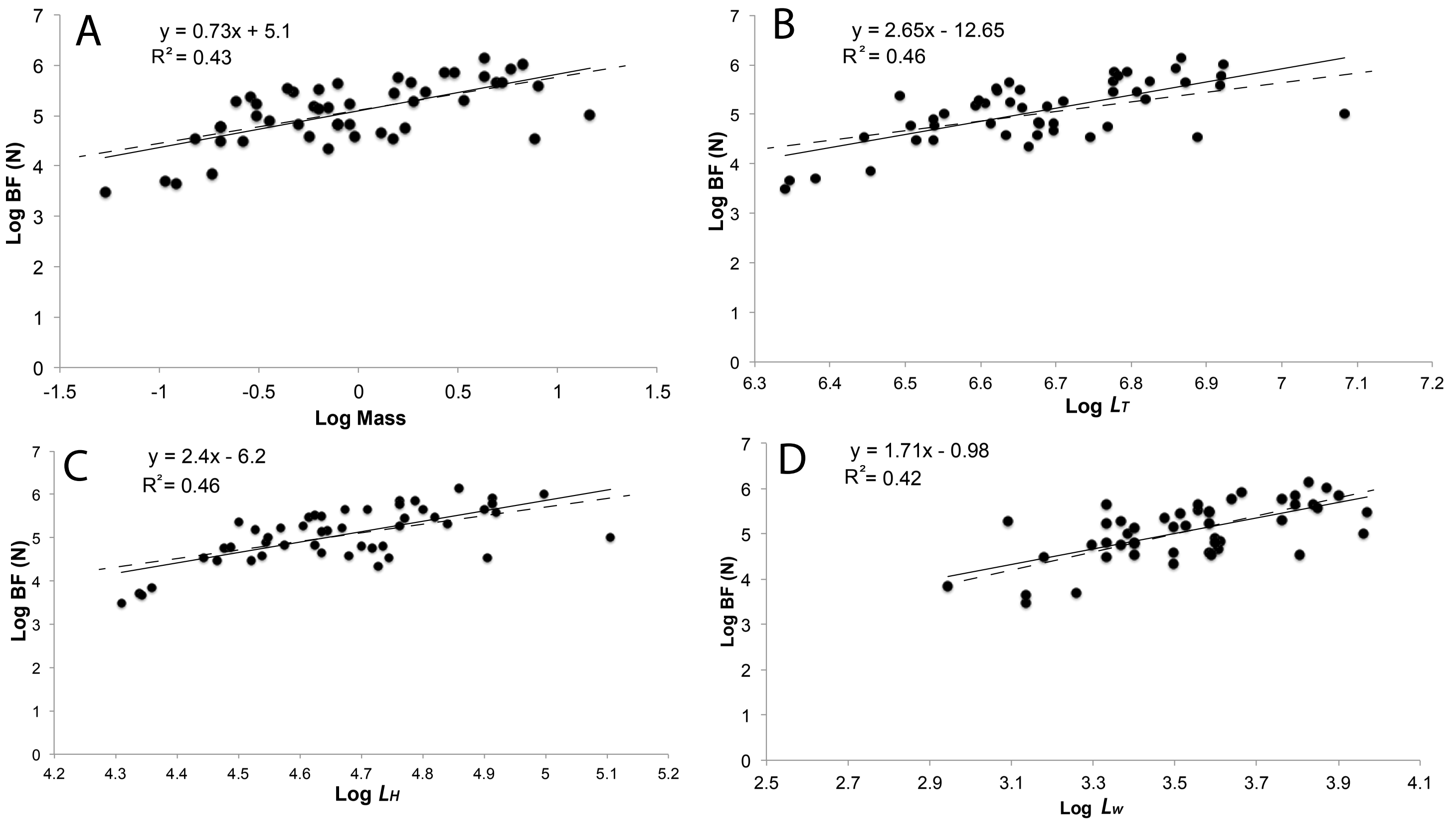

Figure 3.6: Relationships between *G. mordax* bite force (log) and mass (A), total length (B), head length (C) and head width (D). All variables, with the exception of head width, display a positive allometric relationship with bite force (R^2 range: 0.42 – 0.46). Head width exhibited a negative allometric relationship. Dashed lines represent an isometric slope.

Predator-prey size relationships

We measured total lengths (L_T) for 125 wholly intact prey items. The largest dietary item recovered was a kelp bass (297 mm, L_T), which was consumed by the largest moray in our dataset (1195 mm, L_T). This kelp bass length was ~26% of the moray's total length, and ~ 169% of its L_H.

The smallest prey consumed was a kelp crab (11 mm, carapace length), which was extricated from a moray measuring 692 mm in L_T (1.6% of the moray's L_T). There was no relationship between moray L_H and prey length for all prey categories (kelp bass: $p > 0.372$; mixed fishes: $p > 0.644$; invertebrate prey: $p > 0.665$). However, the regression lines between moray L_H and maximum and minimum prey size for kelp bass significantly differed from 0 (maximum and maximum, $p < 0.001$), indicating an ontogenetic shift where maximum and minimum sizes of kelp bass increased throughout ontogeny (Fig. 7). The regression lines for moray L_H and maximum size for mixed fishes and invertebrates also indicated slopes significantly greater than 0 (slopes = 0.12 – 0.24; $p < 0.001$). Maximum invertebrate size was retested without the apparent outlier and still returned a slope significantly different from 0 ($p < 0.001$). Therefore, with invertebrate prey less common in the moray diet, this outlier remained in the dataset. Slopes for moray L_H and minimum size for mixed fishes ($p = 1$) and invertebrates did not differ significantly from 0 ($p = 1$). These results reveal a ontogenetic telescoping pattern for mixed fishes and invertebrate prey but where the minimum prey size does not increase over ontogeny. This suggests that while larger morays do eat larger fishes from a variety of taxa and larger invertebrates, the smallest of these prey do not drop out of their diet as observed with kelp bass prey.

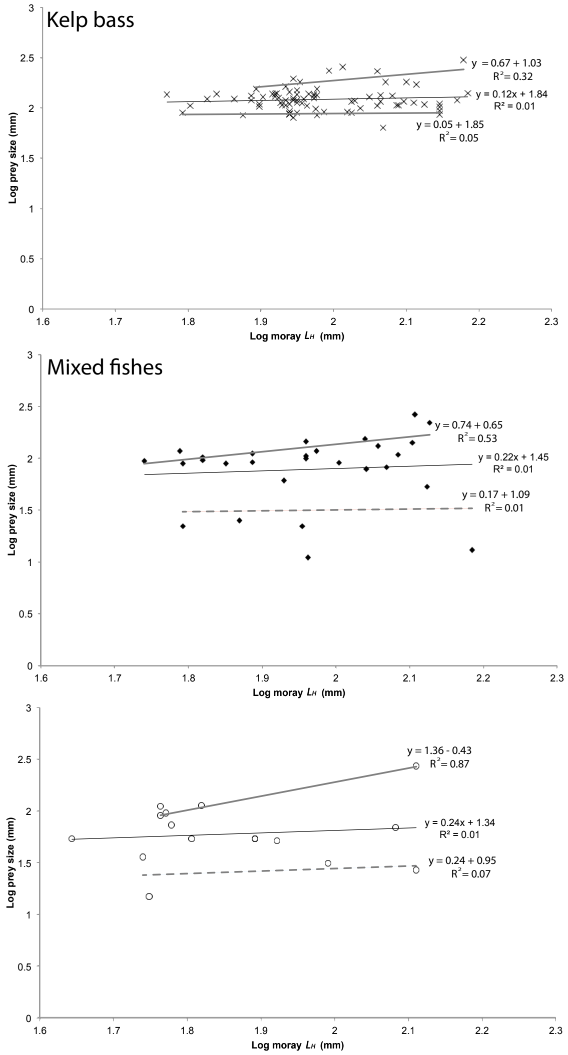

Figure 3.7: Degrees of ontogenetic shift (kelp bass) and telescoping (mixed fishes and invertebrates) using the relationship between *G. mordax* head length (log) and prey size (log) for kelp bass, mixed fishes, and invertebrate prey. Black lines represent the OLS regression through the entire data set for each prey category. Thick grey lines represent OLS regression through positive and negative residual points. In all prey categories, we observe that the slope of the relationship between prey size and head length is significantly different from 0. Solid grey lines indicate slopes significantly greater than 0 for prey in the maximum size category, whereas dashed grey lines indicate slopes not significantly different from 0. For kelp bass prey, larger morays dropped smaller prey items from their diet that reveals an ontogenetic shift in diet, as opposed to ontogenetic telescoping observed in mixed fishes and invertebrates.

DISCUSSION

Functional ecology of *G. mordax*

We provide the first detailed multi-year data set on diet for *G. mordax*, showing that in Two Harbors, Catalina Island, the California moray is a piscivorous predator that specializes on kelp bass. Furthermore, we found a clear pattern of ontogenetic telescoping for kelp bass where maximum prey size increases with moray size but very small prey are dropped from the diet of larger individuals (King 2002; Arnold 1993). However, the inclusion of secondary and typically smaller prey items in the stomach such as mantis shrimp, spiny lobster, blind gobies, and red rock shrimp suggests morays are also opportunistic in their feeding behaviors. Supporting this idea is our finding that crustaceans were the most consumed prey item in 2013 when kelp bass were not abundant.

The inclusion of smaller items in the stomachs of even the largest morays also supports the idea that individuals may be somewhat opportunistic about prey and their relative sizes. Previous studies on predator-prey dynamics in fishes reveal that, contrary to the predictions of optimal foraging models (see Ivlev 1961; Harper and Blake 1988), patterns of prey size consumption by predators do in fact include the retention of smaller prey despite larger predator sizes (Juanes and Conover 1995; Scharf et al. 2000). One hypothesis for why larger fish predators continue to consume small prey is that the importance of size-dependent capture success and differential encounter probabilities outweighs that of handling time (Scharf et al. 2000). Moreover, the abundance of small prey within the system may be significantly greater than those of larger prey, further elevating the likelihood of encounters between large predators and small prey (Scharf et al. 2000). This may in part help explain why we observed significantly smaller kelp bass sizes consumed in 2015 relative to all other years where they had the largest *L* value. During the entirety of 2015, Santa Catalina Island was enveloped by the strongest El Niño since 1983 (Higgins et al. 2017). This resulted in a complete loss of kelp canopy cover (B.H., C.L. and R.M., pers. obs.) that kelp bass use for refuge during daytime hours (Ebeling and Bray 1976). Thus, kelp bass recruits that typically took refuge in the water column likely had to hide within the reef, thereby increasing the encounter rates between small kelp bass and morays. In years where smaller kelp bass may not be as abundant, morays could function as stabilizing predators by opportunistically consuming a wide range of prey in a frequency-dependent regime, as we observed with the increasing, although not significant, proportion of invertebrate prey in the moray's diet in 2013. These findings have strong ecological significance for the community as a whole because a functional specialist such as *G. mordax,* provide a mechanism for maintaining elevated biodiversity through compensatory mortality (Connell 1978).

Predator and prey size shifts across years

While the proportion of prey in the diet of the California moray did not vary significantly across years, we found differences in the average size of kelp basses consumed across years. The average size of kelp bass consumed was smallest in 2015 whereas the average size of kelp bass consumed was largest in 2012. These averages are just below the reproductive size of kelp bass (Fig. 3). Over the course of the five-year study, we observed that moray predators of all different sizes were consuming kelp bass (Fig. 4). Despite the size variation in morays, there was strong overlap in kelp bass size. In our previous study, the distribution and abundance of moray sizes were uneven across different coves within Two Harbors, Catalina Island. The largest morays were trapped only in coves with east/northeastern-oriented faces (Higgins and Mehta 2017). Therefore, morays originating from different trapping sites that displayed different size structuring, would all be consuming kelp bass prey of similar sizes. Additionally, size-based predation frequencies across years may have been determined by fluctuations in reproductive output of kelp bass which would then lead to varying strengths of kelp bass recruitment pulses.

Bite force & predation pressure

Within fishes that utilize biting as the primary mechanism used to capture and consume prey, the size of the gape is often the factor that limits the types and sizes of prey that can be exploited (Kardong 2014). Constraints in cranial growth and/or morphological adaptations, however, often limit the biting ability and therefore may prohibit access to different prey species or prey items of a particular size (Herrel et al. 2006; Bulté et al. 2008; Santana et al. 2010; Pfaller et al. 2011). In this study, we found that morays exhibited a relatively high range of bite forces for their size especially when compared to other apex or secondary predators. For example, *in situ* bite force of the sympatric and almost exclusively durophagus horn shark

(*Heterodontus francisci*) at a mass of 2.95 kg was 160 N (Huber et al. 2005). This is comparable to our *in vivo* bite forces recorded for a moray measuring 2.46 kg (266.54 N). In addition, moray bite forces increased disproportionately as head and body increased in size, suggesting that allometric increases in bite forces may enable the oral jaws to retain larger fish prey during feeding bouts or even provide accessibility to hard shelled prey.

Despite exhibiting allometrically increasing bite forces, our dietary data did not support ontogenetic shifts across all dietary items for morays. For example, morays did not transition from a piscivorous diet to a more durophagous diet (or vice versa) with increasing bite forces, but instead, fed on prey items proportional to moray head length throughout ontogeny. This hypothesis supports previous findings that moray jaw dentition exhibited predominantly isometric growth, suggesting that the oral teeth grow proportionately as individuals increase in size (Harrison et al. 2017). Tooth growth patterns help explain why similar sized items are consumed by morays that vary widely in size as was found in the current study. Fracture forces for hard prey such as lobster and kelp crab are necessary to test the idea that allometric increases in bite forces may enable morays to consume a wider variety (type or size) of hard shelled prey when kelp bass recruits are not abundant.

Based on the strong allometric pattern of bite force, we would expect larger morays to consume fishes that exceed their head lengths. However, we found no significant relationship between prey size and moray bite force. Our results, therefore, suggest that kelp bass size selection is not limited by moray bite force. Rather, other variables such as encounter rates, capture rates, or handling times could limit the sizes of kelp bass prey in the California moray's diet. California morays, similar to other morays (Miller 1987; 1989) or eel species (Helfman and Clark 1986), are known to ram, shake, knot, or use body rotations, to force large prey into their mouths or to remove pieces from larger prey items. In a previous study, we showed that prey size increased total feeding time and prey manipulation duration when morays were fed dead fish or cephalopod prey (Diluzio et al. 2017). Feeding durations and energetic demands necessary to capture and handle large live prey of increasing size would undoubtedly affect the caloric benefits of going after these larger prey.

Frequency of Predation

Of the morays trapped over the five-year period, we found that the overwhelming majority had empty stomachs (85.4%). Previous studies have shown that piscivores have empty stomachs more often than non-piscivores and that nocturnal fishes tend to run empty more often than diurnal fishes. Piscivorous fishes that consume prey whole also tended to have the highest proportions of empty stomachs (Arrington et al. 2002). Our data set revealed that the California moray, a nocturnal piscivore, infrequently turned up with stomach contents averaging ~14.6% over the five year period in summer months. This low percentage of stomach contents could reflect the challenge of capturing kelp bass prey as piscivores tend to be less successful compared to planktivores (Juanes et al. 2002). Capture success in piscivores has also been shown to decrease when prey size to predator size ratio increases (Miller et al. 1988). The challenge of capturing fish prey has lead others to speculate that maximum fishes consumed by piscivores are often considerably smaller than what would be predicted by predator gape size alone (Juanes and Conover 1995; Christensen 1996). Therefore, while predator gape size or cleithrum width may biomechanically limit the sizes of prey a predator may ingest, the behavioral abilities (i.e., evasiveness) of the prey may in fact more tightly regulate the sizes and types of prey consumed before gape morphology of the predator interacts with feeding. Alternatively, California morays have low metabolic rates and individuals do not need to consume prey frequently. Higgins and Mehta (2017) showed that the body condition of morays was relatively consistent across moray size categories and coves suggesting if preferred prey are challenging to capture, it is not reflected in moray body condition.

Trophic placement

Evidence from studies conducted in the tropics suggests that morays are predatory fishes that can be found in densities similar to commercially important predatory fishes such as serranids (sea-basses and groupers) and lutjanids (snappers) (Gilbert et al. 2005) and can alter future community structure by preying upon newly settled recruiting fishes on Caribbean patch reefs (Parrish et al. 1986; Carr and Hixon 1995; Young and Winn 2003). Within the coves of Two Harbors, *G. mordax* is an abundant, static, carnivorous predator (Higgins and Mehta 2017; Harrison et al 2017) that specializes on kelp bass but can consume a relatively wide diversity of prey species throughout ontogeny. These results, therefore, suggest that morays have the densities to inflict consistent and elevated predation pressures on their prey populations as tertiary consumers, however metabolic data would be necessary to understand the effects of *G. mordax* on various prey populations. The California moray was previously categorized as a secondary consumer (Graham 2004). Under this classification, *G. mordax* at Two Harbors is grouped in the same carnivorous fishes category as their primary prey, kelp bass. Our results, suggest that *G. mordax* should be positioned above the carnivorous fishes category and is a tertiary consumer alongside sharks, rays, pinnipeds and birds. While morays are apex consumers in tropical waters (Carr and Hixon 1995; Page et al. 2013), we hesitate to label *G. mordax* as an apex consumer without additional field observations on the habits of other resident marine predators, such as Harbor seals, *Phoca vitulina.*

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AUTHOR’S CONTRIBUTIONS

R.S.M. designed the study. R.S.M., B.A.H., and C.J.L. collected the data. B.A.H. analyzed the data. R.S.M., B.A.H., and C.J.L. interpreted the data. B.A.H. wrote the manuscript. R.S.M. and C.J.L. provided feedback on various iterations of the manuscript.

Compliance with ethical standards

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Supplementary Materials (Methods) for
Eat Whole and Less Often: Ontogenetic telescoping reveals size specialization on kelp bass by the California moray eel, *Gymnothorax mordax*

Benjamin A. Higgins, Chris J. Law, & Rita S. Mehta

A series of underwater transects were placed in the summer of 2013 to examine the potential prey items found in the environment where morays are typically observed (Higgins & Mehta, 2017). We assessed prey distributions by depth, by running eight transects (four pairs of two) parallel to the shoreline at varying depths (3m, 8m, 13m, and 18m). Traps were set at each of these depths and two, 10m transects were laid parallel to the shoreline, resulting in a 20m transect for each trap at each depth. Two scuba divers swam along each arm of the transect recording all vertebrate and invertebrate species observed. As these transects (N = 32), were extremely time intensive to perform, we adopted the annual data monitoring transect surveys by Reef Check for years, 2012, 2014, 2015, and 2016. To determine whether our 2013 surveys could be comparable with Reef Check, we conducted a series of Z-tests to used to examine the differences in distributions of potential prey items detected in both Reef Check and our own surveys of prey items. Our statistical analyses did not detect a significant difference between the proportions of prey items quantified by the transects we conducted in 2013 and those conducted by Reef Check teams during the same year (Z-score range: $0.16 < p < 1$).

Supplementary Materials (Table) for
Eat Whole and Less Often: Ontogenetic telescoping reveals size specialization on kelp bass by the California moray eel, *Gymnothorax mordax*

Benjamin A. Higgins, Chris J. Law, & Rita S. Mehta

Supplemental Table 1: Dietary items recovered from the guts of 196 *G. mordax* via manual palpation.

Dietary item	2012	2013	2014	2015	2016
Blacksmith (*Chromis punctipinnis*)	-	1	-	1	2
Blind goby (*Typhlogobius californiensis*)	-	-	-	1	-
CA moray (*Gymnothorax mordax*)	-	-	-	2	2
CA spiny lobster (*Panulirus interruptus*)	-	-	-	-	3
Garibaldi (*Hypsypops rubicundus*)	-	-	2	1	-
Kelp bass (*Paralabrax clathratus*)	14	21	21	45	13
Kelp crab (*Pugettia producta*)	-	-	-	-	1
Mantis shrimp (*Hemisquilla ensigera*)	-	1	-	-	1
Octopus (*Octopus bimaculoides*)	-	1	1	5	2
Painted greenling (*Oxylebius pictus*)	-	-	-	-	1
Red rock shrimp (*Lysmata californica*)	1	5	2	1	1
Rockfish spp.	-	2	-	-	1
Sculpin spp.	-	1	-	-	-
Striped kelpfish (*Gibbonsia metzi*)	-	-	3	1	1
Unidentifiable crab	-	-	1	-	-
Unidentifiable fish	-	-	-	4	3

Chapter 4

The interaction between ontogeny and temperature in the standard metabolic rate of the California moray (*Gymnothorax mordax*).

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Abstract

Using closed-system respirometry, we measured the standard metabolic rate (SMR) of the California moray eel (*Gymnothorax mordax*) over ontogeny and at two commonly encountered (winter and summer) water temperatures. The SMR for *G. mordax* decreased by 67% (mean: 43.76 mg O_2 kg^{-1} hr^{-1}) when water temperature was reduced from warm (22°) to cold-water (16°) conditions. As expected, body size affected these results; mass-specific metabolic rates were higher for smaller individuals. However, when exposed to colder temperatures, mass-specific SMRs did not show the typical indirect relationship with body size; mass-specific SMRs for smaller individuals were much lower than larger individuals. Also, the SMRs for larger individuals in the cold water treatment did not deviate much from the warm water treatment, suggesting that larger morays (≥1.75 kg) are not as affected by changes in temperature. When compared to other teleosts of comparable body size, such as 0.7 kg and at 15C, *G. mordax* exhibited lower SMRs. However, moray SMRs are more similar to those of more closely related Anguilliformes, studied to date. We also observed that larger morays had a subcutaneous adipose layer along the length of their body that may assist in heat retention and explain the diminished SMR response to lower environmental temperatures.

INTRODUCTION

The metabolic rate of an animal provides the foundation for understanding energy needs and ultimately determines how often predatory species consume prey within their environment (Post and Lee, 1996; Hill et al., 2012). Both empirical and theoretical studies have shown that temperature and body size primarily drive the rate of these aerobic reactions (Xie & Sun, 1990; Kozlowski et al., 2004; Killen et al., 2010). Previous studies have shown that temperature effects on metabolic rates are size specific (Clarke & Johnston, 1999). As all animal populations are size structured, the responses of individuals of a particular size class could have a disproportionate effect on resource acquisition rates, thereby affecting community structure (Lindmark et al., 2018). Despite the importance of temperature and body size in understanding energetic needs, few studies have explored the effects of both variables to understand species-specific responses.

Endothermic animals have repeatedly evolved adaptations to assist in regulating the heat exchange with their environment by developing thermal windows that contain a dense network of capillaries contained within a relatively thin tissue (e.g., elephant ears; Weissenböck et al., 2012). Many terrestrial ectotherms have also developed behavioral adaptations to assist in regulating the difference between core and environmental temperatures (e.g., basking). However, for fishes, behavioral adaptations for thermoregulation via efficient conductive heat transfer are not possible. Thus, the vast majority of the most specious clade of vertebrate life (Nelson, 2006) are poikilothermic organisms. However, some poikilothermic species have evolved morphological adaptations to generate relatively elevated core body temperatures. For example, circulatory adaptations have been found to provide localized endothermy in tunas and sharks (Dickson and Graham, 2004), while whole body endothermy has been found in the opah, by encasing the main site of gas and heat exchange in an adipose layer (Wegner et al., 2015).

The rate in which heat from within an animal can be exchanged with its environment (or vice versa) is largely dependent upon the surface-area-to-volume (SA:V) ratio (i.e., shape) of the organism (Shelomi and Zeuss, 2017). Because volume increases by the cube while surface area doubles with increasing size, we would anticipate that the increase in size of an organism over ontogeny would affect the rate at which heat is exchanged with the surrounding environment. Furthermore, additional factors such as lifestyle and swimming mode were also observed to have significant effect on the metabolic rates of 89 fish species spread across 15 families (Killen et al., 2010), suggesting that neither size, nor shape are solely responsible for determining the metabolic scope of fishes.

The goal of the present study was to test the hypothesis of temperature-dependent intraspecific metabolic ontogeny in the California moray eel (*Gymnothorax mordax*), a Southern California kelp forest predatory fish. We expect to find that the mass specific SMR will decrease as a function *G. mordax* size, a pattern commonly observed in organisms (Kleiber, 1961; Schmidt-Nielson, 1984; Hill et al., 2012; Lindmark et al., 2018). We further predict that when *G. mordax* is exposed to colder temperatures, the mass specific SMR will decrease relative to their warm water rates across ontogeny.

G. mordax is an interesting model for a study of temperature-dependent intraspecific metabolic ontogeny because it is a temperate species and exhibits a sedentary lifestyle (Fitch and Lavenberg, 1971; Higgins and Mehta, 2018). Furthermore, as of this writing, the metabolic rate of this or any other muraenid have not been empirically measured. Therefore, we provide a baseline of comparison for future physiological studies of this specious family (Smith, 2012). Additionally, studies have suggested that individuals of *G. mordax* around Santa Catalina Island are not reproductively active (McCleneghan, 1973; Higgins et al., 2017) and are not highly mobile during the day, further simplifying the energetic demands for this species and allowing for a direct comparisons of metabolic demands to be made across ontogeny. Because the California moray inhabits waters between 2-15 m in depth (McCleneghan, 1973; Higgins and Mehta, 2018), the temperature of its environment is expected to have a large effect on its standard metabolic rate (SMR) (Methling et al., 2011). Furthermore, because *G. mordax* inhabits shallow waters found within the coves of Santa Catalina, seasonal shifts in ocean temperatures that vary from 15^o to 23^o (Gelpi and Norris, 2008) would likely experiences changes in SMR throughout the year, providing a natural system to test how temperature impacts this species across a size range of individuals.

MATERIALS & METHODS

Animal collection & morphometric data

During the summers of 2016 and 2017, 16 *G. mordax* (mean mass: 1.12 kg ± 0.18 S.E.; mean SL: 774.4 mm ± 44.2 S.E.) were collected using custom-built, dual-chambered wire mesh traps (36” x 11” x 9”; Staten Island, NY) at Two Harbors, Santa Catalina Island, CA (33°26’45.4“N, 118°29’31.3”W). Traps were set between 1800-1900 hours each night and baited with thawed anchovies (*Engraulis mordax*). The anchovies were contained in capped plastic bottles drilled with holes. Therefore, morays could smell the bait but, otherwise, bait were not accessible. Trap retrieval occurred the following morning (0700-0800 hours), resulting in a soak time of ~12 hours.

The size range of individuals chosen for experimentation represented as much of the *G. mordax* population size range observed in Two Harbors. Individuals were sedated using MS-222 at roughly 90mg/liter of fresh seawater. Once sedated, total length (tip of snout to posterior-most tip of tail; L_T), head length (tip of snout to gill opening; L_H), and mass (kg) were recorded. The stomach of each moray was manually palped to determine whether it recently fed. Manual palpation, which involves gently pushing any prey items from the stomach out through the mouth, safely removes any previously consumed meals, thus controlling for specific dynamic action during respirometry. After all morphometrics were collected, sedated morays were rehabilitated in a bucket of fresh seawater and then moved into 100-quart coolers for shipment. Coolers were fitted with battery-powered bubblers (PENN

PLAX© Silent Air B11) and transported roughly 19 nautical miles from Two Harbors to the Cabrillo Marine Aquarium (CMA) in San Pedro, CA, where metabolic studies were conducted (see Study Design and O_2 consumption**)**. Once metabolic trials were complete, individuals were either transported back in 100-quart coolers to Two Harbors and released in the same location from which they were originally trapped or transported back to the Long Marine Laboratory (LML) at UC Santa Cruz for additional experimentation. Trapping, release, and collection of all *G. mordax* were in accordance with California Fish and Wildlife Permit #11366.

Study design & O_2 consumption

Individuals arriving to CMA were placed in one of three custom-built metabolic chambers located in the Aquatic Nursery. The chamber dimensions were 60.96 x 30.48 x 40.64 cm with a total volume of 75 L. A custom built acrylic top was fastened to the glass chamber using silicone. The acrylic top also had a 15 x 45 cm rectangular gap, lined with weather stripping tape. Lids were custom made out of 0.63 cm acrylic to cover this gap and fastened to the tank using eight evenly spaced screws with wingnuts. Tightening the eight wingnuts compressed the weather stripping tape between the tank top and lid, creating an airtight seal around the lid. The airtight seal ensured a closed system preventing fluctuations in the ambient O_2 content from influencing the oxygen levels within the chamber. The lids were fitted with two rubber grommets, which were sealed in place with silicone to allow for the insertion of a temperature and an O_2 probe (see below). Aquaria were placed in a seawater table that had a constant supply of fresh seawater running at 22° to provide the chambers with a consistent temperature bath. Individual *G. mordax* were left to acclimate in the chamber for 24 hours. During this acclimation phase, the chambers remained open-system where fresh sea water flowed through all three metabolic chambers. Individuals, which were previously checked for stomach contents, were also fasted during this acclimation period. Upon the commencement of the experiment, the flow-through system was shut off and excess water was siphoned out of the chamber until the water volume in the aquarium measured 68 liters.

Both the dissolved O_2 content and temperature of the seawater inside the chamber were measured using closed (constant volume) respirometry. Both variables were resampled at an interval of 100 miliseconds, with values recorded every 10 seconds throughout the entirety of the trial. Data were collected with an Ocean Optics© NeoFox Sport phase fluorometer. The temperature and fluorometer probes were fitted through the rubber stoppers in the airtight lid and submerged into the seawater. A slotted PVC pipe was fastened to the underside of the lid, directly under the rubber grommet through which the O_2 probe was inserted, to protect the fluorometer from any contact by or movement created by the animal. Experimental trials ended when the animal depleted 60% of the O_2 content in the 68 L of seawater. Oxygen depletion curves obtained from each trial were then converted to mass-specific O_2 consumption rates (mg O_2 kg^{-1} hr^{-1}) or mass-specific standard metabolic rate (SMR) using the following formula (from Palstra et al., 2007):

$$\dot{M}O_2 = (V * \triangle\, [O_2] / \triangle\, t)/M$$

where *V* is the total volume of the metabolic chamber multiplied by the change in O_2 content over *t,* time, and *M* is the mass (in kg) of an individual moray.

Repeatability of Warm Water Trials

The seven individuals that were transported to the LML were first acclimated to the same 22^o temperature regime that they experienced during the warm water trials at CMA. Individuals were left to acclimate to this environment for one month before they were re-tested at 22^o to ensure that SMR values were repeatable and to evaluate the similarity of SMRs to those collected previously. Additionally, the facilities at LML did not have the same sea water table equipment to provide a buffer for holding constant temperatures throughout the metabolic trials. Therefore, these trials were conducted to ensure that potential SMR responses to different temperature treatments were not in error because of changes in the experimental design. A paired t-test was conducted to analyze the differences between the two SMR values at the experimental temperature of 22^o.

Cold water trials

To understand the effect of winter temperatures (e.g., September – February) on the SMR of *G. mordax,* individuals were tested in temperature regimes that Two Harbors Catalina Island typically experiences during a neutral year (i.e., non-El Niño/La Niña) (Gelpi and Norris, 2008). The same seven individuals previously tested in two trials of warm water treatment (22^o) were subjected to a cold-water treatment at 16 ^{o}. We had the opportunity to test an 8th individual, in the cold-water treatment. This individual was collected from Two Harbors in 2016 and transported back to the LML. This individual did not have a warm-water data point as it died prior to any further experimentation.

For the cold-water treatments, all 8 individuals were transferred to flow through aquaria. The slow flow (~1 liter/hr) of freshly filtered seawater from the adjacent Monterey Bay was piped into the tanks at 16^{o}. Air stones were also added to the tanks to ensure the circulation of adequate dissolved O_2 levels. All individuals were allowed to acclimate to the cold water systems for one month before trials began. The experimental design and data collection protocols were identical to those used in the warm water treatment.

Morays were transferred into the metabolic chamber 24 hours before trial commencement to ensure that handling stress did not affect data collection. During this 24-hour window, two-air stones were placed in the chamber to ensure adequate dissolved O_2 levels. Trials began when the air stones were removed and the lid was fastened to the chamber. Similar to the warm water treatment at LML, each metabolic chamber was placed in a 120-quart water cooler and bathed with cold system water (16 ^{o}). To keep chamber temperatures consistent throughout the trial, this water was drained from the cooler and replaced with fresh seawater if it approached a change of ± 0.5^{o}. Trials were monitored twice per hour to ensure that chamber temperature did not vary beyond ± 0.5^{o}. Again, trial duration depended on the time it took the animal to deplete 60% of the original seawater O_2 content in the 68 liters.

Repeatability of warm temperature treatment

We found no difference between the 22^{o} warm water trials conducted at the CMA and those carried out on the same individuals at the LML (n = 5, paired t-test, $P>0.487$). This suggests that morays were appropriately acclimated to experimentation after transport and that the experimental differences (sea water table vs. cooler to maintain a consistent water temperature) had no effects on the metabolic response.

Adipose layer measurements

To describe the adipose tissue present in *G. mordax*, we measured the subcutaneous adipose layer in 20 individuals (size range: 250 – 930 mm L_T; mass range .792 – 2.08 kg). Incisions were made along the ventral side of the animal from the lower jaw to the vent. Muscle was carefully separated from the skin to expose the subcutaneous adipose layer along the length of the individual. Three measurements were taken along the skinned moray: head - directly posterior to opercular opening, body - midpoint as measured from the tip of the jaw to the posterior tip of the tail, and tail - midpoint as measured between vent and posterior tip of the tail). Thickness from the skin to the underlying muscle mass (mm) was measured using a pair of digital calipers.

RESULTS

Effects of body size on SMR

We calculated SMR in 16 individuals varying in size (L_T range: 434 – 992 mm; mass range: 0.160 – 2.14 kg). Total O_2 consumed (units) ranged from 20.2 to 78.6 mg O_2 (Fig 1A). The time it took *G. mordax* to consume 60% of the initial O_2 concentration of fully aerated water within the metabolic chamber (i.e., trial duration) depended on the mass of the individual (non-linear least squares model, d.f. = 14, r^2=0.90, P<0.0001), with smaller individuals taking up to 10.4 hours, and larger individuals taking only 2.3 hours at minimum to deplete 60% of the initial O_2 concentration. As anticipated, we observed that larger individuals consumed less O_2 per kg of body mass compared to smaller individuals (range: 37.2 – 160.8 mg O_2 kg^{-1} hr^{-1} (Fig. 1B).

Effects of temperature on SMR

Eight *G. mordax* had their O_2 consumption rates measured while resting in 16^o seawater, seven of which were tested in the previous warm water (22^o) metabolic trials (Fig. 2). Mass specific SMRs ranged from 10.8 to 30.1 mg O_2 kg^{-1} hr^{-1} showing that as morays increased in body size, individuals exhibited a higher mass-specific metabolic rate than when SMR was measured at 16^o. For example, O_2 consumption decreased from 65.05 mg O_2 kg^{-1} hr^{-1} to 10.81 mg O_2 kg^{-1} hr^{-1} (delta 54.24 mg O_2 kg^{-1} $hr^{-}1$) for the smallest animals in the study (mass = 0.42 kg). At larger body sizes, the differences between mass specific SMRs at 22^o and those at 16^o diminished. Thus,

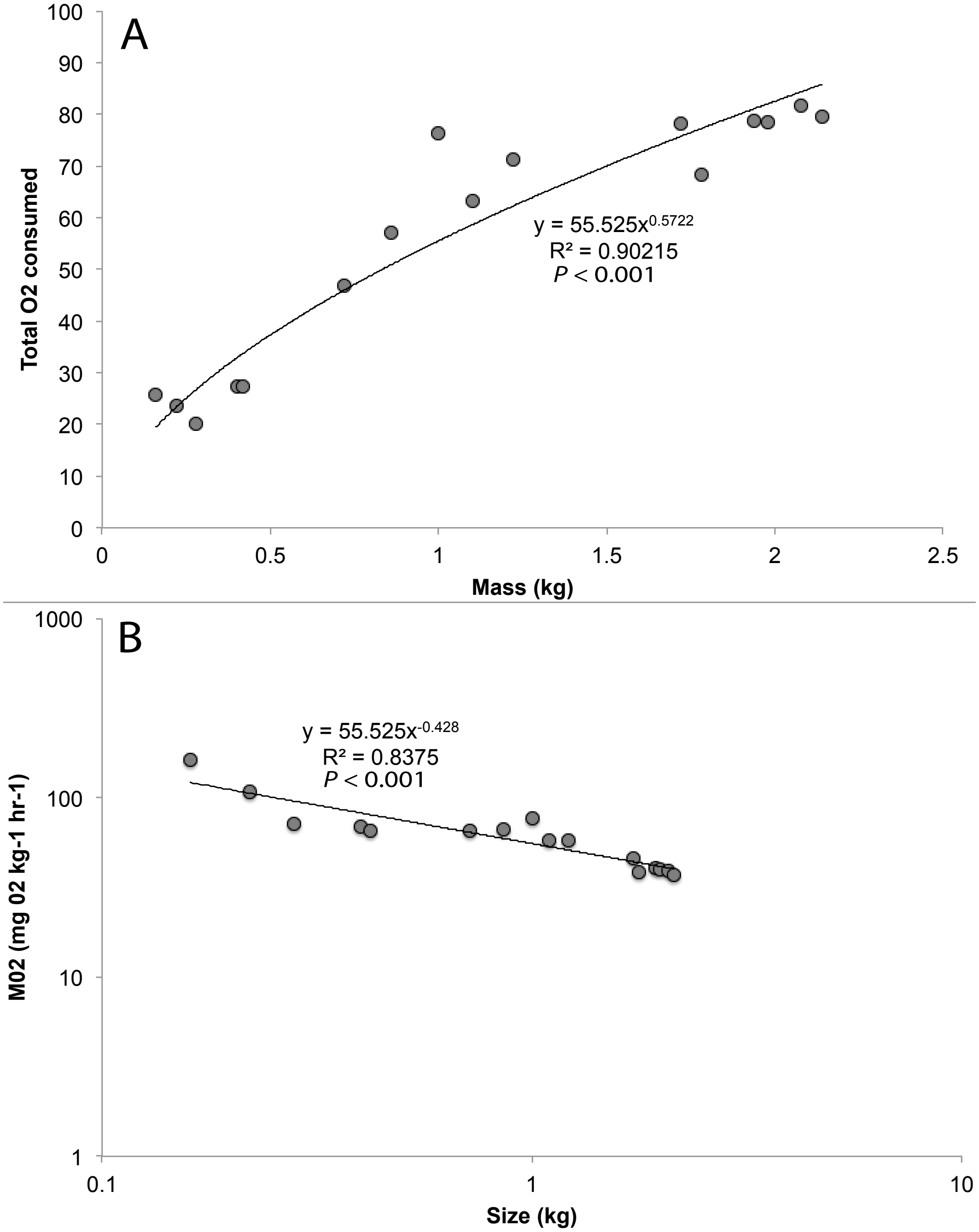

Figure 4.1: A) Total oxygen consumption of an ontogenetic series of *G. mordax* sizes. B) Mass specific SMR of 16 *G. mordax.* Both figures represent individuals tests at 22°. Note logarithmic x and y axis in panel B.

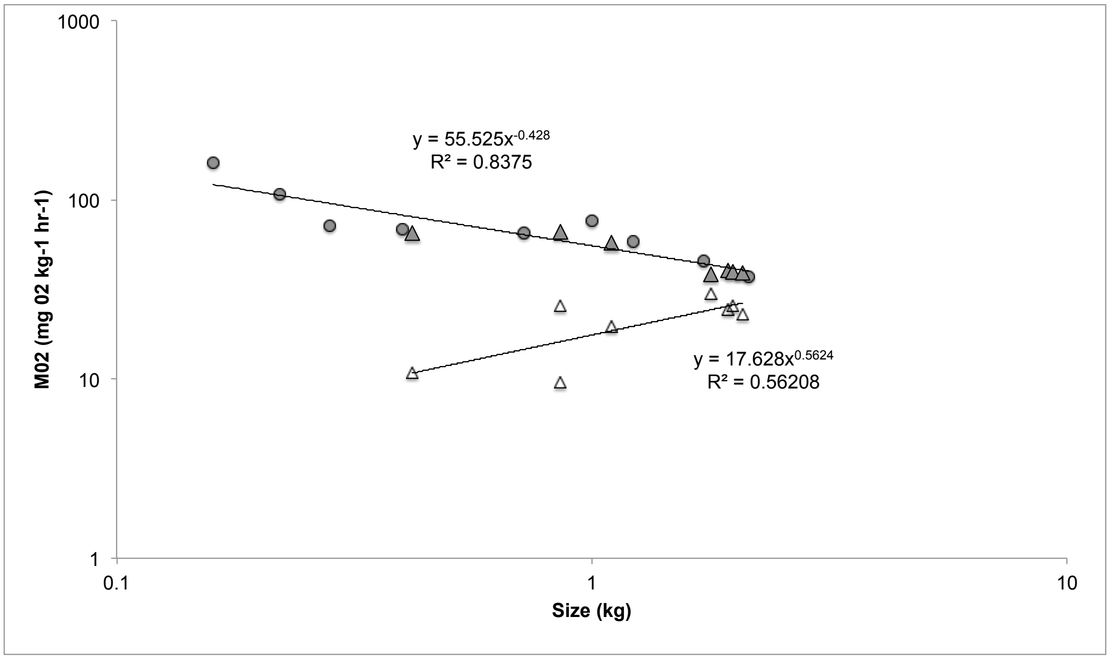

Figure 4.2 Differing responses of metabolic rates relative to summer (22°) and (16°) treatments as a function of mass. Black triangles (n=7) represent the individuals that had SMR also measured at 16° (*i.e.*, paired data points). Note logarithmic x and y axis.

the largest eel in this study (mass = 2.08 kg) had an SMR of 27.89 mg O_2 kg^{-1} hr^{-1} @ 22^o, and only a slightly lower SMR of 23.06 mg O_2 kg^{-1} hr^{-1} @ 16^o (difference of 4.83 mg O_2 kg^{-1} hr^{-1}) (Fig. 3). Despite converging O_2 consumption rates at larger masses, SMRs responses to the two experimental temperature treatments were significantly different (repeated-measures ANOVA, d.f. = 1, F=27.12, P<0.001).

Adipose layer

Dissections of 20 *G. mordax* revealed a subcutaneous adipose layer that ran along the length of the body from the head of the moray to the tail. Adipose layer thickness increased with moray mass (linear model, $r^2 = 0.44$, P<0.001) (Fig. 4A). Moreover, the adipose layer was thickest surrounding the head, and became thinner as measurements were made posteriorly (Fig. 4B). However, the relationship between moray size and adipose layer thickness were significant for only the head and body regions of the moray. Fat layer thickness also scaled allometrically with moray size, as all three regions had slopes significantly different from the expected isometric slope of 0.75 (Standardized major axis regression test [$R^{©}$ package “smatr”] - head: P<0.001; body: P<0.05; tail: P<0.001).

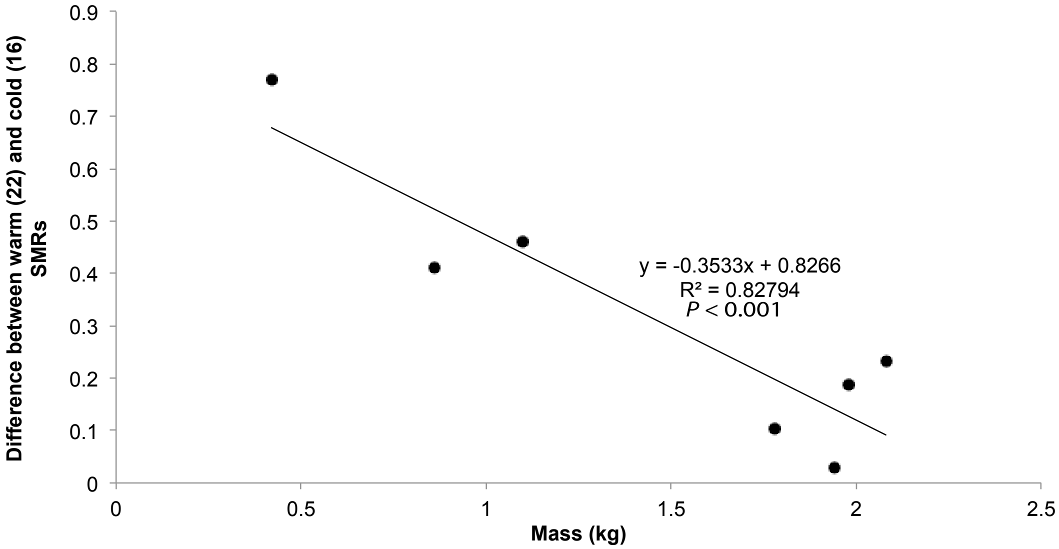

Figure 4.3: Relationship between mass and the differences in paired SMR values of 7 individuals measured at two different (22^{o} and 16^{o}) temperature regimes.

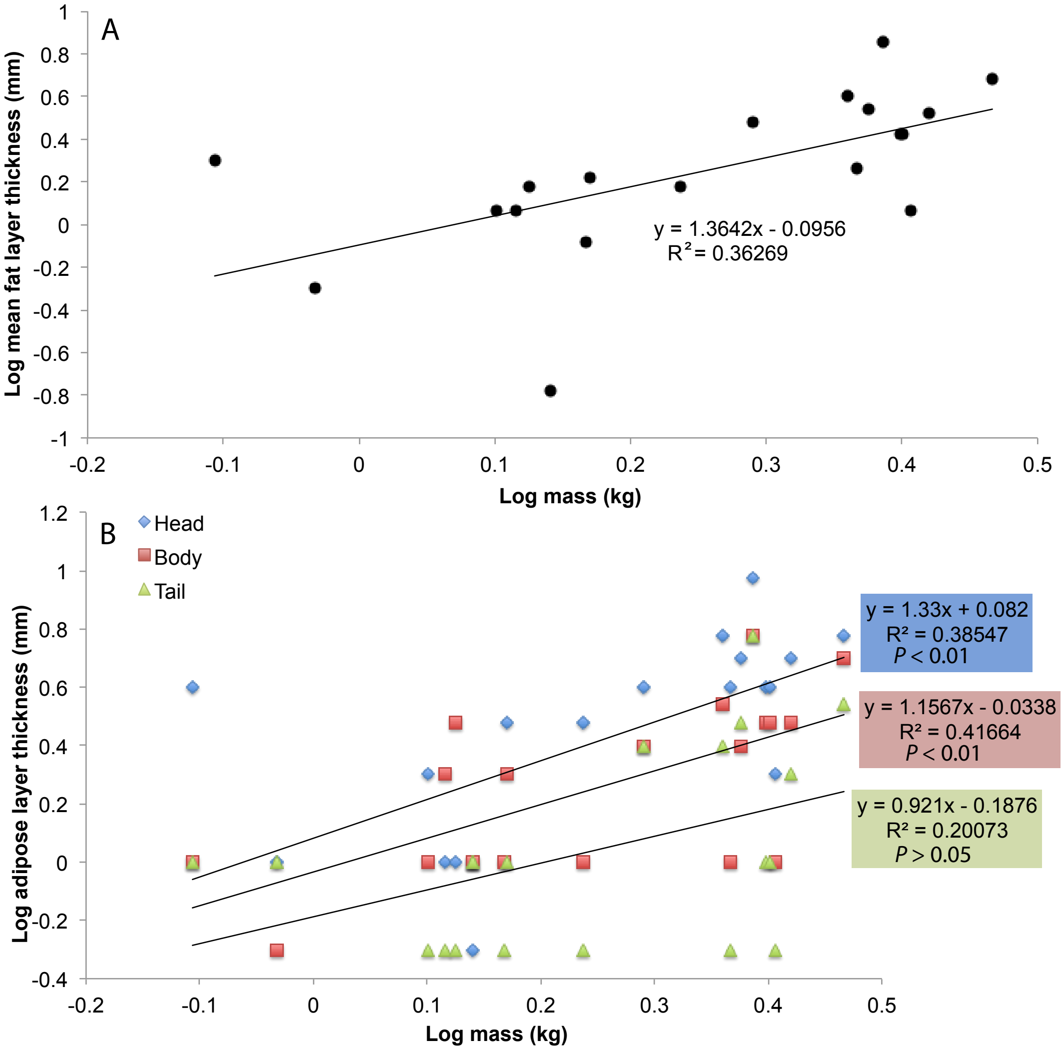

Figure 4.4: A) Log mean subcutaneous fat layer thickness across three areas measured along *G. mordax* body. B) Relationship between log mass and log subcutaneous adipose layer thickness of three different positions along *G. mordax* body.

DISCUSSION

This study provides the first SMR measurements for a member of the Muraenidae, a clade consisting of ~200 predatory species (Smith, 2012). We found that the SMR of *G. mordax* was lower than those reported for other fishes of comparable body mass (Clarke & Johnston, 1999). For a given body size (0.05 kg) and at a similar temperature (15^{o}), anguilliform fishes consumed the lowest amount of oxygen per hour (i.e., lowest resting metabolic rates) when compared to gadiformes, pleuronectiformes, perciformes, salmoniformes, and cypriniformes (Clarke & Johnston, 1999). The SMR recorded for our 0.7 kg *Gymnothorax mordax,* is most similar to other anguilliforms, (silver eel [*Anguillicola crassus*], mean: 39 mg O_2 kg^{-1} hr^{-1} @ 18^{o} [Palstra et al., 2007]; anguilliformes, 58.37 ± 6.91 mg O_2 kg^{-1} hr^{-1} at 15^{o} [Killen et al., 2010]; European eel [*Anguilla Anguilla*], 26.28 ± 11.24 mg O_2 kg^{-1} hr^{-1} [Methling et al., 2011]).

As anticipated, mass-specific SMRs of *G. mordax* were inversely related to body size, with the largest morays exhibiting SMRs roughly ≤50% those of the smallest individuals at 22°. Interestingly, we observed an unexpected trend when the same size range of morays was exposed to 16°. Rather than observe lower SMRs and an inverse relationship between mass-specific SMR and body size at the 6° decrease in temperature, we found that mass-specific SMR increased with increasing moray size. Although the cooler temperatures did result in lower metabolic rates for all individuals, the discrepancy in mass-specific SMR between the 22° treatment and the 16° treatment decreased as moray size increased. These results indicate that larger morays do not exhibit as strong of a physiological response to changes in temperature compared to smaller individuals.

Thermal inertia for larger individuals is a phenomenon that is taxonomically widespread (fishes: Neill and Stevens, 1974; Neill et al., 1976; Dizon and Brill; 1979; mammals: McNab, 1978, and reptiles: Spotila et al., 1973; McNab and Auffenberg, 1976). Because volume increases by the cube while surface area doubles with increasing size, larger morays may respond less to fluctuations in water temperature. Although changes in surface area to volume ratios are magnified in animals that have a long cylindrical body plan, larger morays should still have a much lower surface area to volume ratio than those of smaller individuals. These factors may explain why changes in ambient temperatures affect smaller morays more than larger individuals.

We found that the subcutaneous adipose layer is also thicker in larger individuals. A subcutaneous adipose layer could provide larger morays with an advantage for thermal stability when exposed to colder waters. Despite the strong relationship between adipose layer thickness and size (Fig. 4), a 1.18 kg *G. mordax* exhibited the thickest adipose layer (9.5 mm) but was not the largest individual in the data set. Additionally, this same individual possessed the thickest fat layer in both the body (6 mm) and tail (6 mm). In all but one individual, the head region displayed the thickest adipose layer, followed by the body, and then tail. This suggests that there is some variation in the deposition of subcutaneous adipose. The tail region always had the thinnest subcutaneous adipose layer. However, the extent to which the subcutaneous adipose layer affects overall SMR may depend on where along the body it is deposited and how thick the layer can become.

Fishes lose the vast majority (~80-90%) of their aerobic heat during the passage of blood through the gills (Stevens and Sutterlin, 1976; Brill et al., 1994; Dickson and Graham, 2004). One morphological adaptation expressed in *G. mordax* for dwelling within the crevices of the rocky reefs is a reduction of the operculum. Rather than a large opercular flap that abducts during respiration, morays have a parabranchial pouch with a small opening for water to exit after passing across the gills. The opercles, which in most fishes, are sites with the greatest potential for heat loss, are reduced in morays. While we have no evidence that *G. mordax* exhibits endothermy, the presence of a whole-body subcutaneous adipose layer in conjunction with a reduced operculum may provide physiological adaptations to heat loss. Further research on this and other potential mechanisms (e.g., mitochondrial densities) that have the potential to maintain higher internal core temperatures is warranted. Additionally, it is not known if the development of a thick subcutaneous adipose layer as *G. mordax* grows in size is an adaptation for temperate living or is also found in tropical muraenids.

Only a small number of the roughly 26,000 fish species (Nelson, 2006) have circumvented the low metabolic rates of ectotherms. Mackerel sharks (family Lamnidae), tunas, and their relatives (Scombridae) have all been found to display some level of regional endothermy in their muscle, eye, brain, or visceral tissues (Dickson and Graham, 2004). All of these species use the same mechanism to attain regional endothermy and are continuous swimmers (Dickson and Graham, 2004). The opah (*Lampris guttatus*) has achieved whole body endothermy through mitigating heat loss at the gills (Wegner et al., 2015). Here, heat is retained by the addition of adipose tissues surrounding the rete mirabile within the gill arch (Wegner et al., 2015).

The waters that envelop Santa Catalina Island exist in one of three thermal profiles at any given time. Typical exposures during winter months (e.g., September – February) range from 13° to 16° depending on the depth of the thermocline (Gelpi and Norris, 2008). However, as *G. mordax* mainly reside in very shallow waters (Higgins and Mehta, 2018), the population would likely be exposed to the warmer range of temperatures, perhaps remaining above the thermocline year-round. As Catalina Island is situated within the Southern California Bight, it is also susceptible to the effects of both El Niño and La Niña oscillation events (Gelpi and Norris, 2008; Higgins et al., 2017). Neutral temperatures are present when neither of the two climatic events are imposing either cooler (La Niña) or warmer (El Niño) water temperature regimes. While the current study examined the metabolic response of *G. mordax* to typical seasonal changes in ocean temperature (e.g., winter vs. summer), it is important to note that larger variation over multiple years (e.g., El Niño: 25° @ 4.6 m depth in 1998 vs. La Niña: 11° @ 4.6 m depth in 1999) can result in a greater fluctuation in the standard metabolic rates of smaller to medium sized individuals (Gelpi and Norris, 2008). Moreover, both the frequency and intensity of El Niño events are predicted to increase in the coming century (Cai et al., 2014). As was observed by the changes in metabolic rate in the current study, El Niño events have the potential to increase SMR in the California moray population, especially in the small to mid-ranged moray size classes, thereby elevating predation pressures on kelp bass (Higgins et al. in review, Ch. 3; Harrison et al. 2017).

Recent investigations into the habitat preference and distribution of *G. mordax* show that they are large (mean: 635 mm SL), occur in far greater densities than previously reported, and display high site-fidelity (Higgins and Mehta, 2018). However, only 14% of all individuals recovered from a multi-year trapping effort during the summer months contained dietary items in their guts during manual palpation, suggesting that for most of the time, *G. mordax* appears to be in a post-absorptive state (Higgins et al., *in review*). This was especially apparent for the largest morays analyzed, as individuals that consumed the most prey were typically in the lower to middle end of their size range. Fishes typically don't have empty stomachs, however those that are nocturnal are more often collected with empty stomachs than diurnal species. Furthermore, piscivorous fishes that consume prey whole seem to be the only trophic group that regularly experience long intervals between meals (Arrington et al., 2002). The California moray, although observed to be opportunistic in its foraging behaviors, has a tendency to be a nocturnal piscivore that consumes large prey whole. However, quantifying predation rates by marine predators remains a significant challenge in ecology, as observing predators in general and obtaining the relevant parameters required to produce sufficient bioenergetic models are difficult to obtain (Barnett et al., 2017).

The results of this research also highlight the importance of examining metabolic physiology over an individual's lifetime as metabolic rate can greatly influence the functional role of individuals within a community and affect community interactions and structure. As metabolic rate is a function of organism size, it should be no surprise that the ecological role of a juvenile may be markedly different than that of adults, as different sized organisms expend and acquire different amounts of energy. A discussion of the importance in understanding metabolic ontogeny within teleosts was first mentioned in Post and Lee (1996), where they argue that most metabolic studies included individuals representing only <50% of the change in body mass. In the present study, we report the metabolic rates for *G. mordax* that vary ten-fold in body size. However, because of the equipment used during trapping, individuals ≤ ~400 mm SL did not recruit to the gear and could not be included in our study. Additionally, while larger individuals likely occupy the waters of Two Harbors, they did not recruit to our gear. After six consecutive years of trapping, we have yet to collect individuals larger than those included in the present dataset.

Studying the metabolic demands of adults alone may not provide an accurate representation of how species will respond to changing climates, as juveniles may differ in their physiologic or behavioral response. Within marine habitats, the temperature of our oceans are predicted to cause increased metabolic rates, while simultaneously constraining dissolved O_2, which would in turn restrict organismal aerobic capacities (Fry, 1947; Pörtner and Knust, 2007; Deutsch, 2015). Thus, as the largest group of vertebrates are ectotherms and will likely face physiological challenges and limitations with warming oceans, much work is needed to advance the field of fish metabolic ecology.

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Conclusions

Ecological processes and their inherent functions are maintained by the manner in which the functional roles of species are distributed within an ecosystem (Nystrom, 2006; Sundstrom et al., 2012). As ecosystems and the species therein face a changing world, the burden of maintaining ecosystem stability falls disproportionally across trophic levels. Indeed, while average species lost within a system does affect the functioning of a wide variety of interactions, the magnitude of the effects is ultimately determined by the identities and functional roles of the species that are going extinct (Cardinale et al., 2006). Therefore, studying the functional roles of all species within a community is a critical, first step to addressing significant ecological questions, such as why certain ecosystems exhibit higher degrees of resilience and resistance to perturbations (Schindler et al., 2015) or even why certain systems contain disproportionately more biodiversity than others (Cardinale et al., 2006).

In this dissertation I advanced our understanding of the functional roles and importance of the California moray eel through a multi-year field study. My aging study found that California morays live for at least 22 years, placing it among the longer-lived fishes that commonly inhabit Southern California kelp forest ecosystems (Higgins et al., 2017). This chapter served as the first published record of a wild California moray age, where the previous estimate was derived from a single captive individual (Fitch and Lavenberg, 1971). Furthermore, I tested the hypothesis proposed by McCleneghan (1973) that California morays are brought to Santa

Catalina Island via currents indicative of El Niño events. In 33 individuals randomly culled for otolith studies, I found that 91% of them settled around Santa Catalina Island during years under the influence of El Niño oceanic temperatures and current dynamics. The findings of this chapter suggest that the moray population of Santa Catalina Island is mainly replenished by propagules distributed from the south. With climate models predicating El Niño frequencies and magnitudes to intensify (Cai et al., 2014), this chapter further draws attention to the need to monitor predator populations as they both potentially contract and expand their ranges, likely altering community structure. If these climate models prove to be accurate, moray recruitment will likely increase, raising predation pressures on kelp bass, as well as other prey species described in chapter 3. Furthermore, whether the coves of Santa Catalina Island can support a consistently growing population of morays is also unknown.

In my second chapter, I discovered that the density of moray populations residing in the coves of Two Harbors were up to 100 times greater than previously thought (Froeschke et al., 2006; Higgins and Mehta, 2018). Habitat analysis revealed that morays were most concentrated in shallow waters (< 5 m depth), comprised of mainly rocky and cobble substrate types, with southern facing sites containing higher densities of morays. These discrepancies may be a result of how moray larvae are delivered to and settle within the various coves of Two Harbors.

My third chapter utilized a Linear selectivity index to analyze stomach contents in relation to prey availability and abundance data we obtained from Reef Check. We discovered that the California moray is primarily a piscivorous predator, mainly consuming kelp bass – a tertiary consumer that predates upon a host of species (Quast, 1968; Graham, 2004). Morays also appear to be targeting specific sizes of additional prey species, resulting in ontogenetic telescoping, whereby smaller items are retained in the diets as morays grow in size. The results of this chapter would suggest that the California moray may be an apex predator, and is not a tertiary level consumer in Southern California kelp forests as proposed earlier by Graham (2004). Furthermore, morays may be functioning as stabilizing predators, consuming a wide range of items with frequency dependence. Thus, elevated biodiversity may be maintained in the system because of compensatory mortality (Connell, 1978), where morays prey upon the competitively dominant (e.g., kelp bass) species, or perhaps promote the coexistence of multiple prey species via prey switching. However, predator exclusion experiments conducted across a long-term period would be required to adequately test these hypotheses. Additional, work focusing on predation patterns of morays is needed before the California moray can be confidently described as an apex predator. For example, dietary analyses of other commonly occurring large piscivorous predators, such as harbor seals (*Phoca vitulina)* or giant sea bass (*Stereolepis gigas*) would help to solidify the trophic position of the California moray eel. As of this writing, other than Higgins and Mehta (*in review*) that reported infrequent intraspecific predation, no published data suggests that any other species in the Southern California kelp forests ecosystem frequently consume morays.

While understanding which species morays consume is valuable, those data alone do not provide sufficient information that can be used to elucidate its functional role or importance. To better understand how often morays consume a meal (i.e., frequency of predation), my fourth chapter analyzes the standard metabolic rate (SMR) of morays across ontogeny, and at different seasonal oceanic temperature levels. Similar to other anguilliformes, SMRs of the California moray are considerably lower than those of similar sized teleosts. However, I discovered that while California moray mass-specific metabolic rate decreases as they grow in size (as expected), this pattern is not observed when individuals are exposed to colder waters. Instead, larger individual respond less to a decrease in temperature. In this chapter, I also describe a subcutaneous adipose layer found along the length of the moray body that may provide some level of homeothermic capabilities for larger morays. However, more work is needed to determine if this adipose layer serves as a mechanism for the observed response in larger individuals, or if other mechanisms are contributing to the patterns observed. Beyond building towards my main goal of understanding the functional ecology of the California moray, this chapter also highlights the importance of considering intraspecific metabolic analyses in fishes, and advances our knowledge of how ectothermic predatory species interact with their prey throughout ontogeny against a dynamic environmental backdrop.

Through this groundwork, a future study is in progress to provide a bioenergetics model for the California moray population at Two Harbors, as this dissertation provides much of the required data to do so. From incorporating the prey items described in chapter 3 and the metabolic data of chapter 4, the next step will be to predict exactly how much biomass of particular prey species the moray population consumes during a given time period. Then, utilizing the densities calculated in chapter 2, the metabolic ecology of the California moray can be scaled up to the population-level – a task that has been completed previously only for sharks, tunas, and marine mammals (Barnett et al., 2017). However, caloric contents from the wide range of prey species that morays are known to consume must first be obtained. Furthermore, additional natural history data would help to ensure that other common assumptions of bioenergetic models are satisfied, such as the maintenance or upregulation of somatic and/or gonadal tissues (Deslauries, 2017).

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