

Pelagic calcifiers face increased mortality and habitat loss with warming and ocean acidification

Nina Bednaršek^{a*}, Brendan R. Carter^{b,c}, Ryan M. McCabe^c, Richard A. Feely^b, Evan Howard^d, Francisco P. Chavez^e, Meredith Elliott^f, Jennifer L. Fisher^g, Jaime Jahncke^e, Zach Siegrist^h

^a Southern California Coastal Water Research Project, Costa Mesa, CA, 92626 USA; ninab@sccwrp.org

^b NOAA Pacific Marine Environmental Laboratory, 7600 Sand Point Way NE, Seattle, WA, 98115 USA; brendan.carter@noaa.gov; richard.a.feely@noaa.gov

^c Cooperative Institute for the Study of the Atmosphere and Ocean, University of Washington, Seattle, WA, 98195 USA; rmccabe.ocean@gmail.com

^d School of Oceanography, University of Washington, Seattle, WA 98195 USA; ehoward2@uw.edu

^e Monterey Bay Aquarium Research Institute, 7700 Sandholdt Road, Moss Landing, CA, 95039 USA; chfr@mbari.org

^f Point Blue Conservation Science, 3820 Cypress Drive #11, Petaluma, CA, 94954 USA; melliott@pointblue.org; jjahncke@pointblue.org

^g Cooperative Institute for Marine Resources Studies, Oregon State University, 2030 SE Marine Science Drive, Newport, OR, 97365 USA; jennifer.fisher@noaa.gov

^h System Science Applications, Inc., Renton, WA, 98058 USA; zcsiegrist@gmail.com

*Correspondence Information: Nina Bednaršek; 714-755 3237; fax: 714-755 3299; ninab@sccwrp.org

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Abstract:

Global change is impacting the oceans in an unprecedented way with resulting changes in species distributions or species loss. There is increasing evidence that multiple environmental stressors act together to constrain species habitat more than expected from single stressor. Here, we conducted a comprehensive study of the combined impact of ocean warming and acidification (OWA) on a global distribution of pteropods, ecologically important pelagic calcifiers and an indicator species for ocean change. We co-validated three different approaches to evaluate the impact of OWA on pteropod survival and distribution. First, we used co-located physical, chemical, and biological data from oceanographic cruises and regional time-series; second, we conducted multifactorial experimental incubations using OWA to evaluate survival; and third, we validated pteropod distributions using global carbonate chemistry and observation datasets. Habitat suitability indices and global distributions suggest that a multi-stressor framework is essential for understanding distributions of this pelagic calcifier.

1. Introduction

Human CO₂ emissions have caused significant physical and biogeochemical alterations in the global oceans (Gattuso et al., 2015; Le Quéré et al., 2018; Friedlingstein et al., 2019), causing ocean warming, acidification and deoxygenation (Feely et al. 2004; Doney et al., 2020). These changes are not occurring independently but are interactive and simultaneous (Howard et al., 2020). Multiple lines of evidence suggest that global anthropogenic change from will drive long-term negative ecological consequences for marine organisms (Feely et al., 2008, 2016, 2018; Gruber et al., 2012; Turi et al., 2016; Chan et al., 2017).

Temperature and carbonate saturation state are two major drivers that shape physiological limits of marine calcifiers and define their vulnerability to ongoing ocean warming and acidification (OWA), with a growing body of evidence demonstrating that these changes are already underway (Bednaršek et al., 2020; Fox et al., 2020; Osborne et al., 2020). Yet, mechanism-based risk assessments that integrate multiple lines of sensitivity and specific habitat requirements are limited. Such studies are important not only to delineate potential habitat loss of pelagic calcifiers but also to quantify the risks of various representative carbon emission pathways (RCPs) and to contextualize potential conservation strategies. RCP8.5 assumes “no greenhouse gas mitigation”, and RCP2.6 reflects “strong mitigation”. The latter scenario limits the increase in global mean surface temperature to below 2°C (relative to the reference period 1850–1900) and is

therefore suitable for providing a first estimate for the consequences of keeping global warming to “well below 2°C, if not 1.5°C,” as stated in the Paris Agreement (Oppenheimer et al., 2015).

Among the calcifiers, pelagic gastropod communities, including pteropods, have been identified as particularly sensitive to global changes. Pteropods are globally distributed, with important ecological and biogeochemical roles in the regional ecosystems, like the polar as well as temperate habitats of the California Current Ecosystem (CCE; Bednaršek et al., 2014)—and even more important roles in the subpolar and polar regions of the Arctic and the Southern Oceans (Bednaršek et al., 2012; Wang et al., 2017; Gonzalez et al., 2018). These habitats are projected to experience higher rates of OWA than other areas (Hoegh-Guldberg, IPCC 2014; Siedlecki et al., 2020). Many experimental studies ascribe negative effects on pteropods to OWA (Lischka et al., 2011; Lischka & Riebesell, 2012; Bednaršek et al., 2017, 2018; Gardner et al., 2018; Johnson & Hofmann, 2020). Among pteropods, *Limacina helicina* is the most dominant and ecologically important species with a widespread geographic distribution (Bednaršek et al., 2017). Studies have shown that *L. helicina* is negatively impacted by ocean acidification, while the interactive stressors (OWA) can shape their cellular and physiological responses (Lischka et al., 2011; Bednaršek et al., 2017, 2018; Johnson & Hofmann, 2020). However, currently there are no regional or global scale indices of environmental suitability available for pteropods that use multiple stressors to project biological responses.

A niche refers to the range of suitable conditions and habitats supporting a species, such as temperature (T) and carbonate saturation state (Ω), that shape organismal physiological tolerances. Of these, temperature is considered the dominant factor influencing the physiology and distribution of ectothermic organisms like *L. helicina* (Wethey et al., 2011; Robinson et al., 2017). Carbonate system chemistry can independently induce physiological stress through increased energy requirements to maintain homeostatic strategies, with uncompensated costs leading to the changes in the species' fitness, survival and population distribution. While mechanisms driving biological response related to a single stressor have been well developed (McLaren, 1963; Smith & Teal, 1973), the combined effect of OWA has rarely been investigated, especially at the population level. Yet, potentially irreversible biological responses underscore the need for a better understanding of how multi-stressor change influences marine calcifiers.

Habitat Suitability Indices (HSIs) are emerging tools to predict the likelihood of species occurrences related to seawater properties (Teal & Carey, 1967). So far, few HSIs have been developed specifically for climate change-related stressors, despite a clearly identified need to better characterize the impacts of ocean changes. This is in part because developing and testing HSIs requires synoptic information about species distributions, their physiological traits, and physical-chemical habitat characterization, measurements that are seldom recorded together, thus limiting assessments of population impacts due to multiple stressors.

In this study, we compared concurrent field *L. helicina* observations and *in situ* physicochemical water properties to examine their species distributions. Specifically, we used three synoptic field surveys spanning 2011-2016, in combination with regional co-located time-series observations to develop an empirical habitat suitability index (HSI) based on temperature (T) and the saturation state of aragonite (Ω_{ar}). To test whether this empirical population-level HSI is underpinned by and adequately represents pteropod sensitivity to the dual stressors (OWA), we conducted shipboard multifactorial experimental studies exploring the effects of OWA on *L. helicina*. Finally, we compared globally distributed *L. helicina* observations and climatological hydrography from the World Ocean Atlas (WOA; Garcia et al., 2018) and

the Global Ocean Data Analysis Project for Carbon gridded data product (GLODAP; Lauvset et al., 2016) to evaluate whether the physicochemical sensitivities and HSI generated from our CCE analysis are broadly applicable across the geographic and hydrographic distribution of this species. By combining global and regional observations, experiments and statistical modelling, this study represents the most comprehensive study thus far to explore how multiple drivers (OWA) influence *L. helicina*.

2. Materials and Methods

2.1 Physicochemical and biological sampling

2.1.1 NOAA cruises

During the NOAA West Coast Ocean Acidification (WCOA) cruises in 2007, 2011, 2012, 2013 and 2016, vertical profiles of temperature (T), salinity, macronutrients, oxygen, chlorophyll-a (chl-a), dissolved inorganic carbon (DIC), total alkalinity (TA), and pH were sampled along 17 cross-shelf transects, and $p\text{CO}_2$ and aragonite saturation state (Ω_{ar}) were calculated following the methods described by Feely et al. (2016). Biological sampling was also conducted in 2011, 2013 and 2016. Pteropods were generally collected during nighttime sampling at 48 stations, using 333 μm mesh Bongo nets with 30- to 45-minute oblique tows from 100 m depth to the surface (Figure 1, 2; Bednaršek et al., 2017).

2.1.2 Regional time series

We supplemented the synoptic cruise datasets with three regional time series spanning different periods (Table S3). These time series include *L. helicina* presence or absence observations along with local hydrographic data. In the southern CCE, pteropod presence data for 2014 to 2016 was obtained from the CalCOFI program zooplankton database using vertically towed nets (202 μm mesh PRPOOS) spanned the surface to 210 m, and laterally towed MOCNESS nets for vertically stratified sampling. Central CCE pteropod data between 2011 and 2014 was obtained from the Applied California Current Ecosystem Studies (ACCESS) cruises off San Francisco, CA. Zooplankton was sampled using a 1-m diameter hoop net (333 μm mesh) towed obliquely for 10 minutes from 50 m to the surface. Northern CCE data spanning 2011 to 2016 were obtained from the Newport Hydrographic Line (NH25) off central Oregon, at a station located 40 km offshore over 200 m bathymetric depth. These samples were collected using a vertically towed 0.5 m diameter net (202 μm mesh) between 100 m and the surface. Because the sampling methodologies vary between these time series, we minimized potential biases in abundance between the datasets by restricting our analysis to presence/absence-only data.

Paired hydrographic data were available from the Newport and ACCESS time-series stations, though pH and TA were not sampled and are instead estimated in this work using temperature, salinity, and oxygen concentration dependent regression (Carter et al., 2018; Eqn. 7 with pH adjustments for OA applied). The synthetic Ω_{ar} at the ACCESS and Newport sites was therefore only used for validation statistics presented in the Supplement and does not contribute to training HSI models.

2.1.3 Global databases

Globally distributed *L. helicina* observations were obtained from the Ocean Biodiversity Information System (OBIS; <https://obis.org/taxon/140223>). This database included primarily polar and subpolar presence data (generally not absence)—we used these independent data to test the general applicability of relationships derived from CCE data to the broader species range. The maximum and minimum depths associated with each observation encompassed a large hydrographic range.

Concurrent hydrographic observations were not available for these observations, but in general climatological ocean properties can be useful metrics for assessing the long-term mean environmental sensitivities of species biogeography (e.g., Righetti et al. 2019, Deutsch et al. 2020). Pteropod observations are gridded to standard WOA spatial and depth coordinates for pairing with annual climatological temperatures (WOA version 2018; Garcia et al., 2018). Ω_{ar} for the same coordinates is taken from the GLODAP gridded annual climatology (version 2016; GLODAP gridded field, Lauvset et al., 2016). We use annual climatologies because carbonate system chemical observations are generally too sparse to derive robust seasonal or monthly Ω_{ar} climatologies below the ocean surface.

2.2 Pteropod dual-stressor incubation experiments

To determine the combined effects of thermal stress and low- Ω_{ar} conditions on pteropod survival, we conducted full factorial experiments onboard the WCOA 2016 cruise. Pteropods were examined for mechanical damage, and only intact and actively swimming individuals were placed in a flow-through experimental conditions. Temperature was controlled in the water baths. CO₂ gas was continuously added to the treatments and checked for consistency with pH measurements using Durafet probes calibrated at 11°C with pH-certified Tris buffer. We placed captured pteropods in shipboard flow-through aquaria with pre-acclimatized water to targeted CO₂ levels of 400 (control) and 1200 μ atm (treatment) within \pm 5% at 10°C. This corresponded to Ω_{ar} levels of \sim 0.94-2.2, and two temperature levels of 9–9.5°C and 13.5–14°C (Table S1), representative of the ranges observed in the top 100 m of the water column (Table S1, S2). For validation purposes, TA and DIC were measured at the beginning and the end of the experiments. In addition, discrete pH, oxygen, and temperature were measured daily to confirm the sensors were performing to within expectations.

We maintained pteropods (a total of 480 individuals; Table S2) from 10 different stations for one week to investigate their survival at each treatment level. The organisms were kept in 4L carboys and, were fed one spike of 50 μ L Shellfish Diet 1800, a commercially prepared mix of four marine microalgae (*Isochrysis* sp., *Pavlova* sp., *Thalassiosira weissflogii*, and *Tetraselmis* sp.; $>50,000$ cells mL^{-1}). Pteropod survival was determined under a light microscope, based on the presence of individual heartbeat and movement. To test for differences in survival among treatments, we conducted 2-way mixed model ANOVA analyses. We also note that oxygen was maintained near atmospheric equilibrium (slightly supersaturated) at all times.

2.3 Habitat Suitability Index model development and validation for *L. helicina*

HSIs can be used to identify the environmental conditions in which an organism is typically found. We derived an HSI for the CCE based on WCOA cruise data. Specifically, we used generalized linear modeling, a statistically based empirical modeling approach. In this section we review the construction of the HSI and its validation, showing that an HSI based on T and Ω_{ar} indeed reconstructs *L. helicina* distributions with high skill.

The HSI yields numbers between 0 and 1 with “0” indicating predicted absence and “1” indicating predicted presence. Numbers between 0 and 1 indicate probability of finding *L. helicina* in a net tow using the same tow protocols used on the research cruises.

The HSI model was fit using a “logit” transform of a linear function (LF, ranging from $-\infty$ to ∞) based on seawater properties to estimate the probability of *L. helicina* presence. The LF is the sum of the products of linear regression coefficients (α_i terms) and their associated n measured seawater predictor property values (P terms) plus a constant term α_0 .

$$LF = \alpha_0 + \sum_{i=1}^n P_n \alpha_n \quad (\text{Eqn. 1})$$

HSI is calculated from the LF using the inverse of the logit transformation:

$$HSI = \frac{e^{LF}}{e^{LF} + 1} \quad (\text{Eqn. 2})$$

The α_i regression coefficients in Eqn. 1 are fit using the “stepwiseglm” routine (Matlab v2014b). This routine iteratively adds or removes model parameters based on whether additional terms improve the model fit (X^2 test at 95% confidence). Numerous combinations of predictors and depth surfaces were tested and evaluated based on the skill with which the models reproduced data withheld during training. These trials and the validation metrics are described in greater detail in Supplementary Materials S1. The validation metrics for the model based on the properties of interest (T and Ω_{ar}) equaled or exceeded metrics for all alternative empirical models based on other parameter combinations. After similar testing of depth levels, the property averages over the top 0–100 m were selected and used; this had the best predictive power across models for the WCOA data. This depth range also corresponded to the vertical extent predominantly sampled for *L. helicina* with plankton tows, contains 90% of *L. helicina* observations globally (OBIS 2020), and is the most frequently reported vertical habitat (Lalli and Gilmer, 1978; Bednaršek et al., 2012).

The HSI models were assessed using a model trained only with WCOA observations from 2011 to reconstruct observations from 2013 and 2016, and using a 2016-only model to reconstruct observations from 2011 and 2013. Cruise data from 2013 were not used to train either of the models used for validation because only pteropod presence, and not absence, was recorded. “Skill Improvement” (SI) was our primary model validation metric (Supplementary text S2 and Table S4). SI can be intuitively understood as how much more skillful the model is than a constant probability model, expressed as a percentage of the difference between the skills of a constant model and a “perfect infinite-confidence model”. For reference, the error of a 2011-trained model tested with the 2013/2016 datasets is 35% and the value for the 2016-trained model tested with the 2011/2013 datasets is 44%, whereas the error would be 50% for an evenly distributed signal. The SI is 0% for a constant probability model and 100% for a perfect infinite-confidence model. Lower model errors and higher SI values imply more skillful models.

2.4 Comparison of regional to global *L. helicina* records

We compare global presence observations of *L. helicina* to climatological temperature and Ω_{ar} values in the same locations where the pteropods were observed. Specifically, we binned the presence by 1°C T and 0.2 Ω_{ar} increments. The minimum Ω_{ar} concurrent with pteropod observations at each temperature defines an empirical threshold between pteropod presence and absence over the global range of observations. For

comparison with the HSIs from the CCE, we fit a least-squares regression to these minimum Ω_{ar} between 8°C and 14°C; this is the overlapping temperature range between the predominantly polar OBIS data and the WCOA CCE data (Figure 3). We did not generate an HSI from the global data directly because, unlike the WCOA cruise data, the OBIS database has few absence observations and reflects varied sampling approaches.

3. Results

3.1. Spatial and temporal changes in pteropod distribution in the CCE

Using the coastwide *L. helicina* dataset from 2011, 2013, and 2016 over the CCE, we showed that the spatial and temporal distribution of *L. helicina* is wide-ranging in the spring and summer seasons (Figs. 1, 2). However, *L. helicina* presence was temperature-dependent, with the thermal niche showing a unimodal abundance distribution when related to 100-m averaged temperature. The realized thermal habitat window for this species (averaged over the upper 100 m) spanned approximately 8–13°C, with peak abundances around 10°C (Fig. 3). This temperature distribution occurred consistently over several years regardless of seasonal and interannual variability, suggesting that these ranges are representative of the natural envelope of thermal conditions that defined suitable habitat for *L. helicina* in the CCE. When the temperature in the CCE increased above 15°C, *L. helicina* was largely absent, indicating a relatively stark upper thermal limit. With respect to Ω_{ar} , pteropods occupied conditions in the upper 100 m that are supersaturated with respect to Ω_{ar} ($\Omega_{ar}>1$) and were only occasionally found in $\Omega_{ar}<1$ conditions at colder temperatures.

3.2 Experiments identify multiple stressor impacts on survival

Survival (\pm 1std) under control conditions (low T, high Ω_{ar}) was compared to survival under single (high T/low Ω_{ar} ; low T-/high Ω_{ar}) and interactive (high T/low Ω_{ar}) stressor treatments (Figure 4). Survival was greatest under control conditions ($93\pm9\%$), and significantly declined under exposure to a single stressor to $36\pm25\%$ (high T/ low Ω_{ar} (Fig. S1) and $52\pm26\%$ (low T/ high Ω_{ar} ; Fig. 4a). Complete mortality was observed when the two stressors were combined (high T, low Ω_{ar}). A linear regression model ($R^2 = 0.78$, $p<0.001$ for a null hypothesis of no trend) of all experimental trial replicate data produced Equation (3):

$$\% \text{ mortality} = -19.4 + 11.5 * T - 32.7 * \Omega_{ar} \quad (\text{Eqn. 3})$$

These experiments identified low Ω_{ar} as a secondary driver behind T for *L. helicina* mortality over the observed property ranges. Due to the complete mortality observed in the two-stressor treatments, the possibility that the effects were synergistic rather than additive (Fig. 4b) cannot be ruled out.

3.3 Empirical HSI predicts presence/absence from seawater properties

The linear function for the empirical HSI model fit to the WCOA observations was:

$$LF = 13.49 - 2.475T + 10.10\Omega_{ar} \quad (\text{Eqn. 4})$$

The LF and the resulting HSI were mapped alongside estimated % mortality from T and S (Fig. S1, reflecting patterns visible in Fig. 1).

Coefficients for this and several other HSIs discussed are given in Table S4. We estimated the overall *SI* for our model as 55%, meaning this model gets 55% fewer incorrect predictions than a constant probability model. We estimated this value by averaging the values for the related models obtained from 2016 and 2011 only, and tested with the other years, we did not test models trained from 2013 data due to the lack of species absence data in that year. Synthetic carbonate chemistry data (i.e., estimated from using regional, empirical relationships between Ω_{ar} and T , S , and O_2 , Carter et al., 2017) can be used to estimate HSI at ACCESS and Newport. The HSI has *SI* scores of only 22% and 18% when applied to the ACCESS and Newport Hydrographic time series respectively, though this smaller improvement over a constant probability model is not surprising; estimated carbonate chemistry was necessarily more uncertain in the more dynamic surface and coastal ocean, where environmental variability may decouple the hydrographic variables compared to climatological conditions at depth (Carter et al., 2017). Also, the HSI was fit with data ranging from spring to late summer whereas these time series continued across seasons. For comparison, an HSI formulated with T and S had similar skill for the WCOA data sets but only 0% and 20% *SI* for the ACCESS and Newport time series, respectively.

3.4 Global observations have similar relationships to HSIs from the CCE

Globally and in a long-term average sense, *L. helicina* were predominantly observed where temperature was low and Ω_{ar} concurrently high (Fig. 6). As implied by the experimental and empirical HSIs, the threshold between pteropod presence and absence defined a relationship in which the minimum aragonite saturation ($\Omega_{ar,min}$) associated with observations increases with temperature; *L. helicina* were generally absent below this temperature-dependent threshold. Over the overlapping 8 to 14°C range between the high latitude OBIS data and the CCE data, this relationship was expressed as:

$$\Omega_{ar,min} = 0.23T - 0.72 \quad (\text{Eq. 5})$$

The 95% confidence intervals on the coefficients were 0.07 to 0.40 for the slope ($r^2=0.87$, $p=0.02$ for null hypothesis of 0) and -2.46 to 1.01 for the intercept ($p=0.28$ for null hypothesis of 0). The global database covered a wider range of occupied T and Ω_{ar} environmental conditions than the WCOA observations, leading to the observation that this temperature-dependence may be nonlinear, such that at higher temperatures, $\Omega_{ar,min}$ increased more for each degree of warming. This response was consistent with control by a biological or chemical reaction.

Based on the global OBIS observations, *L. helicina* is widely distributed in the global oceans. These observations suggested that this species is a ‘thermal generalist,’ for which the specific temperature range reflected the hydrographic conditions in different parts of its geographic range. As in the CCE, *L. helicina* was not commonly observed above temperatures of 14°C, though there was very little sampling of subtropical waters represented in the OBIS database. With respect to Ω_{ar} , the global OBIS dataset demonstrated that pteropods mostly occupy the habitats characterized by $\Omega_{ar} > 1$, however there were several observations where they occupied very low- Ω_{ar} habitats, down to approximately $\Omega_{ar} = 0.6$, with this always corresponding to the lowest temperature observations. The consistent slope of the global analyzed datasets meant we could make testable predictions in both space and time.

3.5 Agreement between the empirical and experimental results

We contrasted the empirically-derived T - Ω_{ar} HSI to the % mortality linear fit (% , Table S4) by solving for the combinations of seawater properties at which the two functions suggested 50% probability of presence and 2/3rds probability of mortality, respectively. The choice of 2/3rds probability vs. any other constant probability (e.g., 0%, 50%, or 100%) only affected the intercept of these equations, and 2/3rds was chosen so that the relationships would have a similar average value across the CCE. The HSI based on either the experimental or observational data had comparable validation statistics (Table S3).

Importantly, these functions generated were broadly coherent habitat suitability thresholds in space (Fig. S1) and in property-property space (Fig. 5), and the slopes of all three relationships were remarkably similar: $\partial\Omega_{ar}/\partial T = 0.35$ (experimental CCE), 0.24 (empirical CCE), 0.23 (empirical global). Similarly, the equation of Bednaršek et al. (2018), solved for a constant pteropod abundance, lead to $\partial\Omega_{ar}/\partial T = 0.30$. The comparability of these relationships suggested that population-scale presence and absence was potentially linked to stressor-induced mortality, and that the resulting population scale habitat constraints were consistent across a broad range of environmental conditions.

In summary, high T and low Ω_{ar} values correspond to high mortality and absence for *L. helicina* (bottom right of Fig. 5), whereas high survival and presence were expected in colder and more saturated seawater (upper left of both figures). In the CCE, observations fell near HSI=0.5 at both low and high temperatures because water in the CCE was largely a mixture of cold, low- Ω_{ar} upwelled water (lower left of Fig. 5) and warmer, higher- Ω_{ar} surface and offshore water (upper right of Fig. 5). Because the minimum Ω_{ar} , below which pteropods were rarely observed, varied as a function of temperature, no constant thresholds in temperature or Ω_{ar} alone were sufficient to explain the observations—instead a multi-stressor framework is required. The empirical and experimental HSI metrics successfully captured these patterns of pteropod presence and absence with respect to both variables.

4. Discussion

Global climate change with the predicted shifts in the mean state and frequency and intensity of extremes of temperature and carbonate system parameters may play important roles in species distributions and habitat suitability (Oliver et al., 2018). In this study, we used three complimentary approaches to investigate the sensitivity of pelagic calcifier *Limacina helicina* to OWA. First, experimental incubations suggested that T and Ω_{ar} directly influenced organismal mortality, with low Ω_{ar} being a significant compounding factor for the mortality of *L. helicina* as a function of differences in temperature. Second, regional HSI modeling using cruise data identified the same properties as important factors for this species across multiple years, and suggested that both parameters affected habitat suitability in the CCE. Third, the global, long-term meant spatial alignment of hydrographic conditions and organism distributions were consistent with the regional CCE relationships. Thus, we demonstrated that pteropod biological sensitivities to temperature and Ω_{ar} are interdependent—in the laboratory, regionally, and at global scales.

The sensitivities we found by considering (primarily) spatial variability have a corollary in time. For each 1°C of warming, the minimum Ω_{ar} that *L. helicina* can tolerate is increased by roughly 0.3. This relationship is consistent across the experimental and empirical work presented here. With concurrent OWA, we expect the distribution of this species to contract to a greater degree than implied by its thermal tolerance window

alone. Conversely, climate variability or seasonal changes that result in cooling may allow the pteropods to tolerate lower Ω_{ar} , which can expand habitat options.

Pteropod observations in the global OBIS database appeared to be well bounded by conditions at the bottom of reported depth ranges (Fig. 6), but the maximum depth of *L. helicina* and concurrent hydrographic conditions were not readily obtainable from the WCOA datasets. Thus, it is possible that the predictive power of the HSIs could be improved with a more precise identification of environmental thresholds associated with the pteropods' vertical ranges. Similarly, a better understanding of how the frequency and duration of stressful conditions impact pteropod responses could improve predictability of habitat occupancy.

Our results suggest that a multi-stressor framework is essential for understanding pteropod responses to environmental stressors currently, as well as for future projections due to climate change. However, many studies that investigated long-term pteropod population-level responses have only taken a single driver into account (Howes et al., 2015; Thibodeau et al., 2018), showing no explicit OA effects on the pteropod abundances. As demonstrated from our results, single parameter analysis is not sufficient for explaining population level responses; instead, multiple parameter frameworks have previously been demonstrated to hold greater explanatory power in some instances (e.g. Head and Pepin, 2010; Beare et al., 2013; Beaugrand et al., 2013). While these studies recognized temperature to be a major driver, we also observe that these results can only be generalized for the higher temperatures, which coincided with our observations. We warn that acidification can have simultaneous effects at lower temperature ranges, where the effects may not cause immediate mortality but appear sufficiently large to exclude pteropods from potential habitat. This is particularly concerning given that the high latitude environments where *L. helicina* is most commonly observed also have the lowest and most rapidly degrading carbonate system buffering capacity (Jiang et al. 2019).

For the discussion purposes, we consider two specific climate change scenarios; Representative Concentration Pathway (RCP) 8.5 which assumes “no greenhouse gas mitigation”, and RCP 2.6 which assumes “strong mitigation.” High anthropogenic CO₂ concentrations in RCP8.5 will warm much of the ocean by 2°C or more. Based on the sensitivities in this work, Ω_{ar} would have to increase by 0.5 to 0.7 on average to maintain the present extent of suitable habitat. In that regard, RCP2.6 suggests a higher survival and thus, significantly lower risk for *L. helicina* populations. However, Ω_{ar} is projected to decrease concurrently because of OA. In the absence of strong carbon dioxide removal efforts, even the most stringent mitigation scenarios are likely insufficient to preserve habitat near the present environmental limits inferred from the pteropods' physiological sensitivities. In the CCE specifically, the upper ocean is projected to warm by 1.6-3°C by 2100 under RCP8.5, accompanied by a decrease of -0.37 to -0.75 in Ω_{ar} (Siedlecki et al., 2020). Thus, warming alone is expected to exclude pteropods from most locations sampled during the WCOA cruises that have present temperatures of 9-11°C—this covers much of the CCE. Ω_{ar} decrease also reduce habitat suitability by a similar degree as an additional 1-3°C of warming, which can reduce habitat suitability even at cooler temperatures of 8-10°C. This suggests, barring substantial pteropod adaptive capacity and major mitigation efforts, *L. helicina* to be excluded from large portions of the CCE by 2100.

Beyond considering average changes in the surface ocean, OWA may change the distribution of pteropod habitat with depth as well. All the species within the holoplanktonic gastropod community are epipelagic

diel vertical migrators that experience large changes in their environment daily. This requires rapid metabolic acclimatization that is temperature-dependent, with faster respiration in the warmer surface waters and a metabolic slowdown in the cold and corrosive depths of their daily migration (Smith & Teal, 1973). According to McLaren's hypothesis (McLaren, 1963), epipelagic migrators display uniform patterns of seeking lower temperature at deeper depths, an epipelagic adaptation that serves to conserve their energy (Teal & Carey, 1967; Oliver et al., 2020). This points to the importance of the vertical habitat as a refugia against the upper surface thermal stress. However, when thermal stress extends deeper, pteropods might avoid upper warmer waters by migrating deeper, where they experience higher stress from low- Ω_{Ar} conditions. The lack of suitable vertical habitat thus likely reduces the habitat refugia in which epipelagic vertical migration can conserve energy (Oliver et al., 2020). In addition, increased metabolic requirements from warming could result in food limitations even under a constant food supply. Combined, these stressors might deplete energy pools used for homeostatic strategies and lead to impaired physiology or mortality beyond the limitations we identified here.

We showed that our empirical HSI is consistent with experimental and empirical data at multiple scales of space and time, however the temperature and Ω_{Ar} stresses we identified are unlikely to be the only factors contributing to pteropod distributions. Alternative hypotheses for primary drivers of pteropod distributions include variable food supply (Bednarsek et al., 2018) and physical advection along the coast, which is correlated, but not causally linked, with changing hydrographic conditions. We briefly considered each by way of alternative HSI model formulations and present those results in the Supplemental Materials. However, in brief, available alternative hypotheses were measurably worse at explaining the empirical observations than the simple two factor framework that we present here. Further, neither food limitation nor spurious correlation of hydrography driven by advection were possible factors to be considered in the experimental treatments.

Our findings imply that predicted global and regional CCE-related environmental change could have stark implications for the future of pteropods under OWA. Thus, future modelling efforts should always strive to combine OWA in predicting future outcomes for pteropod populations. The strong parallels between our empirical HSI results and the experimental treatment mortality responses suggest that the model we develop could be applicable for future projections under more frequent or extreme marine heat wave events (Frölicher and Laufkötter, 2018; Oliver et al., 2018), enhanced upwelling, or intensifying anthropogenic OA. Tools such as HSIs inform marine ecosystem vulnerability studies, local pollution impact assessments, climate projections, adaptation strategies, and near-term management responses of sensitive indicators of global climate change.

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Figure Legends

Fig. 1. Physical-chemical observations captured strong hydrographic and chemical gradients of temperature (A–E) and aragonite saturation state (Ω_{ar} ; F–J) in the CCE. Abundances of the dominant pteropod species, *L. helicina*, are included for 2011 and 2016, and *L. helicina* presence/absence is included in 2013. Linear relationship between temperature and Ω_{ar} averaged over 100 m across different geographic regions (K–O).

Fig. 2. Compilation of large scale and regional presence/absence data for *L. helicina* from 2011 to 2016 across latitudinal scales from 25 to 50 degrees N. Blue dots denote *L. helicina* presence, red dots their absence. Background colors are derived by gridding the dots: data are weighted by inverse squared “distance” where temporal (i.e. x-axis) differences were multiplied by 5 °/yr (to make the figure ranges comparable) and with a maximum weight value of 1 (to avoid dots having excessive influences on nearby background colors).

Fig. 3. Abundance distribution of *L. helicina* related to temperature integrated over the upper 100 m. Note that the y-axis is trimmed for clarity. Many samples contained >15 ind/m², however, none of those were associated with average temperatures > 11.6 °C.

Fig. 4. (A) Full factorial experiments included temperature and low Ω_{ar} on *L. helicina* (N=480) using control (low T/high Ω_{ar}), single stressor (low T/low Ω_{ar} ; high T/high Ω_{ar}), or double stressor (high T/low Ω_{ar}) conditions (Table S1). Data was analyzed using 2-way ANOVA and the results with standard deviation show 50% mortality due to thermal stress; 30% mortality due to low Ω_{ar} stress; and 100% mortality due to the combined stress.

Fig. 5. Conceptual T– Ω_{ar} diagram showing habitat compression based on temperature and Ω_{ar} as two stressors. Dots indicate presence (black dots) and absence (red dots) observed along three years (2011, 2013, 2016) of WCOA cruises with the numbers indicating the station numbers. The background color indicates the empirical HSI values for each combination, while the dashed line shows the T and Ω_{ar} combinations at which the mechanistic HSI based on experimental incubations suggests 2/3rds experimental mortality. The proximity of the band of green (~0.5 empirical HSI value) to the dashed line implies a strong similarity between the two relationships, suggesting similar underlying mechanisms account for both. The HSIs show pteropods to be more abundant in the upper left corner, while more likely to be absent in the unsuitable habitats in the lower right.

Figure 6: Global *Limacina helicina* presence (OBIS) with respect to annual mean temperature (WOA) and Ω_{ar} (GLODAP) at the maximum depth of the vertical range reported for each observation. The blue line is the linear fit to the minimum observed Ω_{ar} over the range of 8-13°C ($\Delta\Omega_{ar}/\Delta T = 0.23$, $R^2=0.87$, $p=0.02$ for null hypothesis of no correlation); this represents the overlapping temperature range for the polar and subpolar OBIS observations and subtropical WCOA observations. The solid black line is the empirical HSI=0.99 from the WCOA cruises; the dashed black line is the empirical pteropod relationship from Bednaršek et al. 2018 with abundance=0; the solid red line is the experimental mortality relationship equivalent to HSI=0.99.

Fig. 1:

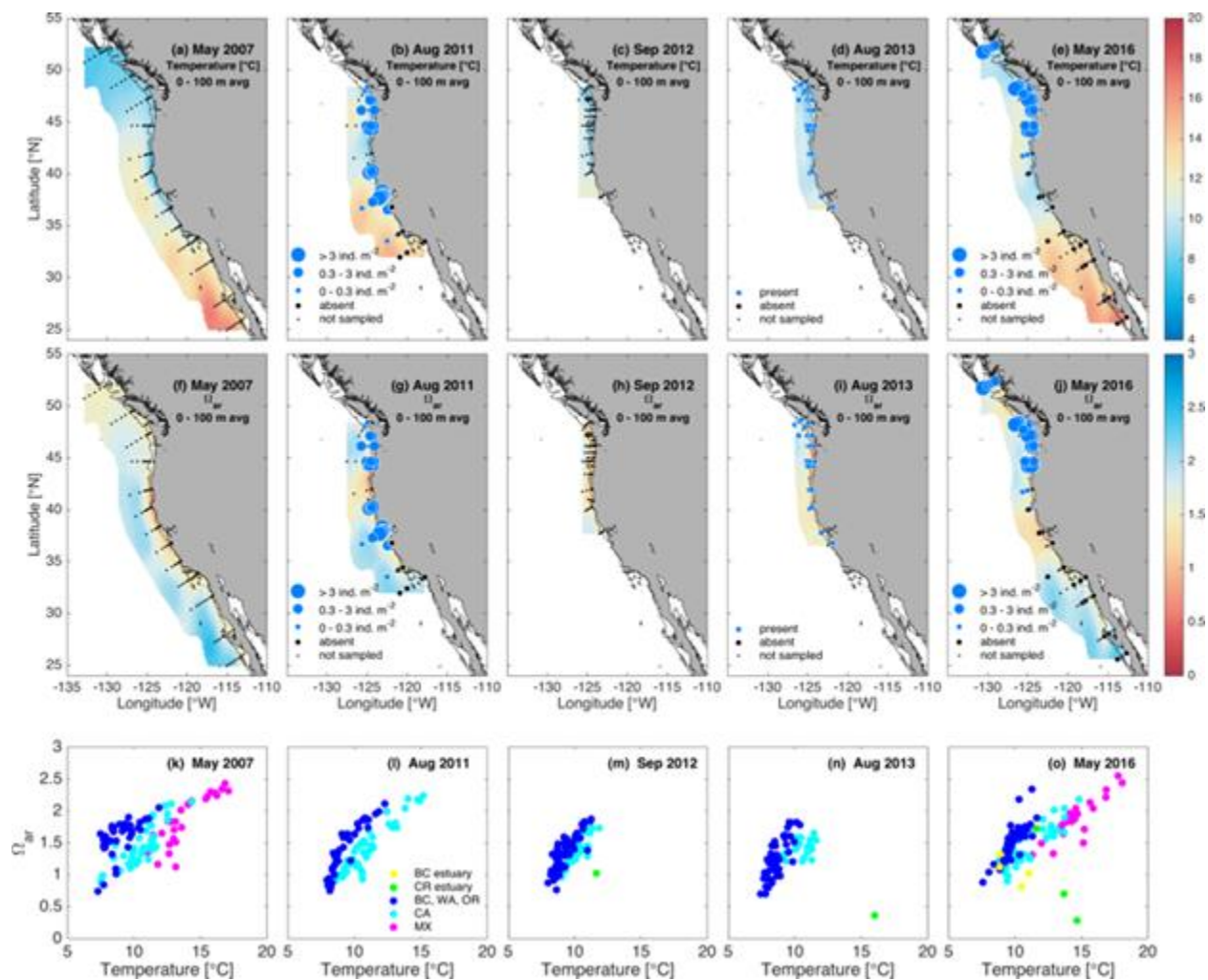


Fig 2:



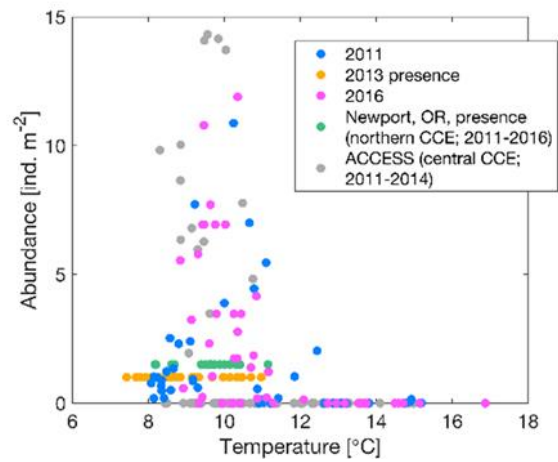


Fig 4:

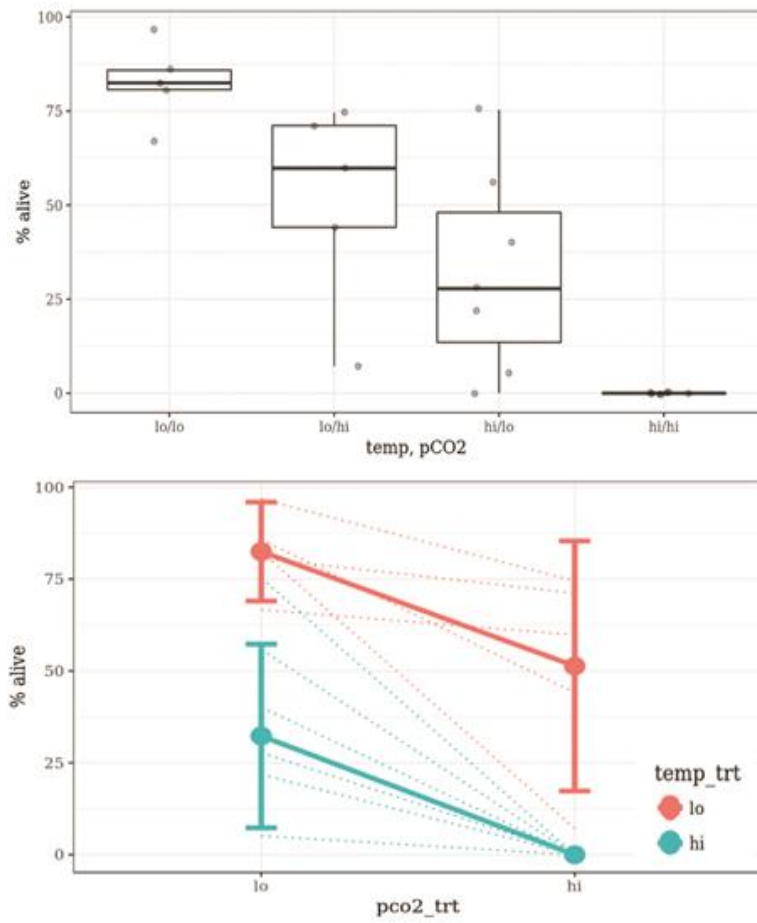


Fig 5:

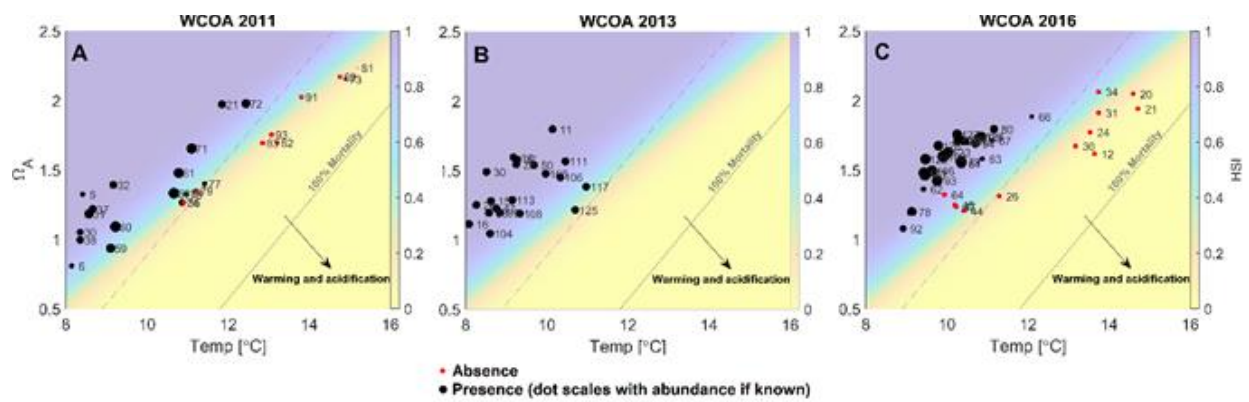


Fig 6:

