

Journal of Fish Biology (2017)

doi:10.1111/jfb.13253, available online at wileyonlinelibrary.com

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

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(Received 27 June 2016, Accepted 23 November 2016)

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.

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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 Bight (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 $\pm 0.5^\circ$ C. Periods where ONI values remained above +0.5 for a minimum of five consecutive months were considered El Niño events, whereas those periods where ONI values dropped below –0.5 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, $r^2 = 0.96$; d.f. = 40, $F_{1,40}$, $P < 0.001$; 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). \circ , 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, $P < 0.001$) (Fig. S3, Supporting Information). There was no significant difference in mean width among the inner three translucent bands (Tukey's HSD, d.f. = 3, $P > 0.05$).

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: $P < 0.05$).

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, $r^2 = 0.56$; d.f. = 40, $F_{1,40}$, $P < 0.001$; Fig. 4). When this specimen was removed from the data set, the age to L_H relationship is strengthened ($r^2 = 0.75$).

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

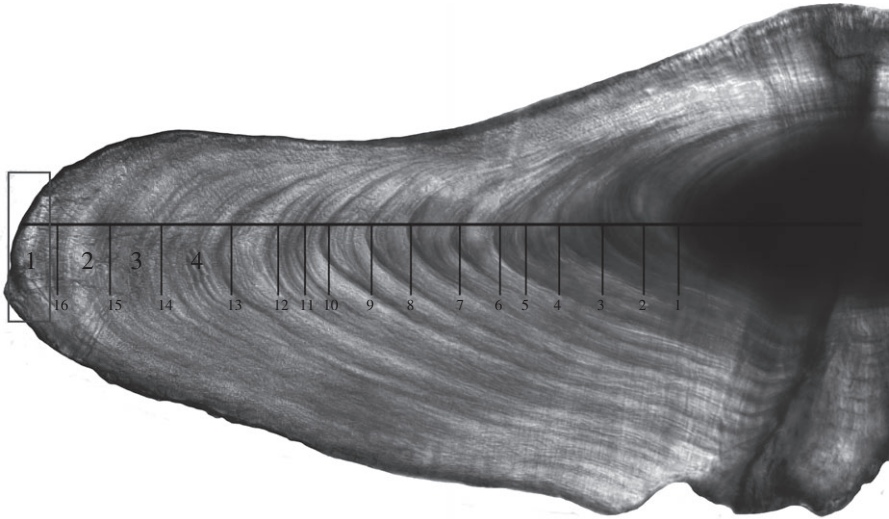


FIG. 2. Thin sectioned otolith of *Gymnothorax mordax* (810 mm total length, L_T) showing annuli (dark bands) counted to estimate ages. Note translucent edge of otolith highlighting \square a summer (September) time of collection. The four outermost translucent zones (large numerals 1–4) were used in 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; $M = 0.30$ 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

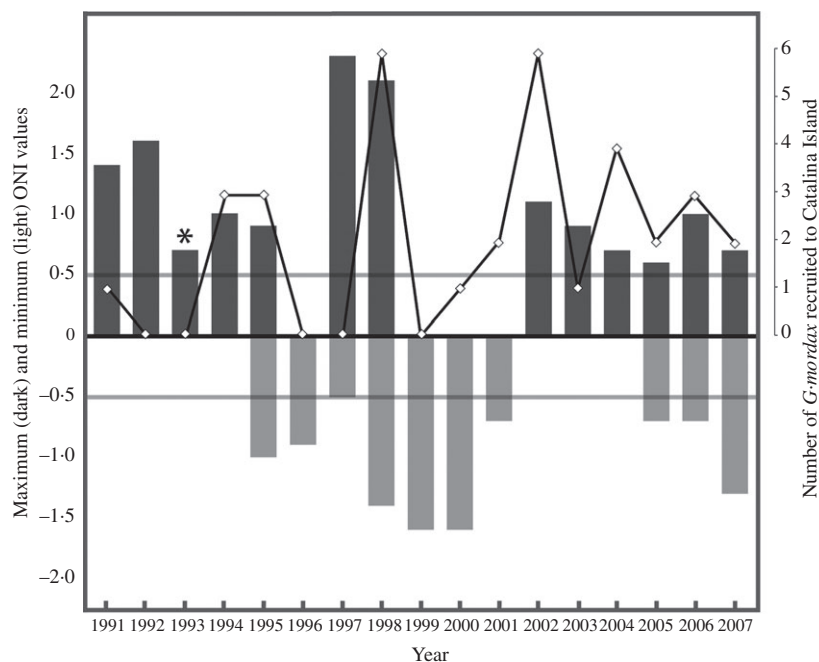


FIG. 3. Number of *Gymnothorax mordax* settled relative to the maximum (■) and minimum (□) Oceanic Niño Index (ONI) values from 1991 to 2007. Years with ONI values exceeding +0.5 indicate an El Niño for that year, while years with ONI values below -0.5 indicate a La Niña for that year. *, The ONI value 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

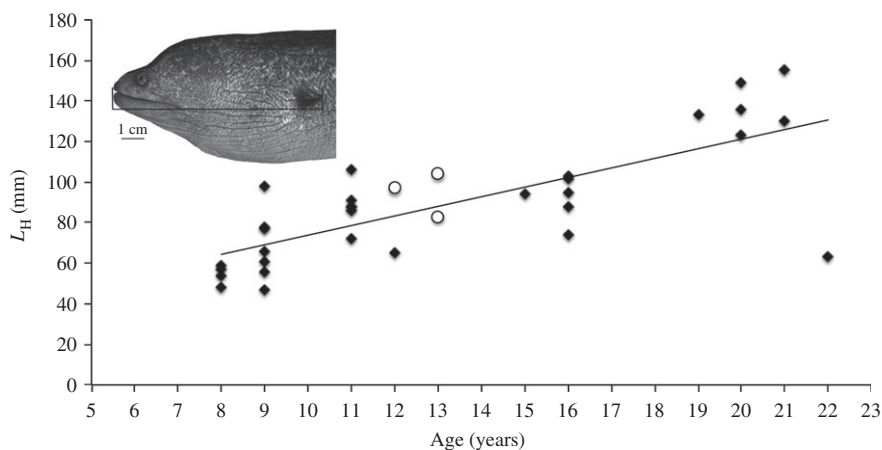


FIG. 4. Relationship between *Gymnothorax mordax* (head length, L_H) and number of annuli (age). ◆, El Niño period; ○, non El Niño period. The curve was fitted by: $y = 4.73x + 26.5$ ($r^2 = 0.56$, $P < 0.001$).

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.

The authors are grateful to M. Beck and the Nature Conservancy, a Hellman Foundation Grant to R.S.M., a grant from the Institute of Marine Sciences at UCSC to R.S.M., donations *via* Experiment.com and J. Kramer for supporting the research; T. Williams, M. Carr, J. Estes, V. Baliga, C. Law, J. Harrison and S. Kienle for providing valuable input and comments on the research; A. Diluzio, S. Eckley, S. Burns and J. Redwine for their assistance with field collections and the staff of the University of Southern California Wrigley Institute for Environmental Studies for logistical support.

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., ($y = 0.14x$; $r^2 = 0.97$).

FIG. S3. Mean \pm 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 ($P < 0.05$).

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