Assessing the impacts of ocean acidification upon tropical tuna

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Introduction

Increasing concentrations of CO_2 in the Earth's atmosphere (IPCC 2007) are causing a gradual warming and acidification of the Earth's oceans (e.g. Barnett et al. 2005; Caldeira and Wickett 2003; Feely et al. 2004). Both warming and acidification have the potential to affect the distribution and population dynamics of many marine organisms (IPCC 2007; Raven et al. 2005; Fabry et al. 2008). Significant advances in knowledge have been made over the last decade that have advanced understanding of how increasing ocean acidity will impact nearshore and coral reef ecosystems (Fabry et al. 2008). Our understanding about the effects of acidification on pelagic ecosystems, however, remains rudimentary. In the Pacific Ocean, improving our knowledge on the possible impacts on the pelagic environment is important, as the Pacific's tuna populations are of one of the largest and most valuable fisheries in the world (Williams and Terawasi 2009). The income derived from tuna fisheries provides a significant contribution to the economies of many Pacific Island countries and territories (Gillett 2009). To ensure such economic benefits are maintained through the sustainable management of this fishery requires an understanding of not only fishery impacts, but impacts of other factors upon population biomass and structure over time. While fishery scientists are now attempting to predict how ocean warming will affect Pacific tuna populations (Lehodey et al. 2010, 2013), no one has previously investigated how ocean acidification (OA) may affect these species and associated fisheries.

To advance our knowledge of the impacts of OA upon tuna populations and fisheries, a pilot study was undertaken at the Inter-American Tropical Tuna Commission (IATTC) Achotines Laboratory in Panama. The objectives of the pilot study were to develop and test experimental protocols to examine the potential effects of OA on yellowfin tuna (*Thunnus albacares*) egg fertilisation, egg and larval development, growth, and survival, and on the rapid selection of resistant genotypes. The following article provides an overview of the project, including a description of the trials conducted and a summary of the results. A full description of the study and the results has been submitted to *Deep Sea Research Part II* for publication.

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Projected changes in ocean acidity

Concentrations of CO_2 in the ocean (pCO2) tend towards equilibrium with the CO_2 in the atmosphere. Since the start of the industrial revolution, the world's oceans are estimated to have absorbed about 30%–50% of global man-made CO_2 emissions, which has lowered the average sea-surface pH by 0.1 units (i.e. making the ocean more acidic and less alkaline) (Feely et al. 2004; Sabine et al. 2004; Orr et al. 2005). It is estimated that uptake of atmospheric CO_2 by global oceans will further reduce sea-surface pH by 0.3–0.4 units by 2100 and up to 0.7 units by the year 2300 (Caldeira and Wicket 2003, 2005).

Concentrations of pH show spatial heterogeneity both between oceanic regions (surface waters) and throughout the water column. Currently, surface layer pH values are lowest in higher latitudes and areas where upwellings may bring subsurface waters with lower pH to the surface. Although the mean seawater pH is expected to decrease globally, the rate of this change is predicted to be greater in high latitudes, and lower in tropical and subtropical waters (Ilyina et al. 2013; Bopp et al. 2013). The degree of change is also dependent on future anthropogenic CO_2 emissions and whether these are higher or lower than "business as normal" IPCC projections, and may be impacted by other predicted consequences of climate change, such as changed ocean circulation patterns (IPCC 2011).

In the Pacific Ocean there is considerable seasonal and vertical/horizontal spatial variation in pH and pCO2. In the eastern tropical Pacific Ocean, surface water pH is on average lower than in the western tropical Pacific, and the pH at 50 m depth (in the eastern Pacific) is on average 0.54 pH units less than at the surface. Across the region of tuna spawning habitat, mean surface water pH is predicted to decrease between 0.26 and 0.49 pH units by 2100 (under the high atmospheric CO_2 scenario of IPCC) (Ilyina et al. 2013). In the eastern Pacific Ocean the pH of surface waters is predicted to decrease from 8.05 to about 7.73 while in the western Pacific Ocean, the mean decline in pH is projected to be 0.40 pH units (with a maximum predicted decline of 0.46) (Ilyina et al. 2013).

Impacts on fish

Our synopsis of the available literature suggests that the early life stages of fish may be more vulnerable to direct OA impacts than adult fish, due to different modes of respiration and ion exchange (Jonz and Nurse 2006; Pelster 2008). Adult fish generally show a stronger capacity to compensate for prolonged exposure to elevated pCO2 due to their ability to control acid base balance by bicarbonate buffering across the gills and to a more limited degree, via the kidneys (Brauner and Baker 2009; Esbaugh et al. 2012). Conversely, exposure to elevated pCO2 has been found to adversely affect embryonic development (Tseng et al. 2013), larval and juvenile growth (Baumann et al. 2011), tissue/organ health (Frommel et al. 2011), and survival (Baumann et al. 2011). Such effects however appear to be species specific, with numerous studies failing to detect direct relationships between "near future" levels of elevated pCO2 and embryogenesis (Franke and Clemmessen 2011), hatching (Frommel et al. 2012), growth and development (Bignami et al. 2013a; Hurst et al. 2012, 2013; Munday et al. 2011a; Frommell et al. 2011, 2012), swimming ability (Bignami et al. 2013a; Munday et al. 2009a) or survival (Frommell et al. 2012; Munday et al. 2011a). Similar results are reported for the growth of otoliths, with increased size and/or density observed in some species (Checkley et al. 2009; Munday et al. 2011b; Hurst et al. 2012; Bignami et al. 2013a, 2013b) but not in others (Frommell et al. 2012; Franke and Clemmessen 2011; Munday et al. 2011a).

The sub-lethal effects of OA may present the largest risk to individuals and populations for many species (Briffa et al. 2012). Somatic impacts such as reduced growth and size at age have been linked to increased mortality in natural fish populations due to increased risks of predation and reduced ability to find food (e.g. Houde 1989; Leggett and Deblois 1994). Otoliths play an important role in detecting sound, acceleration and body position in fish (Bignami et al. 2013b) and altered otolith formation may change predator avoidance and foraging efficiencies of individuals. Neurological and behavioral effects associated with elevated CO_2 levels have also been observed in coral reef fish (Briffa et al. 2012). These include disruption to mating propensity (Sundin et al. 2013), impaired ability to make settlement choices (Munday et al. 2009b), altered timing of settlement (Devine et al. 2012), impaired response to predator and prey olfactory cues (Allen et al. 2013; Cripps et al. 2011; Dixson et al. 2010; Nilsson et al. 2012), reduced escape distances (Allen et al. 2013), altered responses to visual threats (Ferrari et al. 2012a) and auditory signals (Simpson et al. 2011), behavioral lateralisation (Domenici et al. 2012; Nilsson et al. 2012) and a reduced capacity to learn (Ferrari et al. 2012b). Such behavioral changes were recently linked in reef species to the impact of elevated pCO2 upon key brain neurotransmitter GABA-A (Nilsson et al. 2012), with potential implications for other species given the highly conserved nature of GABA-A across species.

Potential vulnerability of tunas

While many of the original studies in this area focused on reef species, recent studies have expanded to include non-reef species (e.g. Bignami et al. 2013a, 2013b; Frommel et al. 2010, 2011, 2012; Sundin et al. 2013; Tseng et al. 2013), but these have not included tuna species. The only experiment known to have tested impacts upon a tuna species (eastern little tuna) tested pCO2 levels that far exceeded those predicted using IPCC scenarios (Kikkawa et al. 2003). Pelagic fish species are considered in general to have evolved in a relatively more stable pH environment than coastal and reef species, and this, in addition to low blood pCO2 levels that can be expected to result from their high rates of gas exchange, may make them more vulnerable to changes in ocean pCO2 and pH (e.g. Nilsson et al. 2012).

Tropical tunas range and spawn in equatorial and subtropical waters from the far western Pacific Ocean to the far eastern Pacific Ocean, and in both near coastal waters and oceanic waters (Schaefer 2001). It is unknown whether the historical level of OA variability across the tropical Pacific has been sufficient to have conferred some evolved resilience in tropical tunas to predicted future levels of OA.

Although the likely effects of OA on tuna populations have not been investigated, such research is clearly a high priority. Decision-makers need timely and appropriate scientific advice for current and future tuna fisheries management and worldwide adaptation planning. In October 2010 the Pelagic Fisheries Research Program (PFRP) recognised this need and funded a collaborative study of the impact of OA on the early developmental stages of Pacific yellowfin tuna. The study, led by the Secretariat of the Pacific Community and IATTC, is investigating the effect of OA upon embryonic development, hatching rates, condition, development, and growth and survival in pre- and post-feeding yellowfin larvae. The collaboration includes scientists from the Max Planck Institute of Meteorology (Germany), Collecte Localisation Satellites (France), the University of Gothenburg (Sweden), and Macquarie University (Australia). As tolerance to OA has been found to be variable on an individual level in other species, the project has included a component to look at whether genotypes (the genetic makeup) of individual yellowfin larvae vary in their responses to different CO_2 levels. This last component is a first step towards determining if OA causes genetic selection of

resistant genotypes in this species. Analyses to estimate the effects of OA on life stage development and rates of deformity, otolith formation and genetics are ongoing and not presented.

Achotines facility

Experimental trials were conducted at IATTC's Achotines Laboratory, Panama, in October and November 2011. The facility was inaugurated in 1985 and is one of only a few in the world with the location, equipment, and expertise to conduct investigations of this type. Achotines Bay is located on a section of coastline (Fig. 1) where the continental shelf drops rapidly and deep oceanic waters are close to shore, allowing researchers to easily access local tuna populations for either field studies of early development or to obtain yellowfin tuna as captive broodstock. At the lab an in-ground concrete tank holds a broodstock population of yellowfin tuna that have spawned on a near-daily basis since October of 1996, providing a reliable source of eggs and larvae for early developmental studies.

Experimental trials

Experimental trials were grouped into three categories: sperm and fertilisation trials, egg and larval trials, and genetics analyses. The egg and larval trials were replicated, with the initial trials in October and the replications in November.

Tank set up and pH control

The experimental setup for the fertilised egg and larval trials consisted of 15 experimental tanks. Each 840-liter (l) capacity tank was nested inside of an 1100-l tank filled with seawater that acted as a buffer/insulator to stabilise the water temperature in the smaller tank during the trials. Water flow, lighting, aeration, and turbulence levels were adjusted to set these parameters as uniformly as possible across all tanks.

Four pH treatment levels (6.9, 7.3, 7.7 and 8.1) were targeted in each trial with three replicate tanks per treatment level (Fig. 2). These levels were chosen based on results from the ocean-carbon-cycle models using the IPCC IS92a Scenario (e.g. the Hamburg Ocean Carbon Cycle model) (Ilyina et al. 2009) and reference to published studies on predicted pH levels (Ilyina et al. 2013; Caldeira and Wickett 2003) and take into account spatial variation in predicted declines, not just the global average predicted declines. Target pH levels 6.9 to 8.1 encompass potential mean ocean pH levels estimated for the current oceans and predicted for near future oceans (to 2300). A fifth treatment with a pH of 6.5 was also included. This treatment was applied as a range test to ascertain that extreme values of pH would result in mortality. This value is well below the lowest predicted pH for the time period to 2300.

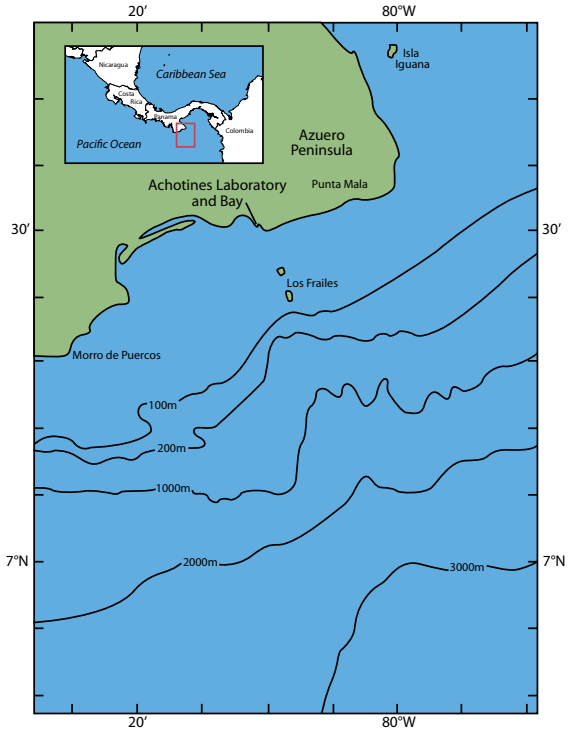

Figure 1. The location of the Achotines Laboratory. The bay in the centre of the photo is Achotines Bay.

Figure 2. The multiple experimental tanks with nested egg incubators used in experiment 1 and experiment 2 of the pilot study.

The local coastal waters that supply the Achotines Laboratory seawater system were very close to pH 8.2 during the trial period and therefore ambient seawater was used for the high pH level. The four lower treatment levels of seawater pH were maintained by regulation of mixtures of compressed air and CO_2 bubbled through air diffusers in each tank. The use of CO_2 was critical to modifying water chemistry (i.e. increasing carbonic acid, increasing H+, lowering pH) in a manner consistent with CO_2-induced ocean acidification.

In all trials, water-quality parameters (pH, temperature, salinity, dissolved oxygen, CO_2, alkalinity) were measured at frequent intervals in each tank. Controlling pH in ocean-acidification experimental systems is a difficult task (Riebesell et al. 2010). For these experiments, sophisticated electronic gas-flow controllers were used to precisely control the mix of air and CO_2 supplied to the tanks in each module. The average pH attained in each module (treatment level) for the first experiment was within 0.15 units of the target pH (and generally much closer). In the second experiment average pH levels in each module varied, at times, by several units from the target pH.

Fertilised egg and larval trials

The effects of OA upon mortality, growth, and development of eggs and larvae of yellowfin tuna were tested by rearing larvae from egg stage to first-feeding stage in 15 tanks comprising the five treatment (pH) levels. Trials were continuous but effectively comprised three phases: egg phase, yolk-sac larval phase, and first-feeding larval phase, with sampling regimes differing in each phase.

To start the experiment, fertilised eggs were collected from a daily spawn in the broodstock tank of the Achotines Laboratory and randomly stocked in each of 15 cylindrical egg-incubation nets nested one per experimental tank (Fig. 3). Eggs were stocked in each egg-incubation net at a density of 177 eggs L^{-1}, and eggs were immediately sampled fresh for weights and measurements. Additional samples of eggs were taken during the incubation period and fixed for subsequent histological examination of tissue and organ development.

Yolk-sac larvae were then dispersed from the egg-incubation nets into their respective experimental tanks 1 hour (h) after hatching. The yolk-sac phase in yellowfin tuna larvae continues until approximately 50–70 h after hatching depending on water temperature. Yolk-sac-stage and feeding larvae were maintained in the same experimental tanks until early on the seventh day of feeding (approximately 8.5 days post-hatching; 9.38 days total from egg transfer), when the experiments were terminated.

Larvae were fed cultured *Brachionus plicatilis* (rotifers) at densities of 3–5 mL^{-1}. Dense blooms of unicellular algae (500,000–750,000 cells mL^{-1}) were maintained in each tank to facilitate rearing (Margulies et al. 2007).

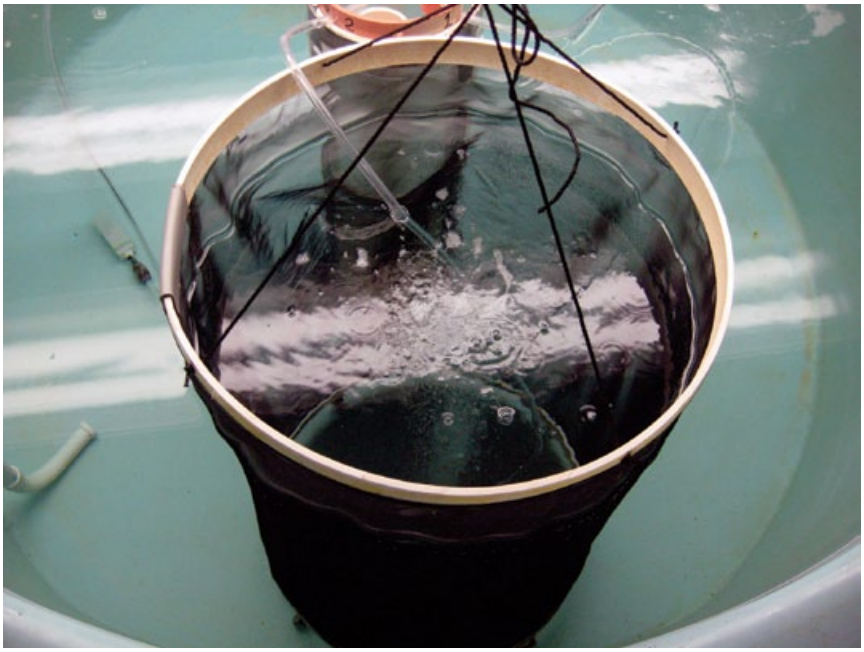

Figure 3. The cylindrical egg-incubation nets used in the pilot study. One net was nested in each experimental tank.

During each phase (egg, yolk-sac, and first-feeding), 15–17 fresh samples were taken at various intervals from each tank to be measured (total length, notochord length, body depth at pectoral, body depth at vent) and processed for dry-weight determination. Samples collected during each developmental phase were also fixed and stored for later analyses of tissue histology and organ development, feeding success, genetic variability and otolith development.

At the termination of the experiment each tank was slowly drained of water and all surviving larvae were removed by beaker and counted. The percentage of expected survival (adjusted for sample removals) was estimated for each tank.

Results and discussion

Our study tested the effect of a range of pH (~6.9–8.2) and pCO2 (330–10,467 microatmospheres [uatm]) conditions upon yellowfin tuna eggs and larvae. This range is broad enough to take into account current and future (to the year 2300) spatial variability in water chemistry across the yellowfin tuna spawning habitat range in the Pacific. Experimental tanks with mean pCO2 of less than 2500 uatm provided conditions that are relevant to the assessment of "near future" (i.e. year 2100) impacts on yellowfin tuna. Over longer time frames (e.g. to 2300) or with further increases in CO_2 emissions, pCO2 may increase further and pH decrease further (e.g. by 0.7 pH units according to Caldeira and Wickett [2003]), in which case our experimental tanks with mean pCO2 between 2500 and 5000 uatm are relevant.

The most consistent impacts across larval yellowfin early life history processes occurred at the highest pCO2 levels tested (>8500 uatm; Table 1). These levels are outside those predicted to occur in the next 300 years. However, there was evidence of significantly reduced survival at mean pCO2 levels of ≥ 4700 uatm (experiment 1) and significantly reduced larval size (experiment 1) and extended egg hatch time (experiment 2) at mean pCO2 levels ≥ 2200 uatm, that are relevant to near future predicted levels (Table 1). Significant effects at near future pCO2 levels were not, however, consistently predicted in both trials.

We observed reduced survival of yellowfin larvae after 7 days of feeding in the first trial with increasing mean pCO2. The mean survival at the control level (pH = 8.23, pCO2 = 368) was not significantly different to survival at pH 7.56 (pCO2 ~2108) but was significantly greater than survival at pH 7.35 (pCO2 ~4732) and pH 6.90 (pCO2 ~8847). The relationship between survival and mean pCO2 in the second trial was neither clear nor statistically significant, due in large part to the high level of intra-treatment variability in survival. There was a sudden mortality event (crash) in tank 15 (pH 8.1) on the last night of trial 2, associated with a very high density of larvae throughout the trial in the same tank. Such events are uncommon but have been observed previously in

Table 1. Experimental results for the pilot study on how ocean acidification may impact yellowfin tuna. Statistically significant differences between control (current day pCO2 levels) and treatment levels are presented as red squares. The green squares represent where statistically significant effects were not detected in experiments 1 and 2. The mean pH and pCO2 for the control tanks for experiments 1 and 2 were 8.2/368 and 8.1/464 respectively.

	Experiment 1			Experiment 2		
	pH range pCO2 range			pH range pCO2 range		
	7.6 2108	7.4 3820	6.9 9824	7.6 1719	7.2 4733	7.0 8847
Egg stage duration						
Survival						
Growth dry weight						
Growth standard length						

high larval density tanks at Achotines after 4–5 days of feeding. High survival in that tank, if it had been included in the analysis, would have provided a declining survival trend with increasing pCO2 in trial 2.

The egg stage and growth results were more consistent between the two trials. Pair-wise comparisons for both experiments indicated a significant difference in dry weights between larvae reared in the control treatment (mean pCO2 ~368 in trial 1 and ~464 in trial 2) and the highest pCO2 treatments (mean pCO2 ~9824 in trial 1 and ~8847 in trial 2) but not between larvae reared at the control and intermediate pCO2 levels. Effects at intermediate pCO2 levels were detected for standard length. Pair-wise comparisons for experiment 1 indicated that larvae reared in the treatment tanks with mean pCO2 ~2108 and mean pCO2 ~4732 were significantly smaller than those reared in the control treatment (pCO2 ~368). Slower larval growth during the first week of feeding may subsequently impact survival by affecting foraging success and by prolonging stage durations, increasing larval size-dependent susceptibility to predation (review in Leggett and Deblois 1994).

A significant positive relationship between mean pCO2 and hours until complete hatching was detected in both experiments. The hatch times at mean pCO2 values less than ~2200 were very similar in experiment 1, and the significant increasing trend in hatch time for this experiment represents an increase in mean hatch time at mean pCO2 > ~8800 (target pH 6.9) as compared to the mean hatch times at the lower pCO2 levels. In experiment 2 the mean hatch time at pH 8.1 was significantly less than that at each of pH 7.3, 7.7. and 6.9. The mean hatch time at pH 7.3 was also significantly less than that at pH 6.9 in this experiment. The difference in hatch time between the current conditions and mean pCO2 > ~8800 was one hour. Similar delays in hatching have also been observed during adverse physical conditions of very low dissolved oxygen levels and extremely high water temperatures (Wexler et al. 2011).

The purpose of the pilot study was to trial techniques to help design more intensive experimental trials. Power analyses of variability in survival responses within and between tanks/treatments indicated that more replicate tanks per treatment are needed to increase the statistical power and sensitivity of the experiments, so that the functional form of survival relationships can be identified and described. This was less of an issue for the growth analyses for which sample numbers were an order of magnitude higher. An additional design consideration for future experiments is the application of elevated pCO2 conditions to the parental stock. Recent research has demonstrated that exposure of broodstock to elevated pCO2 prior to spawning may reduce or remove negative impacts of elevated pCO2 upon behavior of larvae derived from subsequent spawnings (Miller et al. 2012).

Future experimental trials should include a lower pCO2 treatment (~1000 uatm) to test yellowfin larval responses to lower "near future" pCO2 levels. Including the interactive effects of temperature and oxygen, which will also vary under future climate change (Gruber 2011) would also be beneficial. OA and other parameters such as temperature have already been shown to interact for some species (Nowicki et al. 2012; Munday et al. 2009a; Enzor

et al. 2013). Hypoxic zones in the ocean may increase in the future as a result of climate driven changes in temperatures and deep ocean mixing (Hofman and Schellhuber 2009). Survival during the onset of feeding in yellowfin tuna larvae is greatly affected by short-term oxygen deficits at water temperatures ≥26 °C (Wexler et al. 2011). Larval sensitivity to dO2 might increase under elevated pCO2 conditions, and this needs to be tested in future experiments.

The very high fecundity and relatively short generation time of yellowfin tuna may permit them to adapt more rapidly than less fecund, longer-lived species. It will be important to determine the extent to which inter-individual variation mediates different selection responses (Schlegel et al. 2012). Genetic analyses of samples taken from the current trials are in progress to assess whether some genotypes are more robust to changes in pCO2, and these results should provide insights on the designs needed to assess this important question. Results of our supplemental sampling on the feeding patterns, otolith morphology and histological condition of internal tissues of larvae will also permit us to further investigate how acidification affects early life stages. Analyses of samples taken from yolk-sac and early feeding larvae will allow us to assess at what point in development any effects on growth first became apparent.

The ultimate goal of this research is to provide information that will allow models such as the Spatial Ecosystem and Population Dynamics Model (SEAPODYM) to be parameterised to include acidification effects and subsequently enable scientists and tuna fishery managers to better understand how these changes in ocean chemistry will alter the distribution and abundance of yellowfin tuna. Environmental data are used in SEAPODYM to functionally characterise the habitat of the population depending on its thermal, biogeochemical, and forage preferences (Lehodey et al. 2008, 2010). To this end, it will be critical that that further empirical trials are conducted to more clearly identify the functional form of the relationship between pH (or pCO2) and larval survival, and in particular, identify any interactions between pH (or pCO2) and other key physical oceanographic factors such as temperature and oxygen, so as to provide relevant information for appropriately altering the spawning-habitat index in SEAPODYM. Subsequent population level predictions of ocean acidification impacts will enhance the capacity of regional fisheries management organisations to make better-informed decisions regarding the management of the highly valuable tropical tuna resources, particularly with regard to attaining key sustainability-related objectives (Bell et al. 2013).

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