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Rapid Range Expansion of a Marine Ectotherm Reveals the Demographic and Ecological Consequences of Short-Term Variability in Seawater Temperature and Dissolved Oxygen

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ABSTRACT: The distributions of marine ectotherms are governed by physiological sensitivities to long-term trends in seawater temperature and dissolved oxygen. Short-term variability in these parameters has the potential to facilitate rapid range expansions, and the resulting ecological and socioeconomic consequences may portend those of future marine communities. Here, we combine physiological experiments with ecological and demographic surveys to assess the causes and consequences of sudden but temporary poleward range expansions of a marine ectotherm with considerable life history plasticity (California market squid, *Doryteuthis opalescens*). We show that sequential factors related to resource accessibility in the core range—the buildup of large populations as a result of competitive release and climate-associated temperature increase and oxygen loss that constrain aerobic activity—may drive these expansions. We also reveal that poleward range expansion alters the body size—and therefore trophic role—of invading populations, with potential negative implications for socioeconomically valuable resident species. To help forecast rapid range expansions of marine ectotherms, we advocate that research efforts focus on factors impacting resource accessibility in core ranges. Determining how environmental conditions in receiving ecosystems affect body size and how body size is related to trophic role will help refine estimates of the impacts of future marine communities.

Keywords: environmental variability, rapid range expansion, body size, trophic ecology, Gulf of Alaska, California Current System.

Introduction

Understanding how marine ecosystems respond to climate change is at the forefront of contemporary applied ecology, with species extirpations and influxes being a central focus because they cause ecological change through community reorganization (Parmesan 2006; Doney et al. 2012; Ricciardi et al. 2020). Research exploring multidecadal trends shows that the distributions of marine ectotherms are associated with preferred ranges of abiotic conditions (e.g., Pinsky et al. 2013; Deutsch et al. 2015, 2020), illuminating how sustained climate-related oceanographic change could encourage range shifts over the long-term (Lenoir and Svenning 2015). However, more dynamic responses to variability, or environmental fluctuations related to higher-frequency climate stochasticity (e.g., intradecadal), have received less attention. Although corresponding extirpations and influxes of species tend to be temporary (Dayton and Tegner 1990; Cavole et al. 2016),

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depending on their timing and spatial scale, they can cause lasting ecological change (Ruiz et al. 1997), for instance, via priority effects (Gilman et al. 2010). Moreover, dynamic range shifts often portend projected movements associated with long-term environmental change and are therefore useful for understanding how marine communities will reorganize should these range shifts persist.

Marine species with short life cycles more readily shift their distributions in association with long-term climate change than those with slower turnover rates (Perry et al. 2005). Of the former, migratory species are particularly equipped to respond dynamically to environmental variability by altering movement behavior (Bernhardt et al. 2020), sometimes traveling great distances to find suitable conditions in ecosystems outside of their known range (Dingle 2014). Migrations have usually evolved to be preemptive, responding to cues that predict shifts in habitat suitability (Dingle 2014; Bernhardt et al. 2020). As such, the responses of highly motile marine migrants precede responses of planktonic animals (or sessile animals with planktonic offspring) whose geographic shifts are tied to advection (Chelton et al. 1982; Sagarin et al. 1999; Lluch-Belda et al. 2005; Cimino et al. 2021). While theoretical modeling suggests that environmental variability enhances selection for migratory behavior, it can also favor rapid life cycle turnover, small body size, and increased relative fecundity (Southwood 1977; Bernhardt et al. 2020). Animals that are typified by these adaptations tend to exhibit boom-bust dynamics under variable conditions, as their movement behaviors can be restricted, which limits opportunities to explore farther afield (Cornelius et al. 2013; Dingle 2014). Nevertheless, cases of long-distance migrations in small, short-lived (<1 year) insects, which involve sustained movement over multiple generations, demonstrate how such movements can be achieved under variable conditions despite life history limitations (Pedgley et al. 1995; Stefanescu et al. 2013; Dingle 2014).

While it is recognized that intradecadal climate fluctuations are associated with alterations to the migratory patterns of marine species (e.g., Hubbs and Schultz 1929; Pearcy and Schoener 1987; Pearcy 2002; Lluch-Belda et al. 2005; Zeidberg and Robison 2007), it is less understood how oceanographic variability specifically affects migrants and causes them to move. Recent work has linked metabolic physiology with climate-associated temperature increase and oxygen loss in the world's ocean, highlighting the importance of the oxygen supply-demand relationship in governing the distributions of marine ectotherms (Deutsch et al. 2015, 2020; Wishner et al. 2018; Howard et al. 2020). While considerable attention has focused on the factors controlling hypoxia (Deutsch et al. 2011) and how it affects marine ecosystems (Vaquer-Sunyer and Duarte 2008; Gilly et al. 2013), less attention has been given to the effects of relatively small alterations to oxygen supplies at levels well above hypoxic thresholds. Animals have evolved to maximize aerobic activity to meet the highest persistently available oxygen supplies (Seibel and Deutsch 2020), suggesting that relatively small temperature and dissolved oxygen shifts could impact maximum metabolic performance and thus competitive ability.

Dispersal, altered migratory patterns, or range shifts related to climate change can modify encounter rates between competitors or predators and prey and thereby alter species abundances and distributions, leading to community reorganization (Cushing 1990; Sax et al. 2007; Gilman et al. 2010; Blois et al. 2013). Theoretical and empirical research in terrestrial systems suggests that inferior competitors, perhaps as a result of their physiological sensitivities to abiotic conditions, often have a higher proclivity for dispersal (Grime 1977). Ecological release, for instance, via a decline in competitor or predator abundance, can allow such species to expand their ranges faster and farther, potentially into regions with harsher abiotic conditions than typically occupied with competitors present (i.e., with reduced biotic pressures, more of the fundamental niche can be occupied; Keane and Crawley 2002; Bruno et al. 2003). Changing conditions, either experienced over time in a fixed location or the result of modified movement behavior, can alter life history characteristics, such as body size (Post et al. 1999; Hoving et al. 2013; Sugianto et al. 2019). This can have reproductive consequences related to fecundity or courtship-associated competition and can affect the outcome of ecological interactions or even lead to new interactions (Vasseur and McCann 2005).

Although temperature and oxygen supply likely constrain the contemporary and future ranges of marine ectotherms (Deutsch et al. 2015, 2020), it has yet to be demonstrated (1) how short-term variability in these parameters could affect competitive ability and lead to rapid, transient movements beyond typical ranges; moreover, because the migratory capability of many marine species is difficult to study, it is largely unknown (2) how extensive the movements in response to environmental variability can be, (3) how these migrating species interact with communities outside of their typical ranges, and (4) how environmental conditions in new ecosystems impact ecologically relevant life history characteristics in such migrants. In this study we take an integrated approach to investigate these knowledge gaps in a study system with numerous analogs globally.

Squid are excellent model marine ectotherms to investigate how climate-associated variability in oxygen supply could interact with metabolic physiology to affect migratory patterns and how these alterations could lead to ecological consequences. Many squid are abundant, highly motile predators with remarkable life history plasticity (e.g., Hoving et al. 2013) that inhabit dynamic current systems throughout the world's oceans from the surface to the deep sea (Jereb and Roper 2010). Of these species, many are known to compete for resources with ecologically similar fish (Packard 1972), but they possess traits that result in physiological constraints. These include exceptionally high metabolic rates, energetically costly locomotion, and limited blood oxygen carrying capacity and may make such squid particularly sensitive to variability in temperature and oxygen supply (O'Dor and Webber 1986; Pörtner 2002; Seibel 2016). Moreover, squid populations are proliferating globally (Doubleday et al. 2016), which may be related to ecological release via the decline of fish populations (Caddy and Rodhouse 1998). Variability in oceanographic currents (Checkley and Barth 2009), physiological sensitivity, high migratory capacity (Semmens et al. 2007), and ecological release suggest that abundant, highly motile squid are poised to make rapid and drastic alterations in their distribution (Zeidberg and Robison 2007). High metabolic demand, midtrophic function, and life history flexibility suggest that their distribution shifts could have cascading ecological consequences.

The California market squid, *Doryteuthis opalescens*, is a small (<30-cm), short-lived (<1 year), semelparous (single reproductive cycle) squid primarily inhabiting the California Current System (CCS), an eastern boundary upwelling ecosystem in the North Pacific Ocean. There, it is primarily associated with nearshore slope and shelf habitats (Zeidberg 2013). In response to climate-associated oceanographic variability, *D. opalescens* has demonstrated plasticity in life history characteristics and range-wide changes in abundance. During warm climate periods, squid mature at smaller sizes and younger ages and become less abundant relative to cooler periods (Jackson and Domeier 2003; Reiss et al. 2004). This suggests that *D. opalescens*, like many *r*-strategists, exhibits boom-bust cycling (Perretti 2014). Three lines of evidence indicate that *D. opalescens* could also be capable of relatively substantial seasonal or nomadic migrations. First, conservative estimates suggest that 583–816 km could be traveled in an individual's lifetime (O'Dor 1988; Zeidberg 2004; Payne and O'Dor 2006). Second, population genetic analyses demonstrate substantial gene flow over the entire range (Reichow and Smith 2001; Cheng et al. 2020). Finally, geographic trends in *D. opalescens* abundance reflect seasonal shifts in productivity and temperature in the CCS (Zeidberg 2013).

Periodically, *D. opalescens* has appeared in the Gulf of Alaska (GOA; fig. 1), an ecosystem whose southern limit is more than 1,200 km north of the northern extent of the squid's primary range. Past poleward range expansion events of *D. opalescens* (1957–1958: Reid 1961; 1980–1984: Street 1983; Wing and Mercer 1990) were hypothesized to occur in conjunction with climate shifts that caused warmer-than-average conditions and to be associated with ecological interactions between *D. opalescens* and GOA species (Wing and Mercer 1990). However, no quantitative assessment has been made. Over the past two decades, this species has been detected intermittently in the GOA by scientific surveys, most recently from 2015 onward. To investigate how climate-associated variability in environmental conditions could interact with metabolic physiology to encourage alterations to migratory patterns and how these alterations could lead to ecological consequences, we examine the causes and consequences of recent poleward range expansions of *D. opalescens* (fig. 2).

Methods

Multigenerational Poleward Migration and Short-Term Environmental Variability

Unless otherwise noted, all assumptions of statistical tests were met, α was set to .05, and all analyses and data visualizations were implemented using R (ver. 3.5.2; R Core Team 2018). Data underlying all analyses have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.ksn02v75h; Burford 2021).

To examine how poleward range expansion of *Doryteuthis opalescens* could involve long-distance migration sustained over multiple generations, we approximated the poleward progression of *D. opalescens* from 2014 to 2017 using observations of this species from scientific survey data in the CCS (Morgan et al. 2019) and GOA (NOAA AFSC RACE 2017) and from reports by community members in the GOA. The movement capability of *D. opalescens* has been approximated from allometry-based measurements made by remotely operated vehicles (average velocity $= 0.21$ m s^{-1}; Zeidberg 2004) and from acoustic tagging efforts (average velocity $= 0.15$ m s^{-1}; Payne and O'Dor 2006). Averaging these estimates suggests that a conservative approximation of geographic travel distance for *D. opalescens* during its typical life span of 6 months (Zeidberg 2013) is 700 km independent of currents. Consistent with previous work (O'Dor 1988), this estimate assumes 50% travel time (12 h day^{-1}) during the period of maturation (last 3 months of life; Zeidberg 2013).

We determined whether the movement capabilities of this species align with the time and distance between the observations of the poleward range expansion of *D. opalescens* by calculating the time between observations (in generations, with 6 months = 1 generation), the potential travel distance this species could achieve during that time period (700 km $generation^{-1}$), and nearshore distance between observations, or the shortest distance between

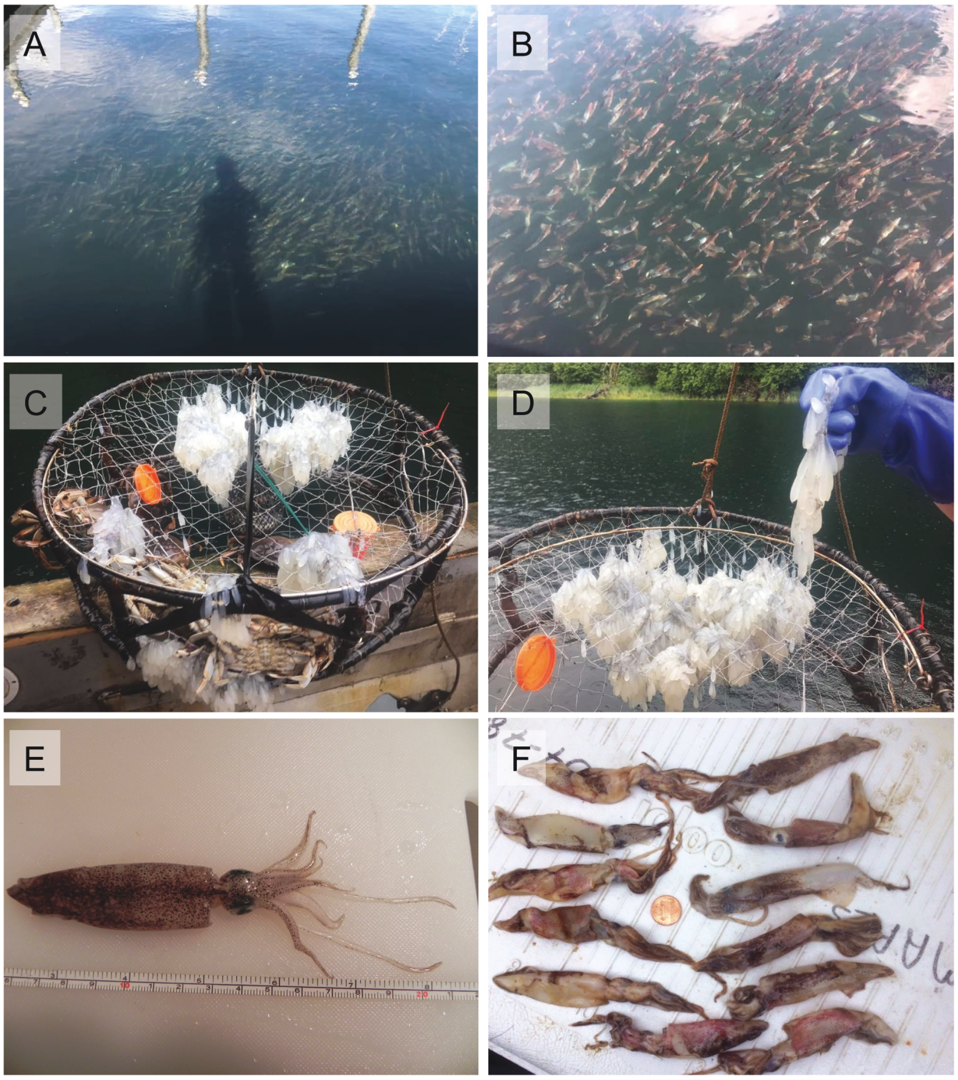


Figure 1: Poleward range expansion of California market squid (*Doryteuthis opalescens*). The poleward range expansion of *D. opalescens* from 2015 to 2019 (and potentially onward) is similar to past events in 1957–1958 and 1980–1984 (Wing and Mercer 1990), with evidence of potential recruitment and ecological activity. *A* and *B* show groups of *D. opalescens* in nearshore waters in Ketchikan, Alaska, in 2019 (photos: Trent Matthews). *C* and *D* show clusters of *D. opalescens* egg capsules attached to a crab pot in Chatham Strait, Alaska, in 2017 (photos: Bryan Todd). *E* shows a juvenile *D. opalescens* found in a Chinook salmon (*Oncorhynchus tshawytscha*) stomach in Sitka Sound, Alaska, in 2017 (Photo: Karen Johnson). *F* shows juvenile *D. opalescens* found in a coho salmon (*Oncorhynchus kisutch*) stomach in Yakutat, Alaska, in 2017 (Photo: Casey Mapes).

observations that does not go over land. Alternatively, if the rate of poleward progression exceeds movement capacity, this would suggest that poleward range expansion involves the proliferation of a small, typically undetected population of *D. opalescens* in the GOA.

Large population size can reduce resource availability via elevated intraspecific competition (Branch 1975; Liow et al. 2011). Thus, we hypothesized that poleward range expansion would be most likely to occur when squid abundance was high in the CCS. However, it is thought that the GOA cannot consistently support *D. opalescens* populations because it is typically too cold for the successful development of *D. opalescens* eggs (Wing and Mercer 1990; Zeidberg 2013), which are laid in the benthos nearshore and have the highest hatching success between 9°C and 14°C (Zeidberg et al. 2011, 2012). Thus, increased abundance in the CCS, when coupled with warming nearshore conditions in the GOA, could be associated with periods of sustained *D. opalescens* presence in the GOA. Alternatively, if poleward range expansion of *D. opalescens*

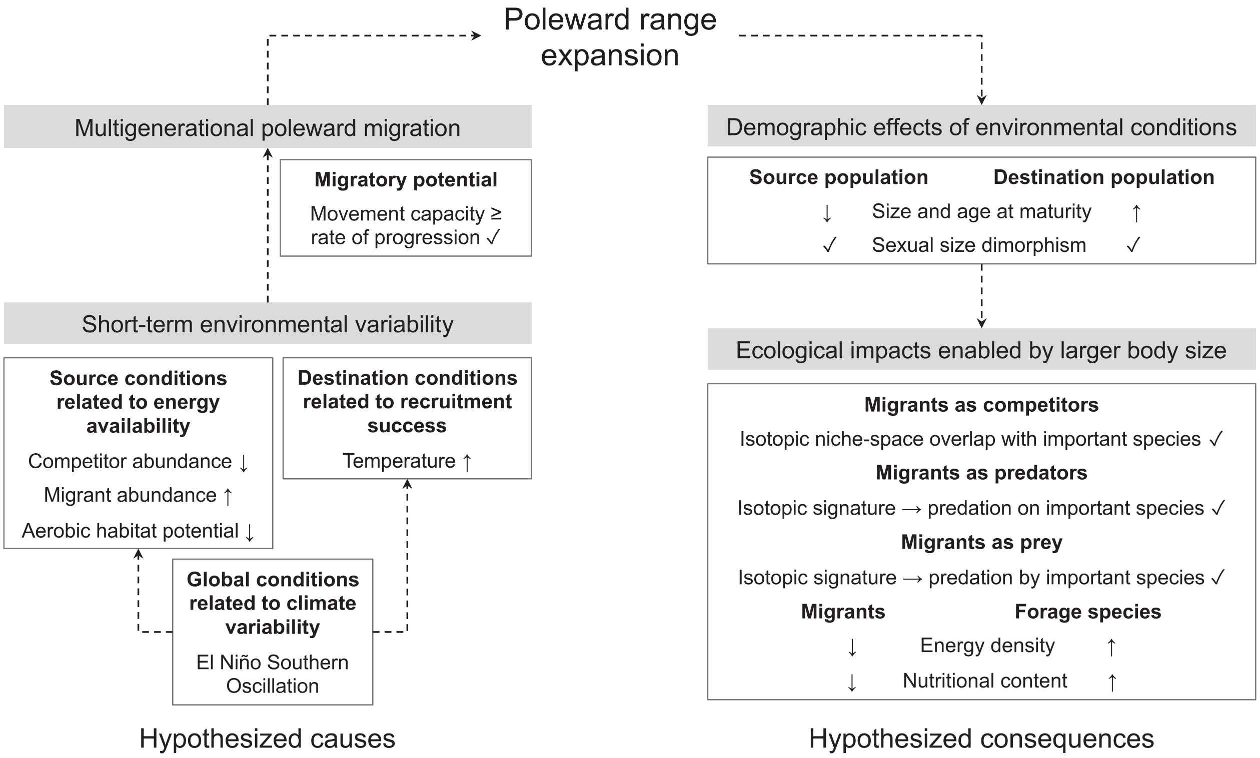


Figure 2: Path diagram outlining the hypotheses of our investigation into the potential causes and consequences of the poleward range expansion of California market squid (*Doryteuthis opalescens*). *Left*, we hypothesized that poleward range expansion was related to multigenerational migration in response to short-term environmental variability. Specifically, global climate variability would encourage poleward movement from lower latitudes by influencing conditions related to energy availability and allow for recruitment at higher latitudes by influencing conditions related to offspring development. The contribution of migration to poleward range expansion would be contingent on the species' movement capacity. *Right*, we hypothesized that poleward range expansion was associated with coupled demographic and ecological consequences. Specifically, populations at higher latitudes would grow larger and live longer than those at lower latitudes; larger body size would be associated with distinct trophic impacts on important species in higher-latitude communities.

is primarily attributable to temperature and has limited association with CCS squid abundance, this would suggest that it primarily involves the rapid growth of a small resident GOA population.

To investigate the environmental context of poleward range expansion of *D. opalescens*, we examined how the probability of *D. opalescens* capture by the National Oceanic and Atmospheric Administration (NOAA) Alaska Fisheries Science Center Groundfish Assessment Program bottom trawl survey (NOAA AFSC RACE 2017; supplemental PDF, supporting methods 1.1) was associated with regional and global environmental factors from 1999 to 2017 ($n = 3{,}101$ hauls; table S1 [tables S1–S7 are available online]) using a generalized additive mixed effects model (GAMM) implemented in the mgcv package (Wood 2011). We included a random effect term (stratum) that accounted for unbalanced sampling of GOA regions with different baseline probabilities for *D. opalescens* capture (i.e., not all regions were sampled equally every year). We modeled catch probability because *D. opalescens* is caught infrequently (and in low abundance) by this survey.

When assessing potential drivers of *D. opalescens* catch probability in the GOA, we considered two region-specific predictors and one global predictor (supplemental PDF, supporting methods 1.2). The regional predictors were average winter/spring (January to May) nearshore seawater temperature in the GOA (NOAA CO-OPS 2019*a*), approximating suitability for recruitment of *D. opalescens*, and average $\log(x + 1)$-transformed *D. opalescens* catch in the central CCS (NOAA NMFS SWFSC FED 2015), representing squid abundance in the core range and thus a potential source population of migrants. The global predictor was average winter/spring multivariate El Niño Southern Oscillation (ENSO)

Index (NOAA ERL PSD 2019), which represents a dominant mode of intradecadal (relatively high-frequency) climate variability that influences environmental conditions in the CCS and GOA (Stabeno et al. 2004; Checkley and Barth 2009).

To account for potential delayed effects between predictors and the response, we examined their correlation at 0–2-year time lags and selected the time lag with the highest correlation to include in the model. CCS squid catch was therefore lagged by 2 years, while ENSO and temperature were not lagged. When assessing collinearity, we found that ENSO had a moderate positive correlation with temperature (Pearson correlation coefficient $= 0.66$, $P < .001$), which caused variance inflation factors to exceed the recommended threshold of 3 (Fox and Weisberg 2011). We therefore removed the ENSO predictor, as temperature is directly relatable to the biology of *D. opalescens*.

We assessed the explanatory value of nonparametric and parametric interactions between *D. opalescens* catch probability and the environmental predictors by fitting multiple GAMMs and selecting the most parsimonious model (supplemental PDF, supporting methods 1.3). To evaluate how predictors were related to the response, we used the most parsimonious model to calculate the response over their full range while holding the other predictor at an average value (temperature $= 9.15°\mathrm{C}$, CCS squid $= 2.47$) and sampling region at that with the maximum probability of *D. opalescens* catch (stratum "50," or shelf habitats shallower than 113 m in the southeastern GOA; von Szalay and Raring 2018).

We hypothesized that the primary mechanism of *D. opalescens* poleward range expansion involved an influx of squid from lower latitudes. Competition and abiotic conditions related to metabolism are known to drive both recruitment success and distribution shifts in other taxa (e.g., Zimmermann et al. 2008; Meier et al. 2012; Deutsch et al. 2015). Such factors may be particularly relevant for physiologically sensitive animals with rapid turnover rates, such as *D. opalescens* and other squid. Northern anchovy (*Engraulis mordax*) and Pacific sardine (*Sardinops sagax*) are particularly relevant competitors of *D. opalescens* in the CCS (supplemental PDF, supporting methods 1.4). Competitive release via the decline of anchovy and sardine populations (Lindegren et al. 2013; MacCall et al. 2016) could therefore lead to higher abundance of *D. opalescens* in the CCS, a portion of which would then undertake poleward movement in response to sustained reduction in aerobic habitat potential. Alternatively, a lack of association between CCS squid abundance and the abundance of fish competitors or aerobic habitat potential would indicate that bottom-up factors influencing prey availability may be more relevant.

To investigate factors that might have affected the abundance and competitive ability of *D. opalescens* in the CCS, we examined how *D. opalescens* catch by the NOAA Southwest Fisheries Science Center Rockfish Recruitment and Ecosystem Assessment pelagic trawl survey (NOAA NMFS SWFSC FED 2015; supplemental PDF, supporting methods 1.2) was associated with regional and global environmental factors from 1999 to 2018 ($n = 576$ hauls; table S1) using a GAMM. By-haul catch per unit effort of *D. opalescens* was adjusted for normality with a $\log(x + 1)$ transformation, and we included a random effect term (station) to account for unbalanced sampling. We modeled catch (instead of capture probability) because *D. opalescens* is caught frequently (and in high abundance) by this survey.

When assessing potential drivers of *D. opalescens* catch in the CCS, we considered ENSO as a global predictor and two regional predictors: average $\log(x + 1)$-transformed combined catch of anchovy and sardine from the CCS pelagic trawl survey, representing the abundance of competitors in the core range, and average winter/spring metabolic index (ϕ; see below) in the CCS, estimating the aerobic activity obtainable by *D. opalescens* in nearshore waters. To account for potential delayed effects between predictors and the response, we examined their correlation at 0–2-year time lags and selected the time lag with the highest correlation to include in the model. All environmental predictors were therefore lagged by 1 year except CCS anchovy and sardine catch, which was lagged by 2 years.

The term ϕ is the ratio of the environmental oxygen supply to the oxygen supply necessary for routine metabolic demand as a function of temperature (Deutsch et al. 2015) and is equivalent to factorial aerobic scope (FAS; Seibel and Deutsch 2020). We calculated ϕ for *D. opalescens* from a seawater temperature and dissolved oxygen time series (2003–2019; Monterey Bay Aquarium 2019; fig. S1*A* [figs. S1–S5 are available online]; supplemental PDF, supporting methods 1.4) and the temperature dependence of hypoxia vulnerability, as measured by critical oxygen partial pressure (P_{crit}; fig. S1*B*). This was determined from closed-system respirometry experiments of groups of *D. opalescens* ($n = 14$ groups composed of 309 individuals) across an ecologically relevant temperature range (7.5°C–19°C; supplemental PDF, supporting methods 1.6). To validate our P_{crit} measurements, we experimentally determined FAS (the ratio of maximum and routine metabolic demand; Halsey et al. 2018) for *D. opalescens* at an intermediate temperature (14°C) using intermittent-flow swim tunnel respirometry (fig. S1*C*; supplemental PDF, supporting methods 1.6) and compared it with P_{crit} at the same temperature.

We assessed the explanatory value of nonparametric and parametric interactions between *D. opalescens* catch and the environmental predictors by fitting multiple GAMMs and selecting the most parsimonious model (supplemental PDF, supporting methods 1.5). To evaluate how predictors were related to the response, we used the most parsimonious model to calculate the response over their full range while holding the other predictors at average values (CCS anchovy and sardine $= 1.16$, $\phi = 3.51$, ENSO $= -0.32$) and sampling station at that with the average *D. opalescens* catch.

Demographic Effects of Environmental Conditions

As a short-lived, semelparous species, size and age at sexual maturity in *D. opalescens* (and other squid with similar life histories) represent the terminal size and age of an individual and are therefore a reliable metric for comparison (Jackson and Domeier 2003; Jackson 2004; Hoving et al. 2013). To assess whether poleward range expansion into the GOA might influence the life history characteristics of *D. opalescens* as opposed to lower-latitude residence in the CCS, we compared the size (dorsal mantle length; mm) and age (days) of sexually mature squid concurrently collected in the GOA and CCS.

The age of *D. opalescens* specimens was estimated by counting increments in the microstructure of squid statoliths (Arkhipkin and Shcherbich 2012; Arkhipkin et al. 2018; supplemental PDF, supporting methods 1.7). Homologues to fish otoliths, statoliths are calcareous structures located in squid's organs of equilibrium (statocysts) in the cartilaginous cranium. As with otoliths, growth increments are deposited on statoliths at regular intervals. Laboratory validation has shown that in *D. opalescens*, statoliths have a daily deposition rate for at least the first 54 days after hatching, and this rate may be assumed for the duration of the life span (Jackson and Domeier 2003).

The GOA is typically cooler and more productive than the CCS (Stabeno et al. 2004; Checkley and Barth 2009); thus, squid that developed in the GOA could have grown larger and older at maturity than squid in the CCS. Alternatively, a lack of size or age differentiation between ecosystems might indicate the ubiquity of relatively warm and unproductive conditions in the northeast Pacific owing to El Niño and coincident high-pressure anomalies during the study period (Bond et al. 2015). We examined the initial effects of poleward range expansion on the life history characteristics of *D. opalescens* by comparing age and size at maturity between GOA and CCS squid collected in 2016 using general linear models (supplemental PDF, supporting methods 1.8). In each model, collection (GOA 2016 or CCS 2016) was the independent variable, and to account for variation attributable to sex and size or age, we included sex (male or female) and size (dorsal mantle length; mm) or age (days) as covariates.

Prolonged warming and limited productivity are thought to be responsible for recent sustained declines in size at maturity of other Pacific squid (e.g., Frawley et al. 2019). Sustained climate shifts encompassing the study period may have led to decreased size at maturity of *D. opalescens* over time in the CCS and GOA. Indeed, the size of *D. opalescens* captured by the fishery in the central CCS (Monterey Bay) declined before our study period (1948–2006; Brady 2008). Alternatively, the absence of such declines in the CCS or GOA may indicate the availability of ecosystem-specific features that enabled squid to maintain or increase size and age at maturity amid prolonged warming, including regional upwelling or localized prey sources.

To investigate how the life history characteristics of *D. opalescens* in higher-latitude populations may have shifted as the poleward range expansion event has progressed, we compared age and size at maturity between GOA squid collected in 2016 and 2017 using general linear models (supplemental PDF, supporting methods 1.8). To understand how life history characteristics of *D. opalescens* in lower-latitude populations may have shifted during the poleward range expansion event, we explored how squid size at maturity has shifted in the CCS from July 2016 to August 2019 (supplemental PDF, supporting methods 1.7) using an analysis of covariance with day of study period (0–1,101) as the independent variable and sex (male or female) as the covariate.

To further contextualize the life history characteristics of *D. opalescens* during the poleward range expansion event, we compared the size of mature squid in the GOA and CCS from our study with similar field-contextualized historical records made more than a half century ago in the CCS. Squid from our study were collected in the GOA from 2016 to 2017 and in the CCS from 2016 to 2019 as previously described. Data from Fields (1965) were used to represent the size of mature squid from 1948 to 1962 in the CCS (supplemental PDF, supporting methods 1.7), which were collected from the commercial fishery in the same location as our CCS squid (Monterey Bay).

Early life history growth rates of *D. opalescens* and close relatives increase with temperature and prey availability, while the effect of salinity is relatively minor (Villanueva 2000; Vidal et al. 2002; Villanueva et al. 2007). Because spring and summer in the GOA encompass periods of relatively high seawater temperature and nearshore primary productivity (Brickley and Thomas 2004; Stabeno et al. 2004), squid that hatched during these seasons would grow to the largest sizes and oldest ages. Squid that hatched in fall and winter, when temperature and nearshore productivity are relatively low (Brickley and Thomas 2004;

Stabeno et al. 2004), would grow to smaller sizes and younger ages at maturity.

To investigate how environmental conditions in early ontogeny might influence the life history characteristics of *D. opalescens* in the GOA, we assessed how hatching season was related to the size and age of mature squid using general linear models (supplemental PDF, supporting methods 1.8) with hatching season (winter, spring, summer, or fall) as the independent variable and sex and year of capture as covariates. Hatching date, which we calculated by subtracting age at maturity from capture date, was used to assign squid to hatching season.

Ecological Impacts Enabled by Larger Body Size

To investigate how *D. opalescens* might affect ecologically and economically important constituents of nearshore GOA communities through interspecific competition, predation, and its suitability as a prey item, we used stable isotope analysis of carbon and nitrogen to assess integrated diet over time (supplemental PDF, supporting information 1.9). We examined *D. opalescens* and several other species also collected in the GOA that were likely to have had direct or indirect trophic interactions with *D. opalescens* (Fields 1965; Karpov and Cailliet 1978; Morejohn et al. 1978; Wing and Mercer 1990). Species selection for this analysis balanced collection feasibility with ecological relevance and did not necessarily represent the complete food web with which *D. opalescens* interacted.

To account for isotopic variation attributable to location and time, samples were collected in the vicinity of Baranof and Chichagof Islands in southeast Alaska (the region containing and adjacent to Sitka Sound) primarily from 2016 to 2018 in winter or spring (table S2). Because of sampling constraints during the period of interest, existing data on stable isotope composition for several species were also used (Fergusson et al. 2018; Hanselman et al. 2018; Strasburger et al. 2018; Kosma 2019; J. M. Straley, unpublished data). Preservation and processing methods of these samples were similar to our own and are described in detail by the published references (table S2).

In the CCS, *D. opalescens* is an opportunistic midtrophic predator that primarily feeds on small crustaceans, such as krill (Euphausiidae; Fields 1965; Karpov and Cailliet 1978; Morejohn et al. 1978; Wing and Mercer 1990). However, at larger body sizes *D. opalescens* will also feed on small fish (Fields 1965; Karpov and Cailliet 1978). Midtrophic GOA species that overlapped with *D. opalescens* in space and time during poleward range expansion, including Pacific herring (*Clupea pallasii*) and juvenile sablefish (*Anoplopoma fimbria*), have similar foraging strategies and prey (Whitehead et al. 1988; Armstrong 1996; Coutré et al. 2015). This would suggest the potential for interspecific competition between *D. opalescens* and these species, which have high socioeconomic importance in the GOA (SeaBank 2018). In particular, if squid grew to larger sizes, they would be in competition for prey with more piscivorous species, such as juvenile sablefish (Armstrong 1996; Sturdevant et al. 2009; Coutré et al. 2015).

To visualize the potential for competition between *D. opalescens* and key constituents of GOA nearshore communities, we represented the isotopic niche space of all species included in this analysis by plotting $\delta^{15}N$ versus $\delta^{13}C$ and calculating 95% prediction intervals (PIs) around the respective bivariate means. From functions in the SIBER package (Jackson et al. 2011), trophic overlap was quantified by calculating isotopic niche width using Bayesian standard ellipse area corrected for sample size (SEAc; ‰^{2}). We then calculated the area of SEAc overlap between *D. opalescens* and species with at least some 95% PI overlap with *D. opalescens* (Parnell and Jackson 2013). Niche space overlap, an index of the potential for competition, was determined as the percentage of a species' SEAc occupied by that of *D. opalescens*.

According to dietary work in the CCS (Fields 1965; Karpov and Cailliet 1978), we would expect *D. opalescens* to primarily feed on krill and other small crustaceans in the GOA. However, if squid grew to relatively large sizes at maturity, then small fish, such as juvenile salmon (*Oncorhynchus* spp.) and herring, with which the squid overlapped in space and time during poleward range expansion, could also comprise their diet. Salmon and herring have high socioeconomic importance in the GOA (SeaBank 2018).

To determine potential trophic links between *D. opalescens* and key constituents of GOA communities, we calculated the contribution of potential prey species to the isotopic signature of *D. opalescens* using Bayesian isotopic mixing models (Moore and Semmens 2008) run from functions in the MixSIAR package (Stock and Semmens 2016; supplemental PDF, supporting methods 1.9). To examine how the diet of *D. opalescens* has changed over the course of the GOA proliferation event, we additionally ran a separate model that included sampling year as a factor (sampling months were relatively consistent; table S2). Large copepods (Calanoida; >2.5 mm in total length), krill, juvenile salmon, and herring were selected as potential prey species to include in both mixing models (supplemental PDF, supporting methods 1.9).

As an abundant midtrophic species, *D. opalescens* is consumed by many important upper-trophic-level species in the CCS (Morejohn et al. 1978), including adult Chinook salmon (*Oncorhynchus tshawytscha*) and coho salmon (*Oncorhynchus kisutch*; Brodeur et al. 2014). During past and present poleward range expansion events, *D. opalescens* has been found in the stomach contents of adult Chinook and coho salmon in the GOA (Wing and Mercer 1990; fig. 1*E*, 1*F*). Thus, given the squid's availability in the GOA, both Chinook salmon and coho salmon would likely prey on *D. opalescens*.

Using Bayesian isotopic mixing models, we investigated the extent to which *D. opalescens* was preyed on by upper-trophic-level species in the GOA by estimating the contribution of *D. opalescens* to the isotopic signature of adult Chinook and coho salmon. Three additional potential prey species from our data set were selected to include in each predator's Bayesian isotopic mixing model: large copepods, krill, and Pacific herring (supplemental PDF, supporting methods 1.9). These species are present and all are known to be preyed on by adult Chinook and coho salmon (Reid 1961; Landingham and Sturdevant 1998; Weitkamp and Sturdevant 2008).

To further investigate the value of *D. opalescens* as a prey item for upper-trophic-level species in the GOA, we compared the energy density of *D. opalescens* with four common forage fish (table S3, pt. A; supplemental PDF, supporting methods 1.10), primarily using data from published references (Vollenweider et al. 2011; Hanselman et al. 2018; Chenoweth et al. 2021). In the CCS, *D. opalescens* has energy density comparable to or slightly lower than forage fish (Morejohn et al. 1978; Zeidberg 2013), and we hypothesized that the same would be true in the GOA. To assess how energy density was related to species while accounting for differences in body size, we used a general linear model (supplemental PDF, supporting methods 1.8) with species as the independent variable and size as the covariate. Size was included in terms of length: dorsal mantle length (mm) was used for squid and fork length (mm) was used for fish.

We also compared the lipid and protein content of *D. opalescens* with two common forage fish (table S3, pt. B; supplemental PDF, supporting information 1.10), primarily using data from a published reference (Vollenweider et al. 2011). In the CCS, *D. opalescens* has relatively low lipid content and high protein content compared with forage fish (Morejohn et al. 1978; Zeidberg 2013), and we hypothesized that the same would be true in the GOA. We calculated 95% confidence intervals (CIs) around the mean lipid and protein content for each species using standard deviations and the *t*-distribution ($n - 1$ df).

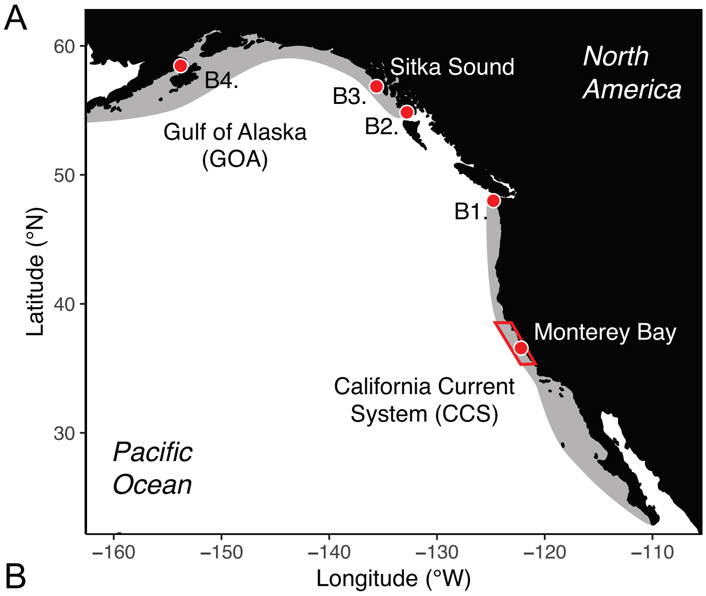
Results

Multigenerational Poleward Migration and Short-Term Environmental Variability

Long-distance migration sustained over several generations is a potential mechanism for poleward range expansion of *Doryteuthis opalescens*. The geographic migratory capability of *D. opalescens*, which we conservatively approximated at 700 km life span^{-1}, accounted for the time and distance between observations of its poleward progression from June 2014 to July 2017 (fig. 3*A*, 3*B*). Accordingly, potential travel distance of *D. opalescens* over this time span exceeded the distance between all observations (fig. 3*B*). This neither precludes nor supports the alternative hypothesis of rapid growth of an undetected resident population.

Poleward range expansion of *D. opalescens* had little association with nearshore temperature in the GOA, which approximated the suitability for recruitment of *D. opalescens*. By contrast, there was a positive association with time-lagged shifts in the abundance of lower-latitude populations—a potential source population of migrants—further supporting the hypothesis of multigenerational poleward migration. The most parsimonious GAMM related the capture probability of *D. opalescens* by the GOA bottom trawl survey to average $\log(x + 1)$-transformed CCS *D. opalescens* catch from 2 years before with a parametric dependency ($z = 2.94$, $P = .003$; fig. 4*B*, 4*C*; table S4, pt. B) and to average winter/spring nearshore temperature with a cubic spline dependency ($z = 3.47$, $P = .21$; fig. 4*A*, 4*D*; table S4, pt. B). The model with predictors fit significantly better than a null (intercept-only) model ($\chi^2 = 65.4$, df = 19, $P < .001$). Average winter/spring multivariate ENSO Index was not correlated with CCS squid catch (Pearson correlation coefficient [PCC] = -0.09, $P = .65$) but had a moderate positive correlation with temperature (see "Methods").

The abundance of *D. opalescens* in the core range, which constitutes a population that could supply migrants to the GOA, had a negative association with the time-lagged abundance of fish competitors, a positive association with time-lagged aerobic habitat potential, and little association with time-lagged ENSO. The most parsimonious GAMM related $\log(x + 1)$-transformed catch of *D. opalescens* by the CCS pelagic trawl survey to average $\log(x + 1)$-transformed anchovy and sardine catch from 2 years before with a cubic spline dependency ($F = 102$, $P < .001$; fig. 4*B*, 4*E*; table S4, pt. D), to average winter/spring metabolic index (ϕ) from the year before with a cubic spline dependency ($F = 23.8$, $P < .001$; fig. 4*B*, 4*F*; table S4, pt. D), and to average winter/spring ENSO from the year before with a parametric dependency ($t = -1.45$, $P = .15$; fig. S2; table S4, pt. D; $R^2 = 0.61$, df = 40, $P < .001$; table S4, pt. C). In 2015 average winter/spring ϕ was lower than any other year in the time series except for 2004 (table S5, pt. B), preceding poleward range expansion of *D. opalescens*. ENSO was not correlated with CCS anchovy and sardine catch (PCC = 0.23, $P = .41$) or dissolved oxygen trends in the CCS



B

	Latitude (˚N)	Longitude (˚W)	Year	Month	Obs. ref.	Time between obs. (mo)	Time between obs. (generations)	Potential travel distance (km)	Distance between obs. (km)
1.	48.227	-124.774	2014	6	1	0	0	0	0
2.	55.214	-133.651	2015	8	2	14	2.33	1631	1005
3.	57.045	-135.329	2016	1	3	3	0.5	350	237
4.	58.261	-154.048	2017	7	2	20	3.33	2331	1212
							6.16	*4312*	*2454*

Figure 3: Poleward range expansion of California market squid (*Doryteuthis opalescens*) could have involved long-distance migration sustained over multiple generations. *A*, Map showing the Gulf of Alaska (GOA) and California Current System (CCS), with both regions shaded in gray. *B*, Approximate progression of the poleward range expansion of *D. opalescens* from 2014 to 2017 aligns with the species' movement capabilities: (1) anomalous abundance of *D. opalescens* in the northern CCS in June 2014, (2) *D. opalescens* captured offshore of Baker Island, Alaska, in August 2015, (3) large numbers of spawning *D. opalescens* observed in Sitka Sound, Alaska, in January 2016, and (4) in addition to other locations, *D. opalescens* captured offshore of Katmai National Park in the northwestern GOA in July 2017. Observation references (Obs. ref.): 1 indicates Morgan et al. (2019), 2 indicates NOAA AFSC RACE (2017), and 3 indicates this study. Distance between observations is the shortest distance that does not go over land. Totals are included below the last three columns to highlight the approximate number of generations it may have taken to travel the distance from the northern CCS to the northwest GOA.

(PCC = 0.33, $P = .23$), but it had a moderate positive correlation with temperature trends in the CCS (PCC = 0.53, $P < .001$); the latter two parameters were the environmental components of ϕ (figure S1*A*). We also derived ϕ from the temperature sensitivity of critical oxygen partial pressure (P_{crit}) in *D. opalescens* (fig. S1*B*). We found that P_{crit} had a weak positive association with temperature; it was lowest at 13°C, but this difference was significant only compared with P_{crit} at 19°C (table S5, pt. A). Measurements of P_{crit} were validated by measurements of FAS in *D. opalescens* (fig. S1*C*; supplemental PDF, supporting methods 1.4); for a 41-g squid at 14°C, P_{crit} (4.84 kPa) was similar to FAS (4.04).

Demographic Effects of Environmental Conditions

Poleward range expansion was associated with changes in life history parameters of *D. opalescens*. Squid in the GOA may have initially achieved larger sizes and older ages at maturity compared with those that resided at lower latitudes (fig. 5*A*). GOA squid in 2016 were on average 67 days older ($t = 7.44$, df $= 36.7$, $P < .001$) and

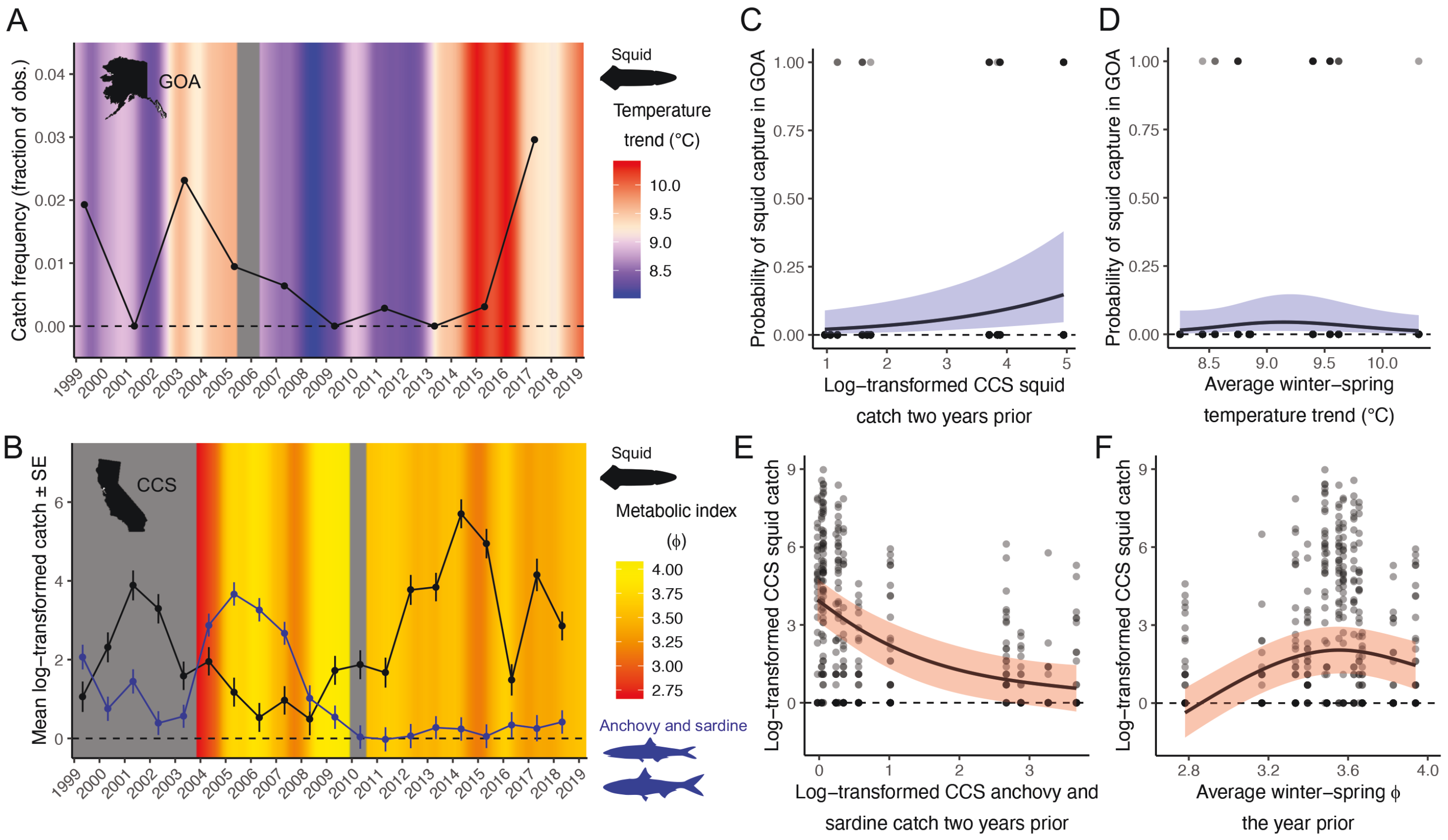


Figure 4: Poleward range expansion of California market squid (*Doryteuthis opalescens*) was associated with climate-related variability in the abundance of competitors, seawater temperature, and dissolved oxygen. *A*, Biennial catch frequency of *D. opalescens* in the Gulf of Alaska (GOA) as recorded by the GOA bottom trawl survey (NOAA AFSC RACE 2017; table S1) overlaid on interpolated monthly nearshore temperature trend (NOAA CO-OPS 2019*a*; gray indicates missing data) recorded in Sitka Sound (fig. 3*A*). Trends were estimated from an average monthly temperature time series using a seasonal-trend decomposition procedure (STL; supplemental PDF, supporting methods 1.2). *B*, Average $\log(x + 1)$-transformed *D. opalescens* catch (black) and average $\log(x + 1)$-transformed sum of northern anchovy (*Engraulis mordax*) and Pacific sardine (*Sardinops sagax*) catch (blue) over time in the central California Current System (CCS; red parallelogram containing Monterey Bay in fig. 3*A*) as recorded by the CCS pelagic trawl survey (NOAA NMFS SWFSC FED 2015; table S1). Averages (±SEs) were obtained from a model-based procedure (supplemental PDF, supporting methods 1.2 and 1.4). Catch time series are overlaid on interpolated monthly nearshore *D. opalescens* metabolic index (ϕ; gray indicates missing data) derived from temperature and dissolved oxygen trends in Monterey Bay (figs. 3*A*, S1). Trends were estimated using STL (supplemental PDF, supporting methods 1.4). On average (±1 SD), ϕ was 3.51 ± 0.26 from late 2003 to early 2019; in 2015, average winter/spring ϕ (3.17 ± 0.03) was lower than any other year in the time series except for 2004 (table S5, pt. B). Probability of *D. opalescens* capture in the GOA with respect to average $\log(x + 1)$-transformed CCS catch from 2 years before (*C*) and average winter/spring nearshore temperature trend (*D*). Solid lines are predictions of the most parsimonious generalized additive mixed effects model (GAMM; table S4, pt. A), with blue bands representing 95% confidence intervals (CIs). $\log(x + 1)$-transformed *D. opalescens* catch in the central CCS with respect to average $\log(x + 1)$-transformed CCS anchovy and sardine catch from 2 years before (*E*) and average winter/spring ϕ from the year before (*F*). Solid lines are predictions of the most parsimonious GAMM (table S4, pt. C), with red bands representing 95% CIs. This model additionally included average winter/spring multivariate El Niño Southern Oscillation Index from the year before (not significant; see "Results"; fig. S2).

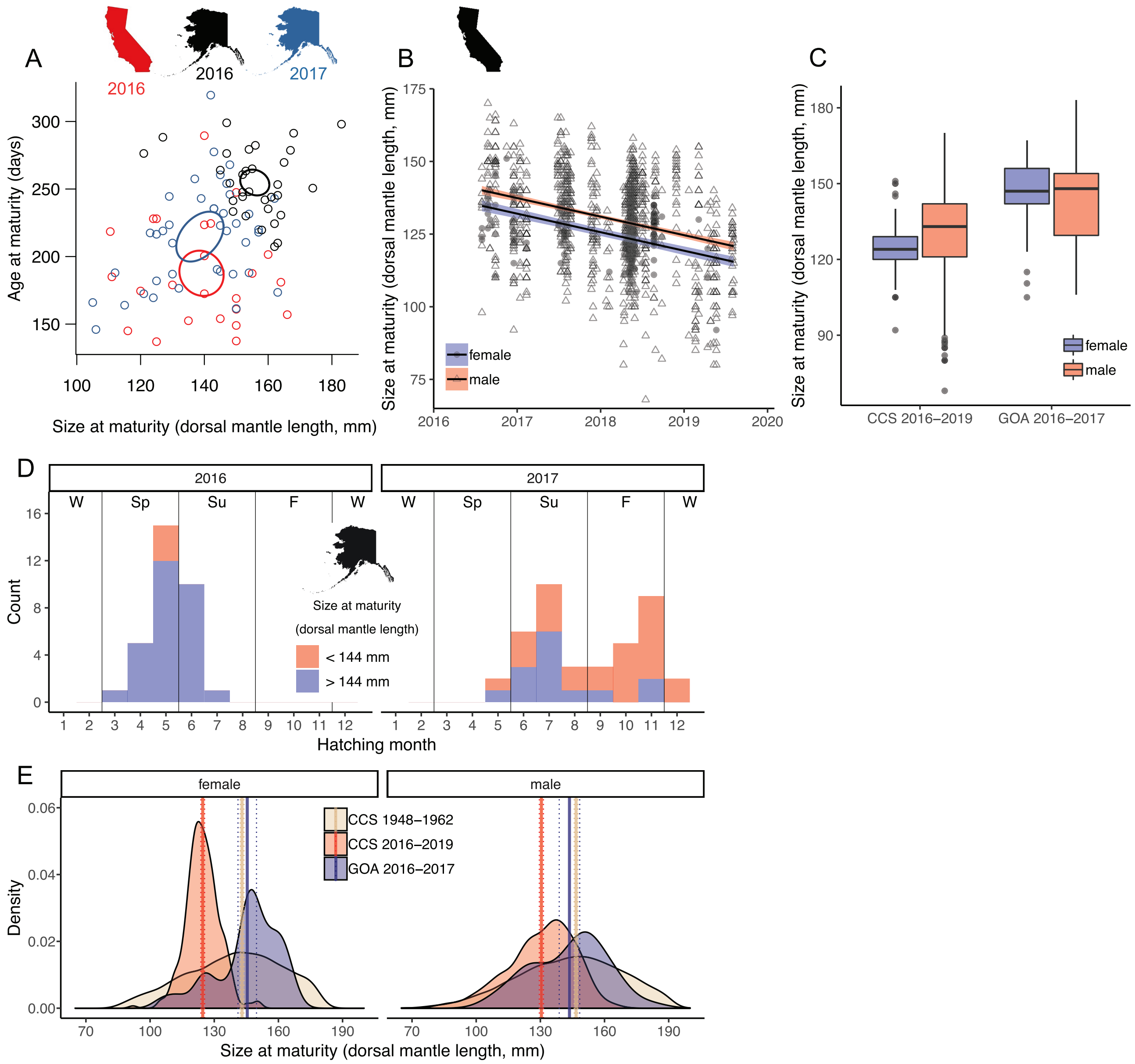


Figure 5: Poleward range expansion was associated with demographic consequences for California market squid (*Doryteuthis opalescens*). *A*, Age and size at sexual maturity of squid collected in the California Current System (CCS; Monterey Bay, CA) in 2016 (red), Gulf of Alaska (GOA; Sitka Sound, AK) in 2016 (black), and GOA in 2017 (blue). Ellipses represent 95% confidence intervals (CIs) of the respective bivariate means. The age and size of sexually mature *D. opalescens* approximate the maximum life span and size, respectively, because this species is semelparous and dies shortly after reproduction. The average age of mature squid in the GOA and CCS in 2016 was 255 and 188 days, respectively; average size was 156 and 139 mm, respectively. In 2017 in the GOA, average age and size at maturity was 215 days and 139 mm, respectively. *B*, Size of sexually mature male and female squid collected in the CCS (Monterey Bay) over time. Lines are predictions of an analysis of covariance model relating squid size to day of study period with sex as a covariate (females are indicated by filled circles; males are indicated by open triangles); shaded ribbons represent 95% CIs. Squid size at maturity in the CCS steadily declined over time, with male *D. opalescens* growing 5.35 mm larger than females on average. *C*, Comparison of size at sexual maturity between male and female squid in the CCS and GOA. Male-biased sexual size dimorphism was present in mature squid in the CCS but absent from mature squid in the GOA (see "Results"). *D*, Size at maturity of squid collected in the GOA in 2016 and 2017 with respect to hatching month and season. Hatching month was determined according to the date of capture and age at maturity. The average size of mature squid in the GOA was 144 mm. W = winter; Sp = spring; Su = summer; F = fall. *E*, Size distributions of sexually mature *D. opalescens* from the GOA (Sitka Sound) and CCS (Monterey Bay) during the recent poleward range expansion event compared with the historical size distribution of squid in the CCS (Monterey Bay) as estimated from data reported by Fields (1965). Solid and dotted vertical lines represent the means and 95% CIs, respectively, of each distribution. The average size of male and female squid (95% CI) was 144 ± 9.6 and 145 ± 8.6 mm in the GOA from 2016 to 2017 (respectively), 147 ± 1.7 and 143 ± 1.7 mm in the CCS from 1948 to 1962 (respectively), and 130 ± 1.9 and 124 ± 1.8 mm in the CCS from 2016 to 2019 (respectively). The age range of mature male and female *D. opalescens* in the GOA was 146–291 and 164–320 days, respectively; the respective size range was 106–183 and 105–167 mm. The age range of mature male and female *D. opalescens* in the CCS was 137–290 and 149–228 days, respectively; the respective size range was 68–170 and 92–151 mm.

17 mm larger ($t = 4.30$, df $= 40.6$, $P < .001$) at maturity than CCS squid collected during the same period. In neither comparison were there significant effects of covariates (sex and size or age).

Life history characteristics for higher-latitude populations of *D. opalescens* may have shifted as the poleward range expansion event has progressed (fig. 5*A*). GOA squid were 40 days older ($t = -2.71$, $P = .008$) and 17 mm larger ($t = -2.66$, $P = .01$) in 2016 than they were in 2017. In these comparisons there was no effect of sex, but there was a significant interaction between size or age and year, with a positive size-age association in 2017 but not 2016 (fig. S3). Including these interactions, age ($R^2 = 0.35$, $F_{3,68} = 13.5$, $P < .001$; table S6, pt. A) and size ($R^2 = 0.35$, $F_{3,68} = 13.5$, $P < .001$; table S6, pt. B) at maturity were significantly related to year in the GOA.

Life history characteristics for lower-latitude populations of *D. opalescens* may have similarly shifted as the poleward range expansion event has progressed (fig. 5*B*). Squid size at maturity in the CCS steadily declined from July 2016 to August 2019 at a rate of 6 mm year^{-1} ($F = 158$, $P < .001$; table S7, pt. A). In this comparison there was a significant effect of sex (males were 5.35 mm larger than females on average; $F = 35.5$, $P < .001$; fig. 5*C*) but no significant interaction between size and sex. Note that in previous comparisons no sexual size dimorphism was detected in GOA squid (fig. 5*C*)

Squid at higher latitudes during poleward range expansion grew to some of the largest sizes and oldest ages documented for this species, reaching sizes comparable to those recorded more than a half century ago at lower latitudes (fig. 5*E*). In contrast, *D. opalescens* that resided at lower latitudes during poleward range expansion were generally smaller than historical sizes (fig. 5*E*), exhibiting some of the smallest sizes and youngest ages at maturity recorded for this species.

Environmental conditions in early ontogeny may have influenced the life history characteristics of mature *D. opalescens* captured in the GOA (figs. 5*D*, S4). Squid that hatched in spring and summer grew larger ($F = 17.3$, $P < .001$; table S7, pt. C) and older ($F = 29.8$, $P < .001$; table S7, pt. D) than squid that hatched in fall and winter. There was a significant effect of capture year in the former comparison ($F = 7.57$, $P = .008$), as squid grew larger in 2016 than they did in 2017 (see above). There was a significant effect of sex in the latter comparison ($F = 4.27$, $P = .04$), with females obtaining slightly older ages at maturity (12 days) than males.

Ecological Impacts Enabled by Larger Body Size

Results are consistent with the hypothesis that *D. opalescens* competed for shared resources with ecologically and economically important constituents of nearshore GOA communities during poleward range expansion. We found substantial overlap in the isotopic niche space of *D. opalescens* and juvenile sablefish (fig. 6*B*): the Bayesian standard ellipse area corrected for sample size (SEAc; ‰^{2}) of *D. opalescens* occupied 56% of that of juvenile sablefish. No other species in our data set (fig. 6*A*) had SEAc overlap with *D. opalescens*.

Results also suggest that *D. opalescens* could have preyed on important constituents of nearshore GOA communities during poleward range expansion. The Bayesian isotopic mixing model estimated that across years (2016–2018), *D. opalescens* had a generalist foraging strategy in the GOA, with no one prey item emerging as markedly dominant (fig. 6*C*). However, when estimates were made for each year, a different picture emerged. Forage fish may have constituted a large proportion of *D. opalescens* diet in 2016, when squid grew largest in the GOA, but small crustaceans appear to be the primary prey in 2017 and 2018, when squid grew smaller. The prey with the highest contribution estimate in 2016 (average ± 1 SD) was juvenile salmon (0.93 ± 0.12), and in 2017 and 2018 it was krill (0.75 ± 0.40 and 0.61 ± 0.36, respectively). In all years, the mixing model estimated a low contribution of Pacific herring (range = 0.04–0.11) and large copepods (range = 0.01–0.19) to squid diet. The model result indicating a large contribution of juvenile salmon to the diet of squid was largely attributed to 2016, the year in which squid were sampled in the winter when juvenile salmon are typically at low availability in nearshore waters (see "Discussion").

During poleward range expansion, *D. opalescens* was likely consumed by important upper-trophic-level species in the GOA. Bayesian isotopic mixing models suggested that out of four prey species, *D. opalescens* occupied the second-highest proportion of adult Chinook salmon diets (fig. 6*D*) and the third-highest proportion of adult coho salmon diets (fig. 6*E*).

Upper-trophic-level species that consumed *D. opalescens* instead of common forage fish in the GOA may have gathered comparable energy supply but lower lipid content and higher protein content. Squid in the GOA had significantly higher energy density than juvenile sablefish ($t = -2.81$, $P = .006$) and comparable energy density to the other GOA forage fish in our data set (fig. 7*A*; table S6, pt. C; $R^2 = 0.38$, $F_{9,95} = 8.23$, $P < .001$). There was no significant effect of size in this comparison, but there was a significant interaction between size and species (table S6, pt. C). Without a size interaction, juvenile sablefish are equivalent in energy density to *D. opalescens*. While the protein content of *D. opalescens* was higher than that of Pacific herring and juvenile sablefish, the lipid content of *D. opalescens* was

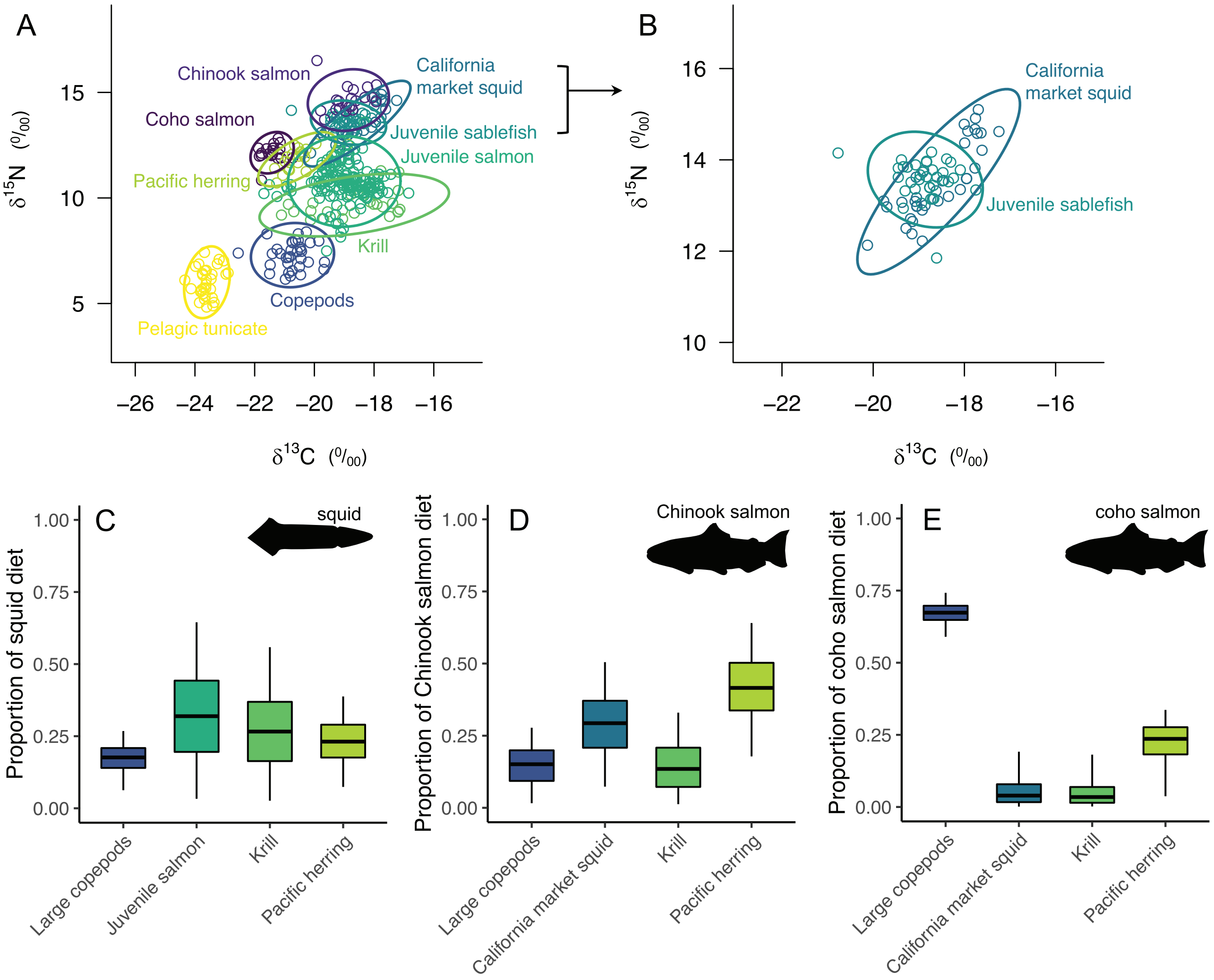


Figure 6: Poleward range expansion was associated with trophic links between California market squid (*Doryteuthis opalescens*) and important species in higher-latitude communities. *A*, Stable isotope signatures of *D. opalescens* and ecologically and economically important constituents of nearshore marine communities in the Gulf of Alaska (GOA): adult coho salmon (*Oncorhynchus kisutch*), adult Chinook salmon (*Oncorhynchus tshawytscha*), juvenile sablefish (*Anoplopoma fimbria*), adult Pacific herring (*Clupea pallasii*), large copepods (Calanoida; >2.5 mm in total length), krill (Euphausiidae), and juvenile salmon (hatchery-raised juvenile coho salmon, hatchery-raised juvenile chum salmon [*Oncorhynchus keta*], and wild juvenile pink salmon [*Oncorhynchus gorbuscha*]). The pelagic colonial tunicate *Pyrosoma atlanticum* represents the signature of an offshore primary consumer. Data are colored by species, with ellipses representing 95% prediction intervals (PIs) to highlight the potential for niche space overlap. *B*, There was a 56% overlap in the Bayesian standard ellipse area corrected for sample size (SEAc; ‰^{2}; not pictured) of *D. opalescens* and juvenile sablefish, indicating a potential for competition. *C*, Bayesian mixing model estimates of the proportions of potential prey contributing to the diet of *D. opalescens* in the GOA. Dark horizontal lines indicate the median values, boxes indicate the inner and outer quartiles, and vertical lines indicate the minima and maxima of the data. The top two prey items in terms of the proportion that they contributed to the isotopic signature of *D. opalescens* across years were juvenile salmon (mean ± 1 SD; 0.32 ± 0.16) and krill (0.27 ± 0.14). *D*, Bayesian mixing model estimates of the proportions of potential prey contributing to the diet of Chinook salmon in the GOA, with boxes and lines representing the same attributes as in *C*; *D. opalescens* occupied the second-highest proportion (0.29 ± 0.11). *E*, Bayesian mixing model estimates of the proportions of potential prey contributing to the diet of coho salmon in the GOA, with boxes and lines representing the same attributes as in *C*; *D. opalescens* occupied the third-highest proportion (0.06 ± 0.05). Upper-trophic-level species, including adult salmon, may have preyed on *D. opalescens* in the GOA during the recent poleward range expansion event (also see fig. 1*E*, 1*F*).

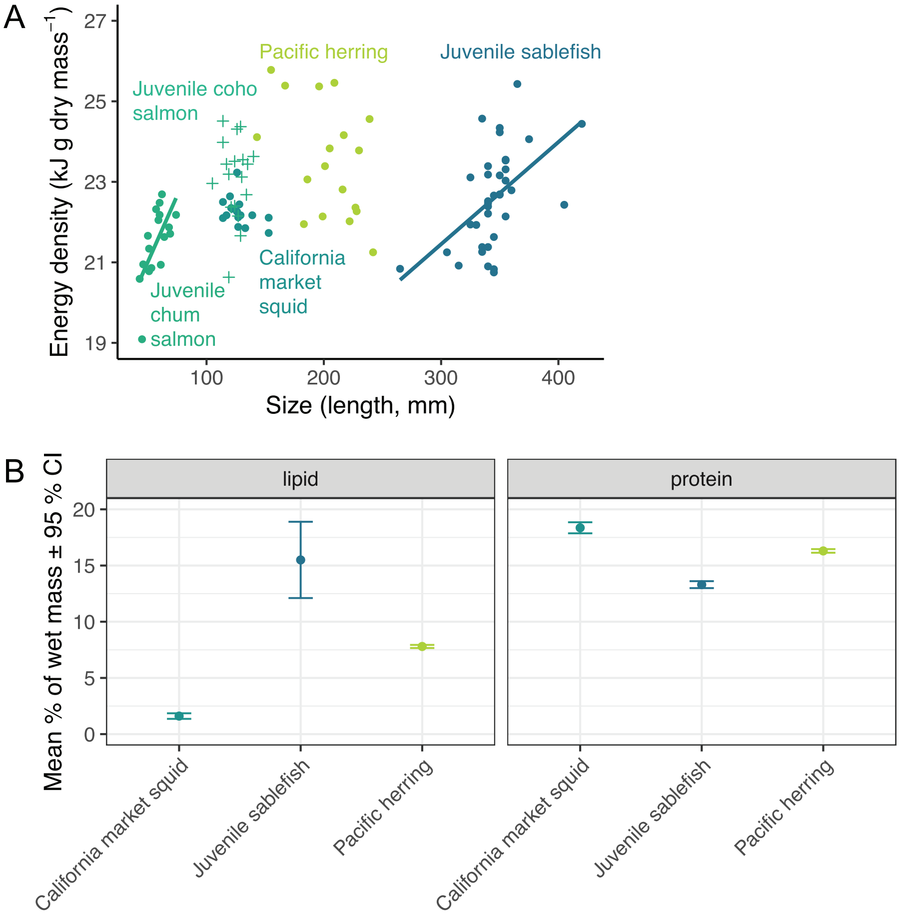


Figure 7: During poleward range expansion, California market squid (*Doryteuthis opalescens*) likely had energy density similar to common forage fish at higher latitudes but with lower lipid content and higher protein content. *A*, Energy content with respect to size of *D. opalescens* collected in the Gulf of Alaska (GOA) compared with that of four key GOA forage fish species: juvenile sablefish (*Anoplopoma fimbria*), hatchery-raised juvenile coho salmon (*Oncorhynchus kisutch*), hatchery-raised juvenile chum salmon (*Oncorhynchus keta*), and Pacific herring (*Clupea pallasii*). Raw values are shown with points; crosses are used to distinguish coho from chum salmon. Length is dorsal mantle length for *D. opalescens* and fork length for fish. There was no significant relationship between energy density and size in juvenile coho salmon, *D. opalescens*, or Pacific herring, but there was a significant positive relationship in juvenile chum salmon ($t = 3.38$, $P = .004$) and juvenile sablefish ($t = 3.57$, $P = .001$). Lines represent the corresponding predictions of significant linear regressions examining the association between energy density and size. Only the energy density–size relationship in chum salmon was significantly different from that of *D. opalescens* (table S6, pt. C). The energy density of *D. opalescens* is comparable to forage fish in the GOA when variation attributable to size is considered—the only significant difference in energy density is between squid and juvenile sablefish, with squid having greater energy density at a common size (128 mm; table S6, pt. C). Relative to squid (22.3 kJ g dry mass^{-1}), there was a difference of -5.17 for juvenile sablefish, 2.96 for Pacific herring, 0.86 for juvenile coho salmon, and 3.91 for juvenile chum salmon (all kJ g dry mass^{-1}). Without a size interaction, juvenile sablefish are equivalent in energy density to *D. opalescens* (difference of 0.34 kJ g dry mass^{-1}). *B*, Lipid and protein content of *D. opalescens* (1.61 ± 0.25 and 18.4 ± 0.49, respectively) compared with that of key GOA forage fish species: Pacific herring (7.8 ± 0.14 and 16.3 ± 0.16, respectively) and juvenile sablefish (15.5 ± 3.39 and 13.3 ± 0.31, respectively).

far below that of Pacific herring and juvenile sablefish (fig. 7*B*).

Discussion

Multigenerational Poleward Migration and Short-Term Environmental Variability

Our data are consistent with the scenario that the causes of poleward range expansion of *Doryteuthis opalescens* began in the contemporary core range of this species, the CCS. We found evidence for a time-lagged association between *D. opalescens* abundance in the core range and the capture probability of this species at higher latitudes in the GOA that aligns with its migratory capabilities (fig. 3*B*; Zeidberg 2004; Payne and O'Dor 2006). Catch probability of *D. opalescens* in the GOA was always very low, likely reflecting limitations of the best available scientific survey data source (supplemental PDF, supporting methods 1.1). However, relative to the mean value, catch probability increased by 288% from the minimum to maximum time-lagged CCS *D. opalescens* abundance (fig. 4*C*). Therefore, influxes of squid that ultimately originated from lower-latitude populations could have at least initially contributed to poleward range expansions of this species, which would suggest that the seasonal or nomadic migratory behavior of *D. opalescens* (Zeidberg 2013) could be augmented to undertake long-distance migration.

These movements are potentially analogous to migrations in small, comparably short-lived (<1 year) insects, such as the nomadic migrations of desert locust (*Schistocerca gregaria*) and the seasonal migrations of the painted lady butterfly (*Vanessa cardui*). Similar to the migrations of larger-bodied, longer-lived migrants, their movements track suitable habitats for foraging and reproduction (Pedgley et al. 1995; Stefanescu et al. 2013; Dingle 2014). However, a key difference is that the migrations of short-lived insects are completed over multiple generations (e.g., sustained movement over six generations is required for *V. cardui* to complete seasonal migrations of thousands of kilometers). Similarly, the hypothesized poleward migration of *D. opalescens* from the northern CCS to the western GOA in 2014–2017, a distance of 2,500 km completed over 37 months, required sustained movement over approximately six generations (fig. 3*A*, 3*B*). This movement, which extended more than 1,000 km beyond any documented occurrence of this species in the GOA (Wing and Mercer 1990; Jereb and Roper 2010), is well within the realm of the highly motile squid's capabilities. In addition, *D. opalescens* could have taken advantage of currents in the northeastern Pacific to further increase its movement potential (Zeidberg 2004; Payne and O'Dor 2006). The prevailing surface currents are equatorward in the CCS, but the deeper (>200-m) Davidson Current flows poleward (Checkley and Barth 2009). Prevailing currents flow counterclockwise in the eastern GOA (North Pacific Gyre), which is effectively poleward (Stabeno et al. 2004).

We hypothesized that warming temperatures in the GOA would facilitate poleward range expansion of *D. opalescens* (Wing and Mercer 1990) by enhancing the recruitment of emigrants. Indeed, two major appearances of this species in the GOA since 1999, one in the early 2000s and another from 2015 onward (fig. 4*A*), overlap with periods of relatively warm nearshore temperature related to ENSO (see "Results") and coincident high-pressure anomalies (Bond et al. 2015). However, we did not detect a significant association between nearshore temperature and capture probability of *D. opalescens* in the GOA (fig. 4*D*; table S4, pt. B). The overall model fit was underdispersed (dispersion parameter = 0.50), which could have masked truly significant relationships. Our analysis used temperature trends in winter and spring based on monthly averages (see "Methods" and supplemental PDF, supporting methods 1.2), which ranged from 8.24°C to 10.3°C over the past 20 years (average = 9.15°C). This overlaps with the lower end of thermal conditions that led to the highest hatching success of *D. opalescens* in lab experiments (9°C–14°C; Zeidberg et al. 2011), which are the same conditions under which the majority of eggs are laid in the CCS (10°C–14°C; Zeidberg et al. 2012). However, it should be noted that our analysis masked higher-frequency temperature fluctuations, which could temporarily drop below 8°C in winter and spring during years when *D. opalescens* was present in the GOA. Daily or weekly fluctuations in temperature are important for ectotherm physiology; for example, when the California mussel (*Mytilus californianus*) is exposed to a 2-h heat-stress bout, it gains improved heat tolerance for up to 3 weeks, encompassing the typical frequency of heat-stress events in the wild (Moyen et al. 2020). The relevance of similarly high-frequency variability in temperature for squid is not clear given our current understanding of squid physiology.

Ecological release during range expansions and invasions is often associated with the occupation of harsher abiotic conditions compared with those typically inhabited in species' home ranges (Keane and Crawley 2002; Gilman et al. 2010). This is due to a reduction in biotic pressures, allowing for a greater proportion of the fundamental niche to be occupied (Bruno et al. 2003). Potential evidence of recruitment (in the form of egg laying and juvenile presence) during the most recent poleward range expansion event (fig. 1*C*–1*F*) and in past events (Wing and Mercer 1990) indicates that temperature may not have overly restricted egg development. Local spawning during poleward migration would have enhanced the pace and extent of the poleward movement of *D. opalescens*.

Our analyses indicate that the poleward range expansion of *D. opalescens* was preceded by competitive release in the CCS. At a fundamental level, species' abundances and distributions are controlled by factors that influence energy supply and demand. Competition can thereby drive population fluctuations by altering the availability of shared energy resources—impacting both resource abundance and the effort required to access the resource (Liow et al. 2011). This may be particularly relevant for active squid, as they compete with ecologically similar fish for shared prey (Packard 1972) but have aerobic constraints related to physiology and metabolism (O'Dor and Webber 1986; Pörtner 2002; Seibel 2016). We found that variability in the abundance of ecologically similar fish competitors, anchovy and sardine (Whitehead et al. 1988; Jereb and Roper 2010), was associated with *D. opalescens* abundance in the CCS (fig. 4*E*; table S4, pt. D): declines in anchovy and sardine were followed by surges in squid abundance 2 years later. Relative to the average value, catch of *D. opalescens* increased by 202% from the maximum to the minimum time-lagged fish value. In 2014 *D. opalescens* abundance had recovered from its lowest levels during higher abundance of anchovy and sardine in the mid-2000s to reach levels greater than those recorded in the previous 20 years (fig. 4*B*). This was also observed in the northern extent of the CCS (Morgan et al. 2019). Competitive release via the crash of ecologically similar fish populations (Lindegren et al. 2013; MacCall et al. 2016) may therefore have allowed large squid populations to develop via improved access to prey (Caddy and Rodhouse 1998; Doubleday et al. 2016). While we do not know the precise influence of anchovy and sardine versus other ecologically similar fishes that are undoubtedly in competition with *D. opalescens* for prey, anchovy and sardine are particularly relevant competitors to consider because their populations have experienced substantial recent and historical declines. The causes of their collapse have been suggested to be a combination of climate-related shifts in ocean conditions, past harvesting pressure, and recent predator recovery (Lindegren et al. 2013; MacCall et al. 2016).

In the struggle for control over energy resources, temperature and oxygen supply have compounding effects on squid and other marine ectotherms: the solubility of oxygen in seawater decreases with increasing temperature (Somero et al. 2015), while oxygen demand increases (Deutsch et al. 2015). Oxygen diffusivity, which increases with temperature, can offset this effect but only partially (Verberk et al. 2011). Hypoxia vulnerability in *D. opalescens*, as measured by critical oxygen partial pressure (P_{crit}), had only a weak positive association with temperature across an ecologically relevant range (7.5°C–19°C). The temperature sensitivity coefficient was 0.1, which falls on the lower end of the range recorded for diverse species (-0.2 to 1.3; Deutsch et al. 2020), with other studied squid having higher values than *D. opalescens* (longfin inshore squid, *Doryteuthis pealeii* $= 0.31$ [Deutsch et al. 2020]; Humboldt squid, *Dosidicus gigas* $= 0.62$ [Trueblood and Seibel 2013]). In fact, aerobic habitat potential for *D. opalescens*, as estimated using the metabolic index (ϕ; Deutsch et al. 2015), changes more strongly with dissolved oxygen than seawater temperature within the ecologically relevant temperature range (fig. S1*D*). Because dissolved oxygen (and seawater temperature) can be spatially heterogeneous in the CCS (supplemental PDF, supporting methods 1.4; Checkley and Barth 2009), using measurements recorded in a single location could have impacted our estimation of how ϕ changed over time.

Our data support the notion that *D. opalescens*, like many species, has evolved to maximize its aerobic activity in alignment with the highest persistently available oxygen supplies in its typical habitat (Seibel and Deutsch 2020). At an intermediate temperature (14°C), we found that FAS for *D. opalescens* (FAS $= 4.04$) was similar to hypoxia vulnerability ($P_{\mathrm{crit}} = 4.84$ kPa), validating our P_{crit} measurements. Compared with the FAS of other studied squid (longfin inshore squid $= 5.85$; Humboldt squid $= 4.38$; Trueblood and Seibel 2013; Deutsch et al. 2020), that of *D. opalescens* was slightly lower. Because ϕ is equivalent to FAS (Seibel and Deutsch 2020), the product of FAS and P_{crit} at the intermediate temperature suggests that 19.5 kPa is the oxygen partial pressure required for maximum aerobic activity in this species (see eq. [1] in Seibel and Deutsch 2020), which is close to air saturation under normal conditions (21 kPa). This is slightly higher than a previous estimate for *D. opalescens* at 15°C (18.5 kPa; Seibel and Deutsch 2020) derived from literature values (O'Dor 1982; Burford et al. 2019).

Large population size can reduce resource availability via elevated intraspecific competition and contribute to decisions to migrate (e.g., Branch 1975), particularly if environmental conditions shift to further reduce resource availability (Liow et al. 2011). Our results indicate that this may have been involved in poleward range expansions of *D. opalescens*. We found that periods of reduction in aerobic habitat potential related to climate variability (see "Results") were followed by declines in squid abundance in the CCS (fig. 4*F*; table S4, pt. D)—suggesting emigration or death and associated reductions in local recruitment. Relative to the average value, *D. opalescens* catch decreased by 178% from the maximum to the minimum time-lagged ϕ. On average, ϕ was 3.51 in the typical habitat of *D. opalescens* in the CCS (fig. 4*B*; i.e., aerobic activity allowed by this habitat is typically 3.5 times greater than routine activity levels). But in January to May 2015, following the peak in squid abundance, ϕ fell to 3.17 (fig. 4*B*), which was lower than all but one winter/spring period in the past 15 years (table S5, pt. B). A ϕ of about 3 is typically associated with the warm limit of a species' range (Deutsch et al. 2015), and this may have forced some portion of the already-large *D. opalescens* population in the CCS to migrate poleward in search of more suitable, less crowded habitat. The associated reduction in recruitment effort or success may have contributed to the sharp decline in *D. opalescens* abundance observed in the core range from 2015 to 2016 (fig. 4*B*). A similar pattern of environmental factors—competitive release, *D. opalescens* population surge, and sustained reduction in ϕ (fig. 4*B*)—may have contributed to similar poleward range expansion of this species into the GOA in the early 2000s (fig. 4*A*). However, we lack the oxygen data to determine ϕ for *D. opalescens* in the core range leading up to this event.

These results support recent hypotheses—relatively small reductions to environmental oxygen supplies, at levels well above hypoxic thresholds (Vaquer-Sunyer and Duarte 2008; Gilly et al. 2013), could elevate the cost of important behaviors, reducing competitive ability and driving species' movements (Deutsch et al. 2015). Our results additionally suggest that ecological release, which can amplify the extent of range expansions once they are underway (Keane and Crawley 2002), may also set the stage for these events to occur under environmental variability in species with boom-bust dynamics, such as *D. opalescens* (Perretti 2014).

A relatively large body of research has focused on periodic poleward invasions of Humboldt squid into the CCS and GOA. Although *D. gigas* differs from *D. opalescens* in some life history, physiological, and behavioral aspects, by integrating this research with our results we can develop a better understanding of why and how squid undertake rapid, drastic movements. Our results suggest that two sequential factors in species' core ranges are likely to drive the initial movement into a new ecosystem: (1) enhanced availability of energetic resources allowing for the buildup of large populations and (2) a subsequent environmental disturbance reducing the availability of energetic resources, forcing some portion of the large population to move. This aligns with the circumstances at lower latitudes before the poleward intrusions of *D. gigas*. Large populations of large-bodied *D. gigas* developed by exploiting seasonal productivity cycles fueled by wind-driven upwelling (Markaida et al. 2005; Robinson et al. 2016; Frawley et al. 2019). Climate variability then interrupted seasonal productivity cycles while increasing temperature (Robinson et al. 2016; Frawley et al. 2019), simultaneously decreasing energy availability and increasing metabolic demand (Rosa and Seibel 2010). Such perturbations were generally followed by declines in body size and fishery landings (but not necessarily biomass) at lower latitudes (Hoving et al. 2013; Frawley et al. 2019) and the appearance of large *D. gigas* in the CCS (Pearcy 2002; Zeidberg and Robison 2007) and GOA (Cosgrove 2005; Wing 2006).

Results from studies exploring the behavior of *D. gigas* suggest two factors that are likely to drive movements once squid are in the new ecosystem: (1) prey availability and (2) suitable spawning habitat availability (Field et al. 2013; Stewart et al. 2013*a*, 2013*b*, 2014). These factors might explain the progression of *D. opalescens* through the GOA during the most recent poleward range expansion event (fig. 3*A*, 3*B*) and why this species has (probably) not yet become permanently established in the GOA. Ontogenetic onshore-offshore and seasonal alongshore migrations of *D. opalescens* known from the CCS (Zeidberg 2013) could be undertaken in the GOA to exploit seasonal onshore-offshore patterns in productivity and consistent geographic alongshore productivity gradients (Brickley and Thomas 2004). Interannual variability in temperature might eventually restrict or negate spawning efforts via cold temperatures and ultimately end temporary intrusions of *D. opalescens* in the GOA (Brickley and Thomas 2004; Stabeno et al. 2004). In a warmer future, however, squid could be released from such limitations.

Our investigation examines a species that, like many other ecologically and economically important squid, is not commonly monitored by scientific survey efforts (Zeidberg 2013; Rodhouse et al. 2014; Arkhipkin et al. 2020). Thus, inferences of abundance and distribution must be made according to data sources that may not completely capture relevant trends (supplemental PDF, supporting methods 1.1 and 1.2). It should also be noted that there are potentially important predictors that we did not consider in our models. Those include bottom-up factors, such as prey availability, and top-down factors, such as fishing pressure. The former tends to be a more common predictor of squid abundance than the latter because commercially harvested squid have rapid population turnover and are therefore thought to be more buffered from top-down pressures compared with their longer-lived vertebrate counterparts (Rodhouse et al. 2014). The goal of this study was to focus on competition and environmental factors influencing competitive ability, as these are known to interact with energy supply and demand to influence population fluctuations and migratory decisions in other taxa (Liow et al. 2011) but are largely unapplied to squid (Rodhouse et al. 2014).

Demographic Effects of Environmental Conditions

Although there are notable exceptions in the deep sea (Hoving et al. 2015; Hoving and Robison 2017; Schwarz et al. 2018), most squid, including *D. opalescens*, are *r*-strategists, with short life spans and semelparity (Jackson 2004; Jereb and Roper 2010). Yet many of such species have remarkable plasticity in life history characteristics at maturity, variation which can be attributable to environmental conditions. Cooler, more productive conditions allow for squid to obtain larger body sizes and longer life spans relative to warmer, less productive conditions (Jackson and Domeier 2003; Hoving et al. 2013; Frawley et al. 2019). For instance, Hoving et al. (2013) reported a 288% flexibility in body size and a 159% flexibility in age at maturity (both with respect to the minimum value) in *D. gigas* specimens collected over a 9-year period in the eastern Pacific Ocean. The largest mature *D. gigas* were collected in the massively productive Humboldt Current System off South America, whereas the smallest mature *D. gigas* were sampled following a warm period in the Gulf of California, Mexico, a semienclosed sea (Hoving et al. 2013). Subsequently, even smaller *D. gigas* have been recorded in the latter region (Hoving et al. 2019). We found 169% flexibility in body size and a 134% flexibility in age at maturity (both with respect to the minimum value) in *D. opalescens* collected over a 4-year period in the northeast Pacific, which we suspect was primarily attributable to differences in the environmental conditions experienced by squid involved in poleward movement versus lower-latitude residence. Squid that reached the GOA in 2016 grew 36% older and 12% larger relative to those that remained in the CCS (fig. 5*A*), suggesting that they were able to exploit cooler, more productive conditions during the initial phase of poleward range expansion.

In polygynous species, such as *D. opalescens*, males and females exhibit different strategies of growth in relation to reproduction, often resulting in sexual size dimorphism where males mature at larger sizes than females. In polygynous and polygynandrous mammals, males and females can exhibit divergent responses to environmental variation (Post et al. 1999; Sugianto et al. 2019); for example, in the red deer (*Cervus elaphus*) warming winters were associated with increased body size in males and decreased body size in females, amplifying sexual size dimorphism (Post et al. 1999). We found no difference in size at maturity between male and female squid in the GOA (fig. 5*C*). Yet during the same time period, typical sexual size dimorphism was apparent in squid that resided at lower latitudes in the CCS, with males growing 4% larger at maturity than females on average (fig. 5*B*, 5*C*). Polygyny and sexual size dimorphism is prevalent in squid—a notable exception being the diamondback squid (*Thysanoteuthis rhombus*), which exhibits monogamy (Jereb and Roper 2010). In the case of *D. opalescens* in the GOA, environmental variability ultimately facilitated residence in an ecosystem with cooler conditions than the typical range (Stabeno et al. 2004; Checkley and Barth 2009). It is not known whether temperature differentially affects the development of male and female squid.

Post et al. (1999) additionally found that early vegetation emergence reduced body size differences between male and female red deer following warm winters because this allowed females to invest more in body condition (and thus grow larger and live longer), whereas males did not make such investments. Within typical ranges, migratory squid that inhabit large, dynamic current systems typically time spawning so that their offspring hatch in alignment with productivity peaks (O'Dor 1992), which can be accomplished by spreading population units to maximize recruitment chance (O'Dor and Coelho 1993). In the GOA, *D. opalescens* that were older at maturity hatched in spring and summer, while squid that matured at younger ages hatched in fall and winter (fig. S4; table S7, pt. D). Primary productivity in the GOA is lowest in winter, and in nearshore waters it is highest in spring and summer, while it peaks in offshore waters in fall (Brickley and Thomas 2004). Access to higher levels of productivity in early ontogeny could therefore have caused female *D. opalescens* in the GOA to delay maturation and reproduction and instead invest more in body condition and growth relative to males.

Body size in *D. opalescens* is positively associated with female fecundity (Macewicz et al. 2004) and presumably male reproductive success, as this species has a lek-like mating system involving male-male competition for access to females (Zeidberg 2013). As a coarse comparison, the potential fecundity difference between squid of average size in the GOA and CCS in 2016, which differed in age at maturity by 40 days, was estimated as 596 oocytes (using eq. [15] in Macewicz et al. 2004). However, any fecundity benefits associated with increased body size in the GOA were potentially moderated by growth rates, which we did not assess. Experimental research shows that the early life history growth rates of squid that are closely related to *D. opalescens* increase with temperature (Villanueva 2000) and decrease in response to periods of low salinity, while the effect of photoperiod is comparably negligible (Villanueva et al. 2007). In the GOA, the lowest seawater temperature and freshwater runoff occurs in winter and spring and the highest occurs in summer and fall (Stabeno et al. 2004). Larger sizes at maturity were obtained by *D. opalescens* that hatched in spring and summer, while those that hatched in fall and winter grew to smaller sizes (fig. 5*D*; table S7, pt. C). In addition to warmer temperatures, *D. opalescens* that were born in spring and summer presumably had greater access to energetic resources (i.e., higher productivity nearshore; Brickley and Thomas 2004) than those born in fall and winter (despite any putative effects of freshwater runoff)—this may have been critical in allowing them to obtain relatively large size and long life span for this species.

Variation in the life history characteristics of *D. opalescens* may also have been related to sustained climate shifts encompassing the study period. The body size of mature squid from 2016 to 2019 in the CCS steadily decreased at 6% year^{-1} relative to the average CCS size (fig. 5*B*; table S7, pt. A). Although we lack a similarly long time series of mature *D. opalescens* body size measurements in the GOA, from 2016 to 2017 age at maturity declined by 17% relative to the average GOA age, while size at maturity declined by 12% relative to the average GOA size (fig. 5*A*). Concomitant size declines over 25° of latitude could reflect broader environmental shifts affecting the entire northeast Pacific Ocean. Frawley et al. (2019) implicated the recent sustained decline in size at maturity of *D. gigas* in the Gulf of California with a 2010 phase shift in decadal oceanic expressions (Pacific Decadal Oscillation and ENSO) that ultimately prolonged warming and limited productivity in that region following El Niño.

Environmental forcing over longer timescales, such as multidecadal cycles (Chavez et al. 2003), may also be relevant. Sustained size declines of *D. opalescens* from 1948 to 2006 have been reported in specimens captured by the commercial fishery in Monterey Bay (Brady 2008). More than a half century ago, male and female *D. opalescens* in the CCS grew 12% and 15% larger than they are today (fig. 5*E*; Fields 1965). In fact, squid that we sampled in 2016–2019 exhibited some of the smallest sizes and youngest ages at maturity recorded for this species. Because there were discrepancies in collection methods, caution must be used when interpreting such size differences (Elahi et al. 2020). While we acknowledge these constraints, our data additionally show that the body sizes of mature *D. opalescens* in the GOA in 2016–2017 were comparable to those recorded more than a half century ago in the CCS (fig. 5*E*; Fields 1965). In addition, mature squid in the GOA achieved older maximum ages than have been recorded in the CCS for over two decades (Jackson 1994; Butler et al. 1999; Jackson and Domeier 2003). This suggests that despite long-term trends (Brady 2008), *D. opalescens* retained the ability to obtain historical sizes, which was putatively unlocked by poleward migration.

Ecological Impacts Enabled by Larger Body Size

Environmentally altered life history characteristics can affect the outcome of ecological interactions or even lead to new interactions (Vasseur and McCann 2005). Thus, in the case of the poleward range expansion of *D. opalescens*, new ecological interactions were facilitated not only by expansion into new habitat but also by the attainment of larger adult body sizes. In the GOA, we found substantial overlap between the isotopic niche space of *D. opalescens* and juvenile sablefish (fig. 6*B*), which indicates the potential for competition between these species. This aligns with the distribution and opportunistic foraging strategy of both species: juvenile sablefish live in nearshore habitats (Armstrong 1996), where adult *D. opalescens* are primarily observed in the GOA, and both species are voracious predators that feed on a range of invertebrates (Karpov and Cailliet 1978; Coutré et al. 2015; Callahan et al. 2021). In addition, fish can dominate the diet of juvenile sablefish depending on their availability (Coutré et al. 2015; Callahan et al. 2021); although *D. opalescens* primarily feeds on krill and copepods in the CCS, fish become more important prey items as squid get larger (Fields 1965; Karpov and Cailliet 1978). Thus, the appearance of relatively large *D. opalescens* in the GOA could have reduced the accessibility of invertebrate and fish prey for juvenile sablefish.

Juvenile sablefish are highly migratory and at 4–5 years of age recruit to deeper waters, where they are pursued by a commercial fishery (Hanselman et al. 2018). Any putative effects of increased competition from lower-latitude emigrants would be reflected by variability in juvenile abundance and distribution and future commercial landings—which are highly dependent on the maturation of juveniles (Hanselman et al. 2018). In 2015, when *D. opalescens* was detected in the southeastern GOA during the initial stages of the most recent poleward range expansion event, reports showed a spike in juvenile sablefish abundance in the western GOA. As *D. opalescens* spread northwest across the GOA through 2017, few reports of juvenile sablefish exist, and dietary analyses showed relatively low stomach contents (Callahan et al. 2021). Larger numbers of juvenile sablefish have returned to sites in the southeastern GOA in fall of 2018, but the body condition of maturing sablefish in recent years was lower than average (Hanselman et al. 2018). At a smaller spatial scale, a similar pattern was observed during the poleward range expansion of *D. opalescens*: the nearshore bays in the Sitka Sound region, which normally support uncharacteristically large populations of juvenile sablefish, were instead devoid of this species and occupied by *D. opalescens*.

In addition to potential competition, predation by invading *D. opalescens* may have affected important species in the GOA. Like invasions of *D. gigas* in the CCS (Field et al. 2013), *D. opalescens* appeared to have a generalist foraging strategy throughout poleward range expansion (fig. 6*C*). In January and February of 2016, when *D. opalescens* in the GOA matured at the largest sizes (fig. 5*A*), our analysis estimated juvenile salmon as its primary prey item (see "Results"). However, this was before the release of that year's juvenile hatchery salmon and the typical out-migration of most juvenile wild salmon (Weitkamp and Sturdevant 2008; Quinn 2018; NSRAA 2020). While this could have resulted from predation on juvenile salmon from the previous year or early out-migrants, it is also possible that squid were feeding on other forage fishes not in our data set, such as Pacific sand lance (*Ammodytes hexapterus*) or juvenile walleye pollock (*Gadus chalcogrammus*). However, squid were observed aggregating near salmon hatchery release sites and actively feeding on juvenile salmon at night in Sitka Sound in the spring of 2016 and 2017 (A. Bowers, personal communication). Squid activity in the GOA aligns with some of the lowest marine survival (<1%) and subsequent return of spawning adults recorded for some salmon stocks in southeast Alaska in the past several decades (ADFG 2019). Numerous abiotic and biotic factors potentially affected salmon marine survival during this period, including marine heat waves (e.g., "the blob;" Bond et al. 2015; Cavole et al. 2016) and predation by other species, such as juvenile sablefish (Sturdevant et al. 2009; Coutré et al. 2015) and humpback whale (*Megaptera novaeangliae*; Chenoweth and Criddle 2019; Kosma et al. 2019). The emergence of a new predator may have interacted with existing stressors to further reduce marine survival of salmon, similar to predation of Pacific hake (*Merluccius productus*) by *D. gigas* during this squid's range expansions into the CCS (Zeidberg and

Robison 2007; Field et al. 2013). Subsequently, in 2017 and 2018, when squid obtained smaller sizes at maturity in the GOA, krill instead appeared to be the dominant prey item, although some of the difference could potentially be attributable to trophic baseline shifting across years, which we were not able to rule out (Wild et al. 2020). This shift in prey during poleward range expansion suggests that environmentally altered life history characteristics, specifically those that allowed squid to obtain larger sizes at maturity, facilitated harmful ecological interactions between *D. opalescens* and important GOA species (Vasseur and McCann 2005).

In the CCS, *D. opalescens* is a valuable prey item for numerous species (Morejohn et al. 1978). Presumably, if upper-trophic-level species in the GOA took advantage of this new resource, then depending on its energetic value, putative effects of *D. opalescens* competition and predation on ecosystem function could potentially be offset. Isotopic mixing models indicated that adult Chinook and coho salmon may have consumed *D. opalescens*, although the proportional contribution to coho salmon diet was quite low (fig. 6*D*, 6*E*). As with the isotopic modeling for *D. opalescens*, gathering prey data for adult salmon balanced collection feasibility with ecological relevance (supplemental PDF, supporting methods 1.9), and our results should therefore be interpreted within these constraints. Salmon diets in the GOA show considerable variability in time and space, and although we were not able to assess all potentially important prey items, the species we included in addition to *D. opalescens* were all present and known prey of both salmon species (Reid 1961; Landingham and Sturdevant 1998; Weitkamp and Sturdevant 2008). Mixing model estimates of salmon predation on *D. opalescens* in the GOA are supported by observations of *D. opalescens* in the stomach contents of Chinook and coho salmon in Sitka Sound and Yakutat, Alaska, respectively, in 2017 (fig. 1*E*, 1*F*). Both salmon species fed on *D. opalescens* when it was present in the GOA from 1980 to 1984 (Wing and Mercer 1990) and are known to feed on *D. opalescens* in the CCS (Brodeur et al. 2014).

Upper-trophic-level species in the GOA that were most likely to eat *D. opalescens* given its availability, such as Chinook salmon, were those that normally pursue forage fish. We found that squid in the GOA had comparable or greater energy density than common GOA forage fish (fig. 7*A*; table S6, pt. C). However, the energy density of *D. opalescens* is primarily derived from protein, whereas the forage fish have much higher lipid content (fig. 7*B*). Protein metabolism is energetically expensive compared with lipid metabolism (Schmidt-Nielsen 1997)—consuming *D. opalescens* instead of common forage fish may have therefore allowed upper-trophic-level species to gather comparable energy supply, but in doing so they likely encountered more difficulty with energy storage. However, realistic quantification of the energetic value of prey should include the energy required to access the prey. For instance, coho salmon, which exhibit relatively high marine survival compared with Chinook salmon, commonly feed on small crustacean prey (fig. 6*E*; Weitkamp and Sturdevant 2008), which are less energy dense than forage fish but are presumably more readily gathered (Weitkamp and Sturdevant 2008). It is unknown how the energy cost of capturing *D. opalescens*, or any social squid for that matter, compares with that required to capture ecologically similar forage fish.

Conclusions

Throughout the world's oceans, squid and other marine ectotherms are poised to undertake rapid movements in response to increasing environmental variability (Thornton et al. 2014), thereby transporting biomass between ocean systems (Arkhipkin 2013). We suggest that these events are likely to occur given the development of large populations followed by a disturbance that affects interspecific or intraspecific competitive ability. In the case of poleward range expansion of *Doryteuthis opalescens*, competitive release may have allowed for large populations to develop at lower latitudes, where subsequent temporary reduction in aerobic habitat potential associated with climate variability likely drove some portion of the population to move poleward. Recent research has related biogeography to long-term metabolic suitability, and our work shows the potential importance of relatively small, short-term variability in determining the movement behavior of physiologically sensitive marine ectotherms. To help contextualize rapid range expansions, we advocate that forecasting efforts consider factors that impact resource accessibility in core ranges, such as competition and environmental conditions that constrain aerobic activity.

Because the invaded ecosystem was generally cooler and more productive than the core range, poleward range expansion unlocked large body sizes that have been relatively absent from lower-latitude *D. opalescens* populations for more than a half century. Large body size likely facilitated new, potentially harmful ecological interactions between *D. opalescens* and important species at higher latitudes and alterations to regional carbon flow. Competition with juvenile sablefish for shared prey and predation on juvenile salmon may have impacts on adult populations and thus socioeconomic consequences. These fish are the basis of fisheries, professions, products, and services collectively worth billions of US dollars annually and are integral to the subsistence and traditions of marginalized native cultures (SeaBank 2018).

More broadly, our results show how the demographic and ecological consequences of marine ectotherm range expansions are coupled. Understanding how body size is associated with relevant environmental gradients, such as temperature (Verberk et al. 2020) and trophic interactions (Keppeler et al. 2020), will therefore improve the resolution of the ecological impacts of future marine community reorganization. Such information will help forecast how invaders behave and interact in receiving ecosystems (Ricciardi et al. 2020), which will help resolve complexities in theoretical generalizations of ecosystem function, such as allometric trophic networks (Martinez 2020), resulting from dispersal and migration. Because of the importance of ecological, physiological, and behavioral variation, relationships determined at the level of taxon or functional group will probably be more informative for specific ecosystems than generalized relationships.

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Statement of Authorship

B.P.B., L.A.W., and R.S. designed research; B.P.B., H.-J.T.H., J.M.S., and M.W.D. acquired funding; B.P.B., L.A.W., R.S., and N.C. developed methods and experimental design; B.P.B., L.A.W., R.S., E.M.C., and A.S. collected data; B.P.B. and L.A.W. analyzed data; B.P.B. validated and visualized data; B.P.B., L.A.W., R.S., E.M.C., N.C., H.-J.T.H., J.M.S., and M.W.D. provided resources; R.E., H.-J.T.H., J.M.S., and M.W.D. provided supervision; B.P.B. wrote the original draft of the manuscript; and B.P.B., L.A.W., R.S., E.M.C., R.E., N.C., H.-J.T.H., and M.W.D. edited the manuscript.

Data and Code Availability

The data generated in this study have been deposited in the Digital Dryad Repository (https://doi.org/10.5061/dryad.ksn02v75h; Burford 2021). Data gathered from published work or online data sets have been collated for reader convenience but are also available from the corresponding references. The R code necessary to reproduce results using the data provided is available on GitHub (https://github.com/benjaminpburford/alaska-squid) and Zenodo (https://doi.org/10.5281/zenodo.5722595).

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California market squid, *Doryteuthis opalescens*. Photo credit: B. Burford.