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Ocean warming has a greater effect than acidification on the early life history development and swimming performance of a large circumglobal pelagic fish

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Abstract

Ocean warming and acidification are serious threats to marine life; however, their individual and combined effects on large pelagic and predatory fishes are poorly understood. We determined the effects of projected future temperature and carbon dioxide (CO_2) levels on survival, growth, morphological development and swimming performance on the early life stages of a large circumglobal pelagic fish, the yellowtail kingfish *Seriola lalandi*. Eggs, larvae and juveniles were reared in cross-factored treatments of temperature (21 and 25°C) and pCO_2 (500 and 985 μatm) from fertilisation to 25 days post hatching (dph). Temperature had the greatest effect on survival, growth and development. Survivorship was lower, but growth and morphological development were faster at 25°C, with surviving fish larger and more developed at 1, 11 and 21 dph. Elevated pCO_2 affected size at 1 dph, but not at 11 or 21 dph, and did not affect survival or morphological development. Elevated temperature and pCO_2 had opposing effects on swimming performance at 21 dph. Critical swimming speed (U_{crit}) was increased by elevated temperature but reduced by elevated pCO_2. Additionally, elevated temperature increased the proportion of individuals that responded to a startle stimulus, reduced latency to respond and increased maximum escape speed, potentially due to the more advanced developmental stage of juveniles at 25°C. By contrast, elevated pCO_2 reduced the distance moved and average speed in response to a startle stimulus. Our results show that higher temperature is likely to be the primary driver of global change impacts on kingfish early life history; however, elevated pCO_2 could affect critical aspects of swimming performance in this pelagic species. Our findings will help parameterise and structure fisheries population dynamics models and improve projections of impacts to large pelagic fishes under climate change scenarios to better inform adaptation and mitigation responses.

KEYWORDS
carbon dioxide, critical swimming speed, early life history, larval development, morphology, *Seriola lalandi*, temperature, yellowtail kingfish

1 | INTRODUCTION

Oceans are warming, increasing in CO_2 content and decreasing in pH, due to the continued emission of anthropogenic CO_2 into the atmosphere (Rhein et al., 2013). Approximately one-third of all anthropogenic CO_2 released into the atmosphere is absorbed by the ocean (Sabine et al., 2004; Zeebe, Zachos, Caldeira, & Tyrrell, 2008), increasing the partial pressure of CO_2 (pCO_2) at the ocean surface and causing a decline in pH through a process known as ocean acidification (Doney, Fabry, Feely, & Kleypas, 2009). At the same time, the additional CO_2 accumulating in the atmosphere causes warming of both the atmosphere and the ocean. Thus, marine ecosystems must contend with the combined effects of both warming and acidification (Doney et al., 2012). Many recent studies have experimentally tested the effects of ocean acidification on marine organisms (Hendriks, Duarte, & Alvarez, 2010; Wittmann & Pörtner, 2013) and there is an increasing recognition of the need to investigate the potentially interacting effects with ocean warming, because higher temperatures may either exacerbate or counter the effects of ocean acidification (Kroeker et al., 2013; Riebesell & Gattuso, 2015). Yet, the vast majority of ocean acidification research has been on small benthic species that are amenable to experimental manipulation. Much less is known about the effects of ocean acidification and warming on large predatory species because their large size and high mobility make them inherently difficult to study. This is a major knowledge gap in ocean acidification research because large predators are critical to the structure and functioning of marine ecosystems and drive top–down responses in marine food webs (Frank, Petrie, Choi, & Leggett, 2005; Heithaus, Frid, Wirsing, & Worm, 2008; Myers, Baum, Shepherd, Powers, & Peterson, 2007; Myers & Worm, 2003).

Large pelagic fishes are the ocean's predominant top predators. They also comprise a large proportion of the total harvest from wild capture fisheries and are essential to the subsistence and livelihoods of millions of people in coastal regions throughout the world (FAO, 2016). Coupled ocean-biophysical population-dynamics models are one of the tools used to predict the effects of climate change on large pelagic fishes, because they can make spatially explicit the projections of biomass under different climate change scenarios (Bell et al., 2011). For example, Lehodey, Senina, Calmettes, Hampton, and Nicol (2013) modelled the effects of warming on larval distribution and adult biomass of skipjack tuna, predicting that both will shift towards the eastern Pacific under future warming.

Spatially explicit population-dynamics models aim to model the effects of natural environmental and anthropogenic forcing throughout the life history of pelagic fishes (Lehodey, Senina, & Murtugudde, 2008). To do this, an age-structured spatial population model is linked to anthropogenic and environmental forcing and the dynamics of lower trophic levels on which the fish feed. To assess the impacts of climate change on a focal species, the model must be informed by the knowledge of environmental forcing on survival, growth and movement throughout the fish's life history. The dynamics of larval and juvenile stages are vital to the dynamics of the adult population, especially in pelagic fishes (Chambers & Trippel, 1997; Cushing, 1995). Furthermore, the early life stages of fishes are generally assumed to be more sensitive to the direct effects of environmental change than larger juveniles and adults (Houde, 1989; Pankhurst & Munday, 2011; Rombough, 1997). Therefore, establishing the effects of elevated temperature and pCO_2 on the early life history stages on pelagic fishes is a priority for determining the effects of global change on these species.

A major challenge in estimating the effects of ocean warming and acidification on large pelagic fishes is that most species cannot be spawned and reared in captivity. To date, only a handful of studies have tested the effects of elevated pCO_2 on the early life history stages of large pelagic fishes, studying cobia, *Rachycentron canadum*; dolphinfish, *Coryphaena hippurus*; yellowtail kingfish, *Seriola lalandi*; and yellowfin tuna, *Thunnus albacares*. No consistent effects of up to 2,100 μatm pCO_2 were detected on early life history traits in cobia (Bignami, Sponaugle, & Cowen, 2013) or dolphinfish (Bignami, Sponaugle, & Cowen, 2014), but oxygen consumption and swimming ability were reduced in dolphinfish at >1,400 μatm pCO_2 (Bignami et al., 2014; Pimentel, Pegado, Repolho, & Rosa, 2014). Munday, Watson et al. (2016) found no effects of 1,000 or 1,700 μatm pCO_2 on survival and growth of yellowtail kingfish to 3 days post hatching (dph), but oil globule reserves declined, indicating possible energetic consequences for newly hatched larvae. Similarly, Bignami, Sponaugle, Hauff, and Cowen (2017) observed lower starvation resistance in larval cobia reared at 1,700 μatm pCO_2, which is consistent with increased energetic demands at elevated CO_2. Finally, Bromhead et al. (2015) reported negative effects of elevated pCO_2 on growth and survival of yellowfin tuna, but the effects were predominantly observed above 4,000 μatm and were strongest and most consistent above 8,500 μatm, well beyond future climate change projections (Collins et al., 2013).

The paucity of studies and variable results indicate an urgent need for more research into the effects of projected future CO_2 levels on the early life histories of these species. Moreover, recent physical modelling of ocean acidification has identified likely hot spots of intense pCO_2 amplification (5- to 10-fold higher than global averages) in the southern equatorial Pacific and North Atlantic oceans (McNeil & Sasse, 2016). These hot spots coincide with the predicted change in the core distributions of several pelagic fishes in response to ocean warming (Dueri, Bopp, & Maury, 2014; Lehodey et al., 2010, 2013). Only one study to date (Bignami et al., 2017) has examined the combined effects of ocean acidification and warming on the early life history of a large pelagic fish, and thus, we cannot yet assess the relative importance of these stressors in predicting the impacts of climate change on these ecologically and economically important fishes.

The yellowtail kingfish *S. lalandi* has emerged as a potential model species for testing the effects of environmental change on large pelagic fishes because it is one of the few species that can be reliably reared in captivity (Sicuro & Luzzana, 2016; Symonds et al.,

2014). The yellowtail kingfish is a large coastal pelagic fish with a circumglobal distribution in subtropical waters. Individuals can reach 2.5 m in length and over 70 kg in weight (Bray, 2017). The yellowtail kingfish is a powerful swimmer adapted to a pelagic lifestyle and supports an important recreational and commercial fishery in New Zealand, Australia, Japan and other subtropical regions (Lowry, Molony, & Keag, 2016; McKenzie, 2014; Sicuro & Luzzana, 2016).

Here, we tested the effects of projected future ocean temperature and pCO_2 on the early life stages in a New Zealand population of yellowtail kingfish. This population of kingfish experiences long-term mean summer temperatures of 21°C (Shears & Bowen, 2017). We used temperature and pCO_2 levels consistent with projections for the open ocean by the year 2100 under RCP 8.5. Atmospheric CO_2 levels are projected to exceed 900 ppm by the end of this century under RCP 8.5 (Collins et al., 2013). This will lead to ocean warming in the range of 2–4°C (Collins et al., 2013). Surface ocean pCO_2 is rising at the same rate as atmospheric CO_2 (Doney, 2010); however, recent models suggest that seasonal variation in pCO_2 will be amplified as atmospheric CO_2 levels rise, which means that ocean pCO_2 will be considerably higher than in the atmosphere for many months each year (McNeil & Sasse, 2016). Therefore, our nominal experimental treatments were (a) current-day average summer temperate of 21°C and ambient pCO_2 of 500 μatm, (b) current-day average summer temperate of 21°C and projected future pCO_2 of 985 μatm, (c) projected future summer temperature of 25°C and ambient pCO_2 of 500 μatm, and (d) projected future summer temperature of 25°C and projected future pCO_2 of 985 μatm.

We focused on the effect of elevated temperature and pCO_2 on larvae and small juveniles (1–25 dph) of yellowtail kingfish as they are likely to be more sensitive to environmental stress than later life stages (Melzner et al., 2009) and because decreased survivorship or performance during these early life stages can fundamentally affect population dynamics (Beverton & Holt, 1993; Chambers & Trippel, 1997; Houde, 1987). We investigated the effects of elevated temperature and pCO_2 on survival, growth, morphological development and swimming performance, including critical swimming speed (U_{crit}) and burst swimming (escape responses). These variables were selected as they are key metrics of individual performance and will be informative for parameterising population-dynamics models under climate change scenarios.

2 | MATERIALS AND METHODS

2.1 | Broodstock, eggs and larval culture

This study was conducted at the National Institute of Water and Atmospheric Research (NIWA) Northland Marine Research Centre, Ruakaka, New Zealand. Spawning stocks of yellowtail kingfish were maintained outdoors in 20 m^3 circular tanks. Each broodstock tank contained up to six locally sourced, wild-caught fish that had been domesticated in tanks for up to 9 years (approximately equal sex ratio in each tank). Each outdoor tank was supplied with 130 L/min seawater filtered to 10 μm at ambient ocean temperature (maximum seasonal range 13–24°C) and with ambient photoperiod. Broodstock were fed a mixture of pilchard (*Sardinops sagax*) and squid (*Notodarus* spp.). Spawning occurred without manipulation and to maximise genetic variation, eggs were collected from multiple broodstock tanks. In the current study, experiments were conducted in conjunction with a spawning event that occurred on the night of 23 January 2017. Four broodstock tanks containing a total of nine females, nine males and one of unknown sex contributed to spawning. Time of spawning was consistent across all tanks, occurring within the last 2 hr of daylight. Although long-term mean summer temperatures for the region are 21°C (Shears & Bowen, 2017), local ocean conditions vary naturally and ambient water temperature was 19–20°C in the 5 days immediately prior to spawning and then dropped to 18.2°C on the night of spawning. Ambient pH_T and pCO_2 were 7.91 and 589 μatm, respectively (Table 1).

Kingfish eggs were collected using an external egg collector as described by Moran, Smith, Gara, and Poortenaar (2007), with a 500 μm mesh net to retain eggs from the surface overflow of each tank. Eggs were sampled in the morning, approximately 12 hr post fertilisation. A representative proportion of floating eggs from the four contributing tanks (range of 4%–50% of total eggs per tank) were mixed, rinsed with oxygenated seawater for 5 min and disinfected with tosylchloramide (chloramine-T) at 50 ppm for 15 min. Eggs were then rinsed with seawater and distributed into 24 conical 400 L incubation tanks at a density of approximately 100,000 eggs per tank at 12:45 hr on 24/01/2017. The average number of eggs stocked per tank was 101,778 ± 9,860 (*SD*).

Each 400 L incubation tank received flow-through seawater at either 21 or 25°C with a photoperiod of 14 hr light and 10 hr dark

TABLE 1 Experimental water chemistry

Treatment CO_2	Treatment temperature	Temperature (°C)	Salinity	pH_{total}	Total alkalinity (μmol/kg SW)	pCO_2 (μatm)
Broodstock—ambient	Broodstock—ambient	19.4 (0.4)	35.6 (0.1)	7.91 (0.02)	2,329.6 (6.1)	589.4 (38.0)
Control	21°C	21.1 (0.1)	35.6 (0.1)	8.00 (0.03)	2,318.8 (7.2)	462.0 (42.8)
Control	25°C	24.8 (0.4)	35.6 (0.1)	7.94 (0.01)	2,319.9 (7.7)	538.3 (15.6)
Elevated	21°C	21.1 (0.1)	35.6 (0.2)	7.72 (0.03)	2,319.0 (3.8)	959.8 (57.3)
Elevated	25°C	24.9 (0.4)	35.6 (0.1)	7.70 (0.01)	2,320.0 (6.2)	1,010.6 (30.4)

Mean (±*SD*) temperature, salinity, pH_{total}, total alkalinity and pCO_2 in experiments with yellowtail kingfish (*Seriola lalandi*) eggs and larvae. Water chemistry in broodstock tanks was measured in the week up to spawning. Temperature, salinity, pH_{total} and total alkalinity were measured directly; pCO_2 was estimated from these parameters using CO2SYS.

and at a flow rate of 3 L/min. Gentle aeration was maintained within each tank with a weighted 4 mm airline. All tanks were at ambient ocean temperature (18.2°C) at stocking. Heating was turned on at 15:30 hr and allowed to slowly rise to the treatment set points of 21 and 25°C overnight. Eggs hatched 2 days after stocking at 25°C and 3 days after stocking at 21°C and larvae were reared for a further 1 day in the incubation tanks before transfer to grow-out tanks. Dead eggs, larvae and egg shells were removed daily from the incubation rearing tanks by draining from an outlet at the bottom of each tank and counted.

At 1 dph, larvae were transferred from their rearing tanks into 24 reciprocal grow-out tanks at a density of approximately 45,000 larvae per tank. The average number of larvae transferred was 44,227 ± 2,152. Grow-out tanks were 1,500 L circular tanks with slightly sloping bottoms with a black internal surface. Each grow-out tank received flow-through seawater at either 21 or 25°C with a photoperiod of 14 hr light and 10 hr dark and at a flow rate of 3 L/min. Gentle aeration was maintained within each tank with a weighted 4 mm airline. Larvae were fed with enriched rotifers up to 4 times per day. Dead larvae were removed daily from the grow-out tanks by siphoning into a bucket and the number of dead larvae from each tank were counted daily.

2.2 | Experimental system and water chemistry

Seawater pumped from the ocean was filtered through mixed media (sand), bag filtered to 5 μm, UV light treated to 150 mW/cm and delivered to large header tanks. Oxygen diffusers in the header tanks maintained baseline minimum dissolved oxygen (100% saturation) and foam fractionators removed any additional organics. Seawater from each header tank was gravity-fed into eight separate 100 L sump tanks where temperature was maintained at ambient control 21°C or elevated to 25°C and pCO_2 was maintained at ambient control (~500 μatm) or elevated (~1,000 μatm) pCO_2 in a fully crossed 2 × 2 experimental design (Table 1) with two replicate sumps for each treatment. Seawater from each of the eight treatment sumps was pumped into three of the 400 L incubation tanks during the egg incubation stage and three of the 1,500 L rearing tanks during the grow-out stage, so that there were six replicate experimental tanks at each temperature and pCO_2 level throughout the experiment.

An aquarium pump (Hailea HX-6540) pumped water from each treatment sump to the experimental rearing tanks containing kingfish eggs or larvae. A second aquarium pump (AquaOne Maxi 103) in each sump ensured that the water was well mixed and served as the dosing point for the elevated pCO_2 treatments. Elevated pCO_2 seawater was achieved by dosing treatment sump tanks with CO_2 to the desired pH set point using a pH computer (Aqua Medic, Germany). CO_2 was introduced to the pump inlet where it was immediately dissolved by the impeller. A needle valve was used to regulate the flow of CO_2 into the powerhead to ensure a slow, steady stream of CO_2 into the sump. This slow dosing and rapid mixing in the treatment sump tanks ensured that each experimental rearing tank received a steady supply of well-mixed water. All treatment sump tanks and experimental rearing tanks were housed in environmentally controlled rooms.

The pH_{total} and temperature of each rearing tank were measured daily (SG8 SevenGo Pro, Mettler Toledo, Switzerland). The pH electrode was calibrated with Tris buffers obtained from Prof. A.G. Dickson (Scripps Institution of Oceanography, batch number 26). Water samples for carbonate chemistry analysis were taken from all rearing tanks at the start, middle and end of the experiment, closely matching the fish sampling at 1, 11 and 21 dph.

Water samples were immediately poisoned with a saturated solution of mercuric chloride (at 0.05% of the sample volume) and later analysed for dissolved inorganic carbon (DIC) and total alkalinity (TA) at the University of Otago Research Centre for Oceanography, Dunedin, New Zealand. DIC was determined on a SOMMA type extraction system (Johnson, Wills, Butler, Johnson, & Wong, 1993) coupled to a UIC Coulometer (model 5015), using UIC Anode Reagent and Cathode Reagent (UIC Inc., Joliet, IL, USA) following the methodology of Dickson, Sabine, and Christian (2007). Alkalinity was determined by potentiometric titration in a closed cell (Dickson et al., 2007) using a Metrohm Dosimat burette (model 765; Metrohm, Switzerland), a Fluke model 8846A voltmeter, and with 0.2 M HCl (nominal concentration, fortified with NaCl to the ionic strength of seawater) added in 0.1 ml steps. The total alkalinity was determined from the titration data using a least squares minimisation technique. The DIC and TA systems were both calibrated with certified reference material (CRM) consisting of sterilised natural seawater of known DIC and TA preserved with mercuric chloride (Prof. A.G. Dickson, Scripps Institution of Oceanography, U.S., batch number 152). CRMs and samples were water-jacketed at 25°C. Measurement standard deviations of DIC and TA were within 2 and 1 μmol/kg of CRMs, respectively, determined from repeat analysis of CRMs, run in conjunction with study samples. Salinity was measured on the bottle sample using a YSI Pro30 salinity probe.

Carbonate chemistry parameters in each tank were calculated in CO2SYS using the measured values of pH_{total}, salinity, temperature and TA and the constants K1, K2 from Mehrbach, Culberson, Hawley, and Pytkowicz (1973) refit by Dickson and Millero (1987), and Dickson for $KHSO_4$. The estimated daily pCO_2 in tanks was cross-calibrated with calculations in CO2SYS using DIC and TA for the days that water samples were collected. Seawater carbonate chemistry parameters are shown in Table 1.

2.3 | Sampling protocols for life history traits

The number of fish remaining in each tank (i.e. survivorship) at 1 dph was estimated during transfer from the larval rearing tanks to grow-out tanks and by absolute counts at the end of the experiment at 25 dph. The 1 dph count involved mixing the fish within each rearing tank using aeration and gentle mechanical mixing with a handheld agitator. Five samples of 520 ml were then taken with a beaker and larvae counted on a 500 μm mesh flat screen and the average of the five counts was then used to calculate the total number of fish in each rearing tank (using the sample volume to tank

volume ratio). Throughout the experiments, no sampled fish were returned to tanks. Survival percentage was calculated as proportional survival from initial numbers at egg incubator stocking to 1 dph and 1 to 25 dph. The total number of fish sampled from each tank between days 18 and 22 for morphometric traits and physiological and behaviour tests was added to the final count at day 25 as it was assumed that these fish would have otherwise survived to the end of the experiment. To avoid excessive disturbance of the fish during the critical developmental stage around flexion, counts to estimate survivorship were not taken at 11 dph.

Morphometric traits were measured in a random subset of 30 fish sampled from each tank at 1, 11 and 21 dph. At 11 dph, fish were sampled from the first 16 grow-out tanks only (four tanks per treatment). For all other time points, fish were sampled from all 24 tanks. We measured a range of standard morphometric traits that are indicators of growth and performance in larval fishes: wet mass (weight), standard length (SL), total length (TL), body length (BL), muscle depth at vent (MDV), total depth at vent including fins (or "fin depth at vent") (FDV), eye diameter (ED), mandible length (ML), yolk length (YL), yolk depth (YD), yolk area (YA), mean oil globule diameter (OGD), head length (HL), head depth (HD) (Figure 1). For 11 dph fish, the observer also recorded if the tip of the notochord remained straight, or if it inclined upwards, indicating the commencement of flexion. Measurement landmarks followed Chambers et al. (2014). Each sampled larva was photographed with a Leica DFC 420 camera fitted to a Leica MZ7.5 stereo microscope or, for larger individuals, a Canon G16 series camera fitted to a stand. Morphometric traits were extracted from the photographs using ImageJ software with the image displayed on a high-resolution computer screen. The observer was blinded to the treatments when extracting morphological data from the photographs.

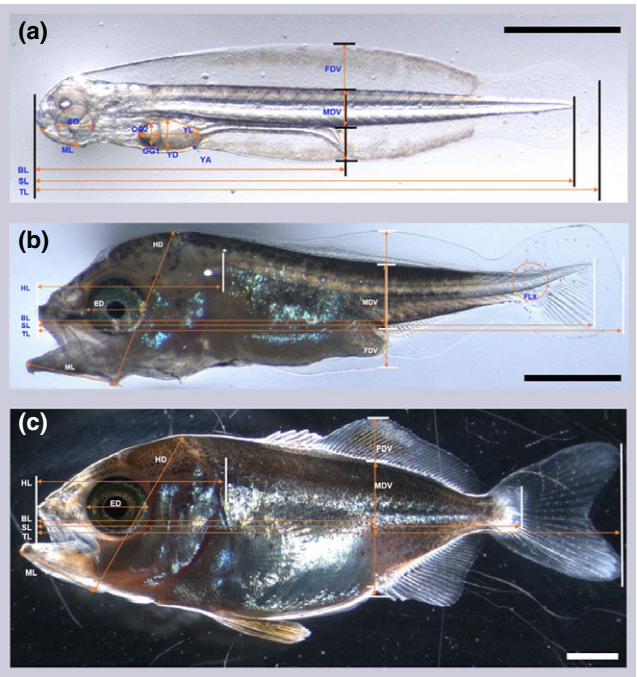

FIGURE 1 Morphological traits measured at each developmental stage. (a) 1 dph, (b) 11 dph, (c) 21 dph. Scale bars represent 1 mm

2.4 | Swimming and escape performance assays

All performance assays were conducted on larvae between 18 and 22 dph. Juvenile kingfish were sampled randomly from experimental rearing tanks. All assays were conducted in seawater at the same temperature and pCO_2 level as the experimental treatment of the individuals tested.

2.4.1 | Swimming performance

The U_{crit} swimming performance of juvenile kingfish was tested using a multilane swim flume as described by Stobutzki and Bellwood (1997) and used by Fisher, Leis, Clark, and Wilson (2005), Munday, Donelson, Dixson, and Endo (2009) and others. The flume contained five individual lanes with dimensions 180L × 30W × 50H mm. The swim flume was positioned over a large rectangular tank that received continual flow of seawater at the same temperature and pCO_2 level in which each fish was reared. The swim flume was connected to a large pump with water flow controlled by a calibrated gate valve. A wall of narrow tubes at the entrance to each lane created laminar flow through the chamber. Water flow was calibrated in 2 cm/s increments against the angle of the gate valve marked on a horizontal rigid plastic disk during three calibration trials.

During trials, the pump was primed and the water velocity began at 2 cm/s. A single fish was placed gently into each lane in the swim flume and the lid secured. Fish were allowed to habituate for 2 min. The trial commenced after this 2 min habituation period, with the water velocity remaining at 2 cm/s for a further 2 min. Water velocity was then increased every 2 min by 2 cm/s (approx. 2 body lengths/s) to determine critical swimming speed (U_{crit}) (after Brett, 1964). The time and speed at which each fish could no longer sustain swimming (U_{crit}) were recorded. The fish was judged to be fatigued when it could no longer maintain its position and was swept downstream onto the retaining mesh grid continuously for >5 s. Each individual was tested only once (n = 40–49 per treatment), and each trial took up to 28 min. Trials were conducted between 09:00 and 17:30 hr over six consecutive days. Swimming performance was videographed with a Canon Powershot G16 digital camera placed on a tripod directly above the swim flume. Time to fatigue was quantified subsequently from video playback.

U_{crit} was calculated using the following equation from Brett (1964):

$$U_{crit} = U + U_i * (t/t_i)$$

where U is the penultimate speed before the fish stopped swimming; U_i is the flow speed increment (2 cm/s); t is the time elapsed in the final increment during which the fish stopped swimming; and t_i is the amount of time individuals maintained at each speed (2 min).

2.4.2 | Escape performance

Fast-start arena and protocol

The fast-start arena consisted of a transparent circular arena (diameter 200 mm) placed within a 60 L white-sided container (350 × 400 × 250 mm) that had a clear Perspex base. The wall of the central arena was perforated to allow the flow of aerated water during habituation. The water level was maintained at 60 mm to reduce movement in the vertical plane. The outer tank was illuminated by an LED light strip (750 lumens) wrapped around the outside of the tank placed just above the water surface with light penetrating with even illumination through the white plastic sides.

At the beginning of a trial, an individual fish (n = 36–41 per treatment) was transferred to the test arena via a water-filled container and allowed to habituate for 5 min. The high-speed video recordings commenced at the end of the habituation period. Fast-start responses were elicited by the release of a black, cylindrical weight with a tapered end onto the water surface at the centre of the arena. The metal weight was controlled by a lanyard that was just long enough to allow the tapered tip to touch the surface of the water. This was achieved by remotely turning off an electromagnet to which the metal weight was attached. In order to provide a sudden stimulation and allow calculation of the escape latency, the stimulus was released through a white PVC tube (550 L × 40 Ø mm) suspended above the experimental arena, with the bottom edge at a distance of 10 mm above the water level. The cylindrical weight was released when the fish moved to the middle portion of the tank, allowing it to move an equal distance in any direction and standardising for the fish's position relative to the stimulus. Escape responses were recorded at 480 fps (Casio EX-ZR1000) as a silhouette from below obtained through pointing the camera at a mirror angled at 45°. Fish escape variables were only measured when a C-start was initiated. The water in the test arena was the same temperature and pCO_2 as the corresponding treatment water in which the fish was reared. To minimise any change in temperature and pCO_2 in the arena water, the arena was drained and reset with fresh treatment water every 20 min. The rate of pCO_2 loss from the testing arena has been found to be negligible within this time frame (Munday, Welch et al., 2016). Trials were conducted between 08:00 and 16:00 hr over three consecutive days. From the videos, we quantified latency to initiate an escape, directionality, proportion of non-reactors, response distance, response speed and maximum response speed. The analysis of the videos was conducted with the observer blind to the treatments.

Kinematic variables

Kinematic variables associated with the fast-start response were analysed using the image-analysis software ImageJ, with a manual tracking plug-in. The centre of mass (CoM) of each fish was tracked for the duration of the response. The following kinematic variables were measured:

1. Response latency (s) was measured as the time interval between the stimulus onset and the first detectable movement leading to the escape of the animal.
2. Directionality: escape responses were divided into "away" and "towards" responses when the first detectable movement of the head was oriented away or towards the stimulus, respectively.
3. Proportion of reactors was defined for each treatment as the proportion of animals that responded with a sudden acceleration after being startled, out of the total number of fish.
4. Response distance (mm) is a measure of the total distance covered by the fish during the first two flips of the tail (the first two axial bends, i.e. stages 1 and 2) defined based on Domenici and Blake (1997), which is the period considered crucial for avoiding ambush predator attacks (Webb, 1976).
5. Response speed (m/s) was measured as the distance covered within a fixed time (24 ms). This fixed duration was based on the average duration (22.8 ms) of stage 1 and 2 (as defined above).
6. Maximum response speed (m/s) was measured as the maximum speed achieved at any time during stage 1 and stage 2.

2.5 | Statistical analysis

2.5.1 | Survival

Survival among temperature and pCO_2 treatments was compared with generalised linear models (GLM) using the estimated number of individuals in each tank from egg stocking to 1 dph and 1 dph to a final count at 25 dph. A Gaussian distribution was used to assess survival from the egg to 1 dph, while a quasi-poisson distribution with a log-link function was used to compare survival from 1 to 25 dph.

2.5.2 | Morphology

Morphometric traits were analysed from 30 randomly selected fish per rearing tank for each of the three developmental stages (1, 11 and 21 dph). Linear mixed effects models (LME) for each morphological variable, with temperature and pCO_2 as fixed effects and tank as a random effect, were used to determine any potential effect of elevated temperature or pCO_2 on morphometric traits. Because of the expected covariance of variables describing morphology of the same individual, these data were reduced by principle component (PC) analysis (Table S1) and loadings on the first and second (if applicable) axes were tested as the dependent variable. Each trait was also tested separately to demonstrate any potential differences in morphology with temperature or pCO_2. A generalised linear mixed model (GLMM) with a binomial distribution and logit-link function (logistic regression) was used to assess the effect of temperature and pCO_2 on the proportion of fish that had reached notochord flexion at 11 dph. As above, tank was a random effect in the model.

2.5.3 | Swimming performance

Critical swimming speeds (U_{crit}) were compared among temperature and pCO_2 treatment levels using LMEs with fish size Ln(wet mass), temperature and pCO_2 as fixed effects and tank as a random effect. U_{crit} calculated in body lengths per second was also

compared among temperature and pCO_2 treatment levels using LMEs with temperature and pCO_2 as fixed effects and tank as a random effect.

2.5.4 | Escape performance

The proportion of fish that responded to the startle stimulus and the direction turned were compared among treatments using generalised linear mixed models (GLMM) with temperature and pCO_2 as fixed effects and tank as a random effect. A binomial distribution and logit-link function were used. Escape performance traits (distance moved and maximum speed) were compared among temperature and pCO_2 treatment levels using LMEs with fish size Log(wet mass), temperature and pCO_2 as fixed effects and tank as a random effect. Latency was compared among temperature and pCO_2 treatment levels using LMEs with distance from stimulus, temperature and pCO_2 as fixed effects and tank as a random effect.

Analyses were performed in TIBCO Spotfire S+ 8.2 and R (R Development Core Team, 2017). Heterogeneity of variance among tanks was included where it improved model fit. Akaike information criterion (AIC), likelihood ratio tests and residual analysis were used to examine model fit and assumptions of analyses.

3 | RESULTS

3.1 | Time to hatching

Kingfish eggs hatched 1 day earlier at 25°C than those at 21°C. Consequently, 1 dph larvae from the 25°C treatments were moved into the grow-out tanks one calendar day earlier than larvae from 21°C.

3.2 | Survival

Elevated temperature ($t_{21} = 2.091$, $p = 0.049$) but not elevated pCO_2 ($t_{21} = 0.158$, $p = 0.876$) reduced survival from the egg stage to 1 dph. Similarly, elevated temperature ($t_{21} = 2.927$, $p = 0.008$) but not elevated pCO_2 ($t_{21} = 0.150$, $p = 0.882$) reduced survival from 1 to 25 dph (Figure 2).

3.3 | Morphology

3.3.1 | 1 dph

There was an effect of temperature and pCO_2 on kingfish morphology at 1 dph. Fish were smaller at 25°C compared with 21°C, possibly because they hatched 1 day earlier and thus had 1 day less embryogenesis. SL, TL, BL, YL, YA and OGD decreased in fish at 25°C compared with 21°C, but ML increased at 25°C compared with 21°C. Elevated pCO_2 increased SL, TL and BL. There was a significant effect of temperature and pCO_2 on principle component (PC) 1, and a significant effect of temperature on PC2 (Figures 3 and 4) (see Table S2 for statistical results).

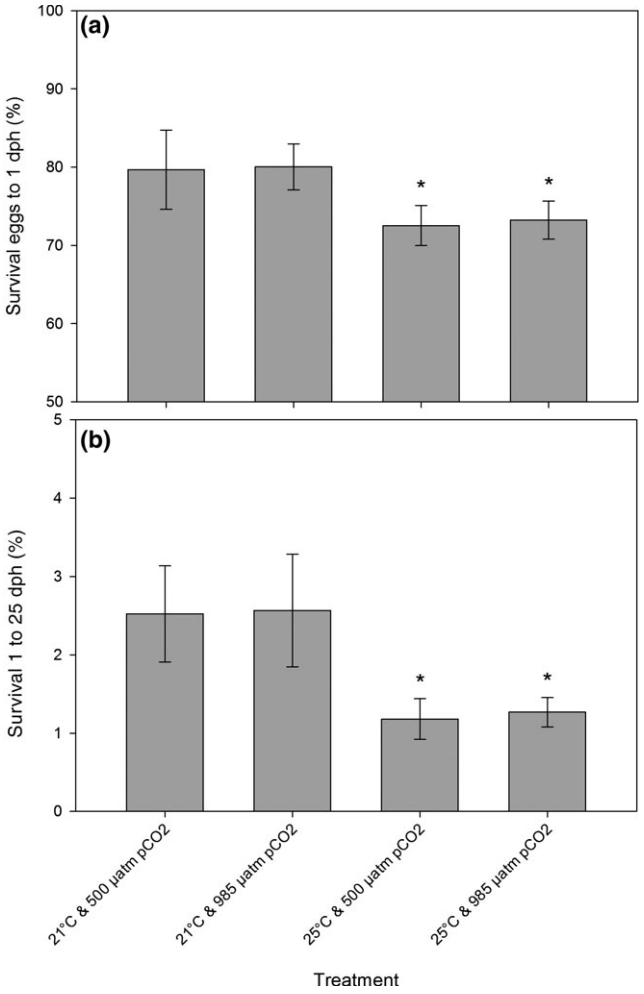

FIGURE 2 Kingfish survival, (a) survival from the egg stage to 1 dph and (b) survival from 1 to 25 dph. Data are means ± 1 SE. Asterisk (*) denotes a significant difference from the control treatment

3.3.2 | 11 dph

At 11 dph, there was a significant effect of temperature on MDV, FDV, ED, ML, HL, HD. Kingfish larvae at 25°C had increased MDV, FDV, ED, ML, HL and HD compared with larvae at 21°C. Temperature had a significant effect on PC1 and PC2. There were no effects of elevated pCO_2 on any of the morphological traits measured at 11 dph (see Table S2 for statistical results). Temperature ($z = 4.566$, $p < 0.0001$) but not pCO_2 ($z = -0.121$, $p = 0.9036$) influenced the number of fish that had reached flexion by 11 dph, with a greater proportion of fish exhibiting notochord flexion at 25°C compared with 21°C (Figures 3 and 5).

3.3.3 | 21 dph

At 21 dph, there were significant effects of temperature on all morphological traits measured: wet mass (weight), SL, TL, BL, MDV, FDV, ED, ML, HL and HD. Temperature had a significant effect on PC1 (the proportion of variance explained by PC1 was 0.967, Table S1). There were no effects of elevated pCO_2 on morphological traits at 21 dph (Figures 3 and 6) (see Table S2 for statistical results).

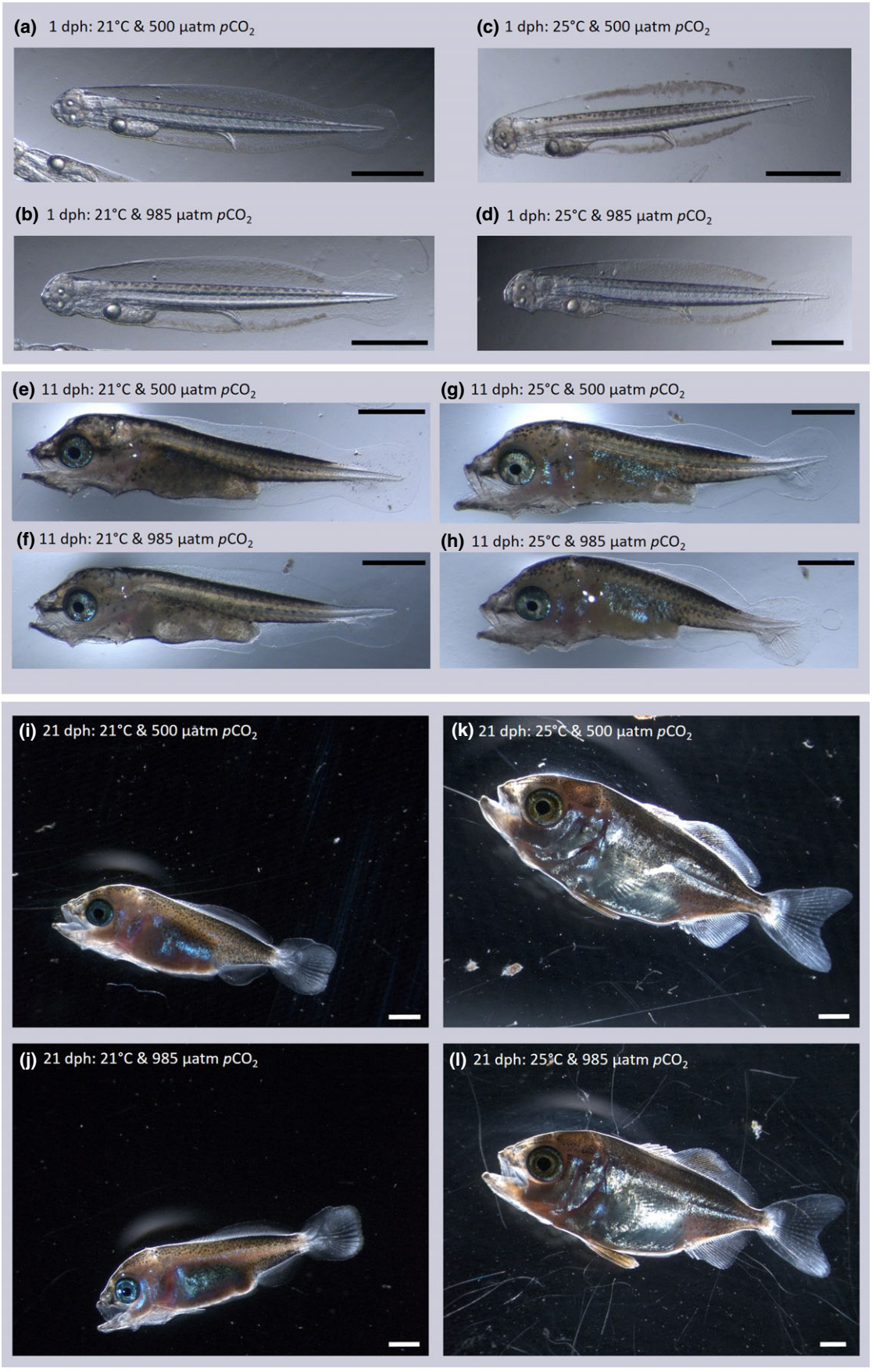

FIGURE 3 Kingfish at 1 dph (a–d), 11 dph (e–h) and 21 dph (i–l). Scale bars represent 1 mm

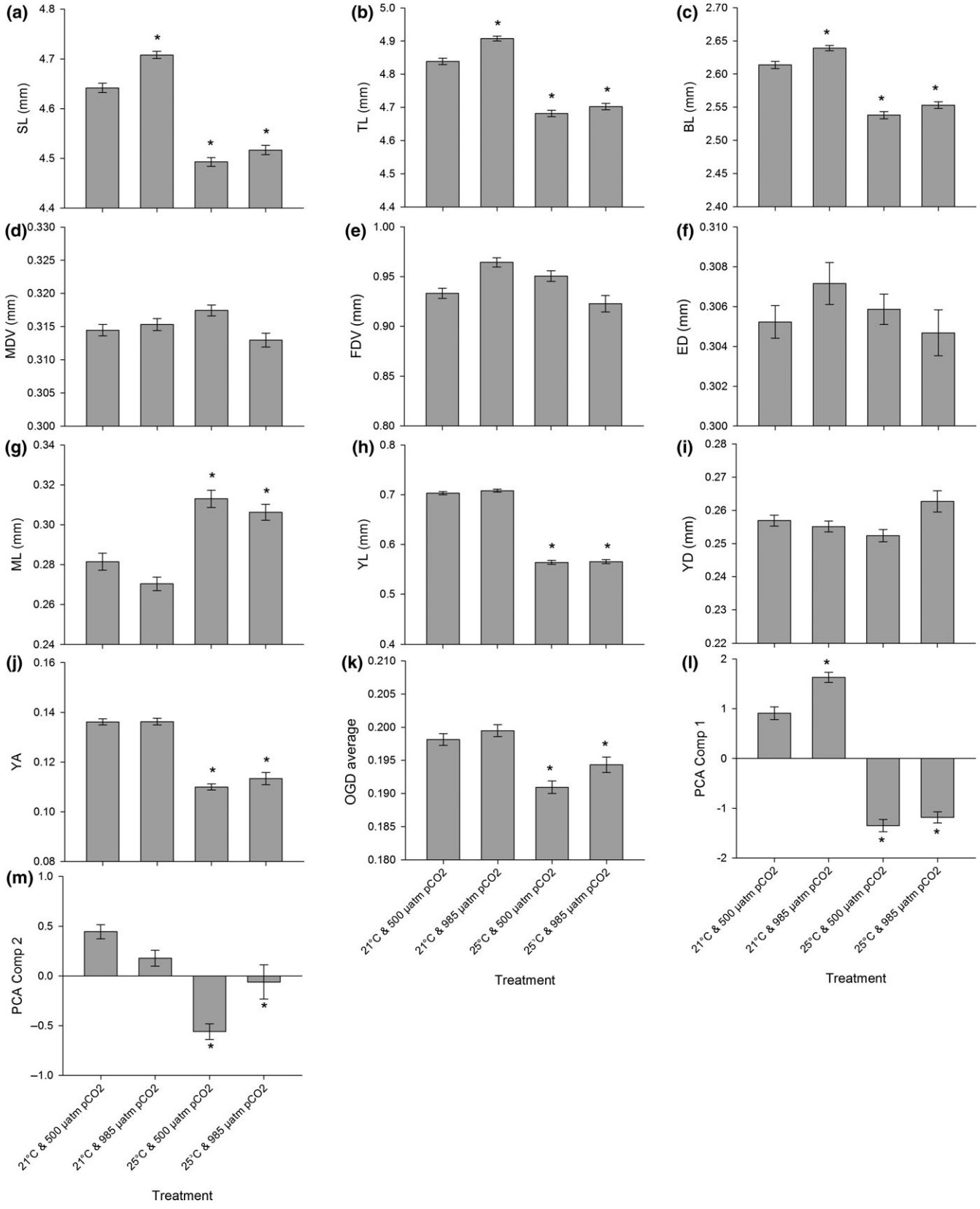

FIGURE 4 Kingfish morphology at 1 dph, (a) standard length (SL), (b) total length (TL), (c) body length (BL), (d) muscle depth at vent (MDV), (e) total depth at vent including fins (or "fin depth at length") (FDV), (f) eye diameter (ED), (g) mandible length (ML), (h) yolk length (YL), (i) yolk depth (YD), (j) yolk area (YA), (k) mean oil globule diameter (OGD), (l) PCA component 1, (m) PCA component 2. Data are means ± 1 SE. Asterisk (*) denotes a significant difference from the control treatment

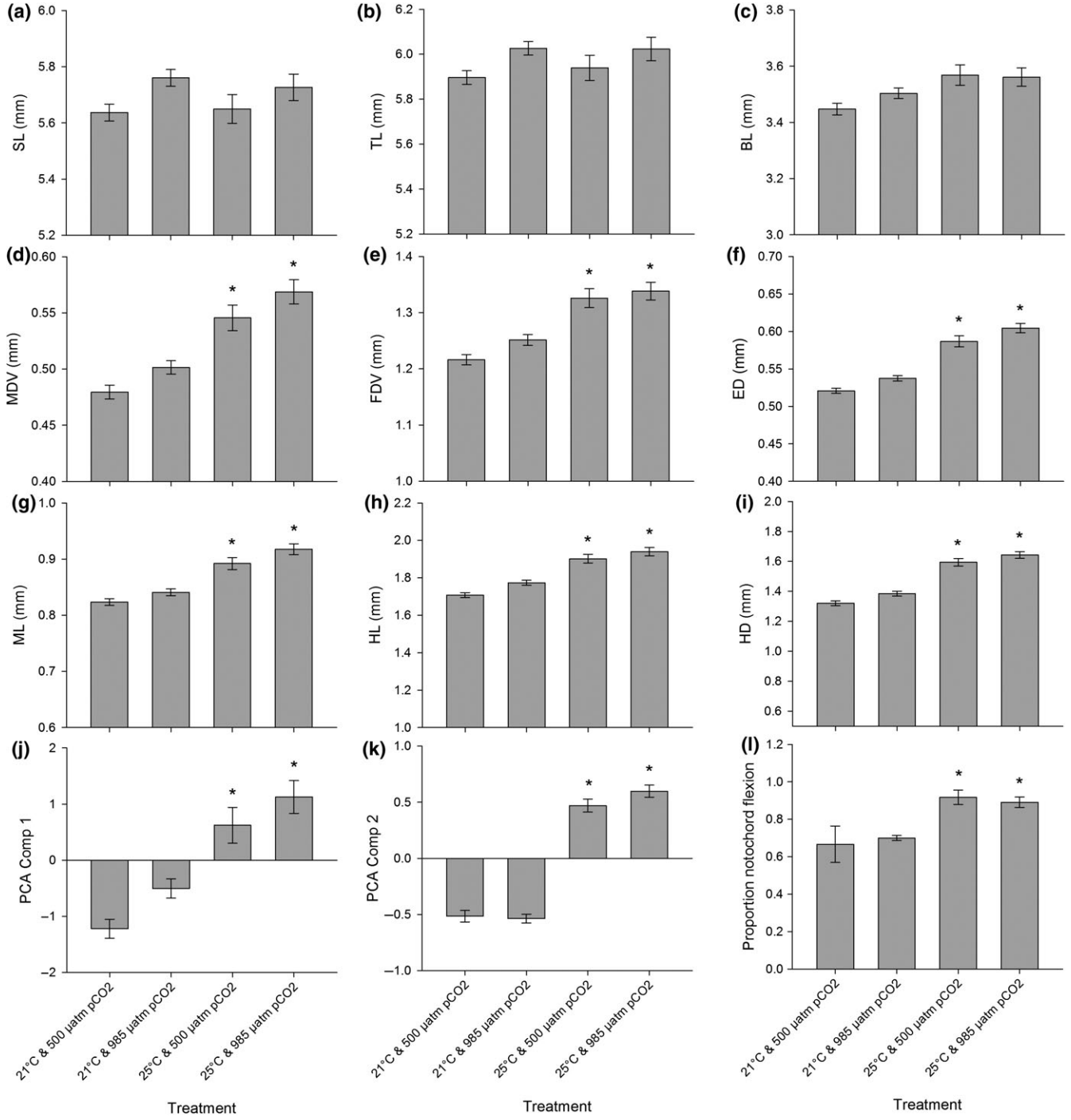

FIGURE 5 Kingfish morphology 11 dph, (a) standard length (SL), (b) total length (TL), (c) body length (BL), (d) muscle depth at vent (MDV), (e) total depth at vent including fins (or "fin depth at length") (FDV), (f) eye diameter (ED), (g) mandible length (ML), (h) head length (HL), (i) head depth (HD), (j) PCA component 1, (k) PCA component 2, (l) proportion of individuals that reached notochord flexion. Data are means ± 1 SE. Asterisk (*) denotes a significant difference from the control treatment

3.4 | Performance traits

3.4.1 | Swimming performance

U_{crit} was affected by fish mass ($F_{153} = 9.627$, $p < 0.0001$), temperature ($F_{21} = 6.046$, $p < 0.0001$) and pCO_2 ($F_{21} = -3.699$, $p = 0.0013$); moreover, there was an interaction between fish mass and pCO_2 ($F_{153} = -3.330$, $p = 0.0011$) (Figure 7). Fish reared at 25°C had a higher U_{crit} compared with fish reared at 21°C. By contrast, fish reared at elevated pCO_2 had reduced U_{crit} relative to fish reared at control pCO_2 and this effect was dependent on fish size. U_{crit}, analysed additionally by body lengths per second, was similarly affected by temperature ($F_{21} = 9.211$, $p < 0.0001$) and pCO_2 ($F_{21} = -2.368$, $p = 0.0276$) (Figure S1).

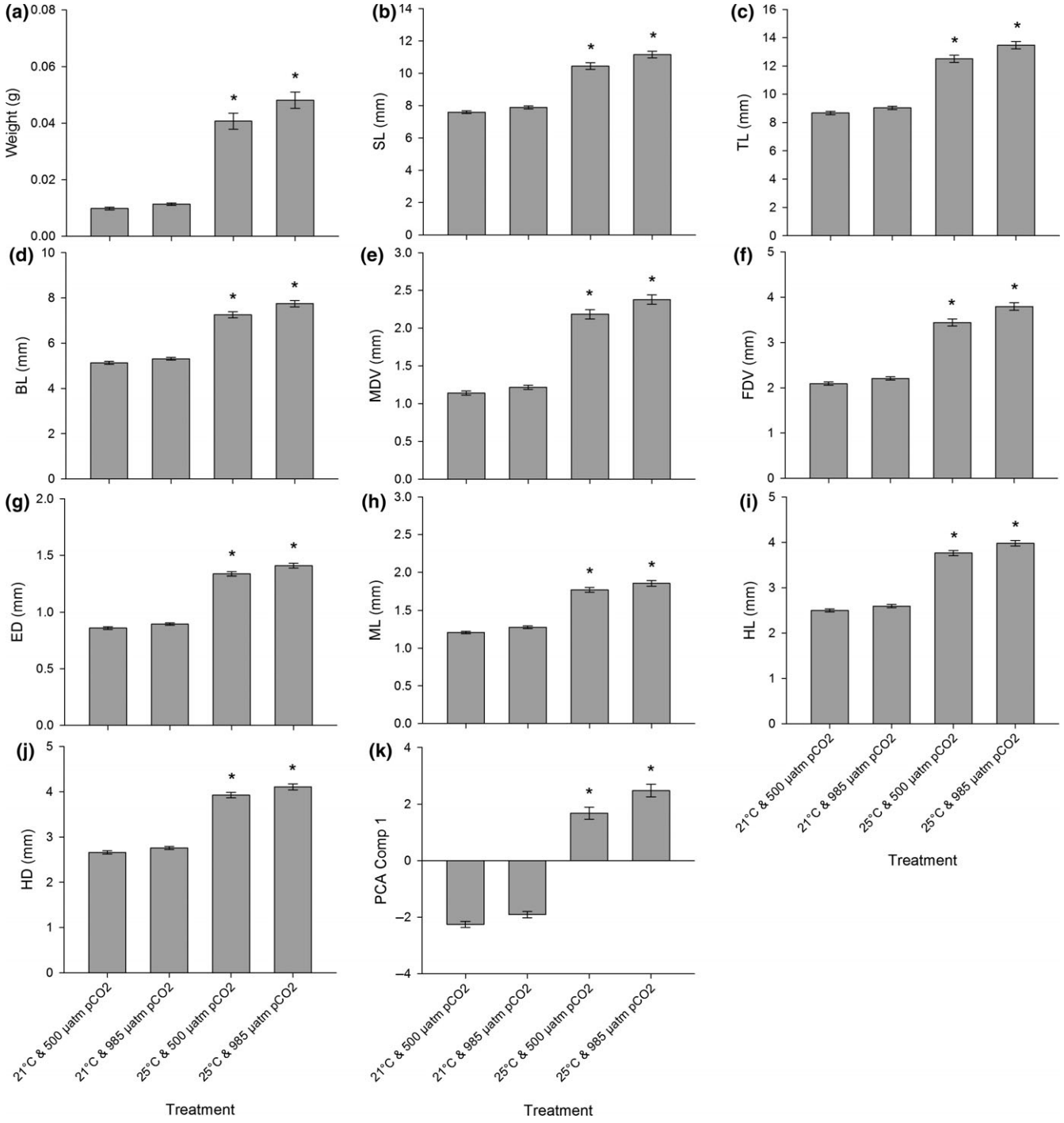

FIGURE 6 Kingfish morphology 21 dph, (a) weight, (b) standard length (SL), (c) total length (TL), (d) body length (BL), (e) muscle depth at vent (MDV), (f) total depth at vent including fins (or "fin depth at length") (FDV), (g) eye diameter (ED), (h) mandible length (ML), (i) head length (HL), (j) head depth (HD), (k) PCA component 1. Data are means ± 1 SE. Asterisk (*) denotes a significant difference from the control treatment

3.4.2 | Escape performance

A greater proportion of kingfish reared at 25°C reacted to the startle stimulus compared with those reared at 21°C ($z = 5.075$, $p < 0.001$), but pCO_2 ($z = 1.004$, $p = 0.3154$) had no effect on the proportion of kingfish that reacted to the startle stimulus (Figure 8a). For those fish that did respond to the stimulus, the direction turned, whether away from or towards the stimulus was not influenced by temperature ($z = -0.302$, $p = 0.7924$) or pCO_2 ($z = -0.195$, $p = 0.8456$) (Figure 8b). For responders, the distance moved during escape was affected by fish mass ($t_{73} = 4.459$, $p < 0.001$) and pCO_2 ($t_{20} = -2.212$, $p = 0.0387$), but not temperature ($t_{20} = -0.541$,

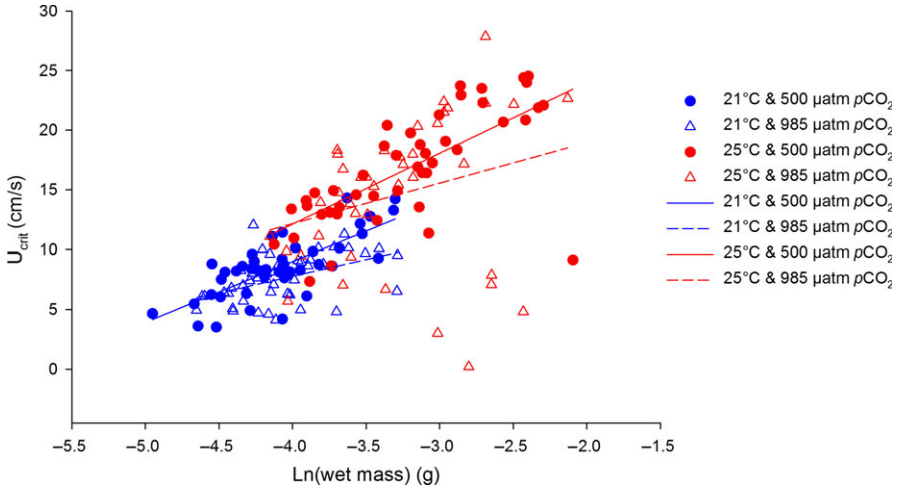

FIGURE 7 Swimming performance, measured by U_{crit} on fish mass

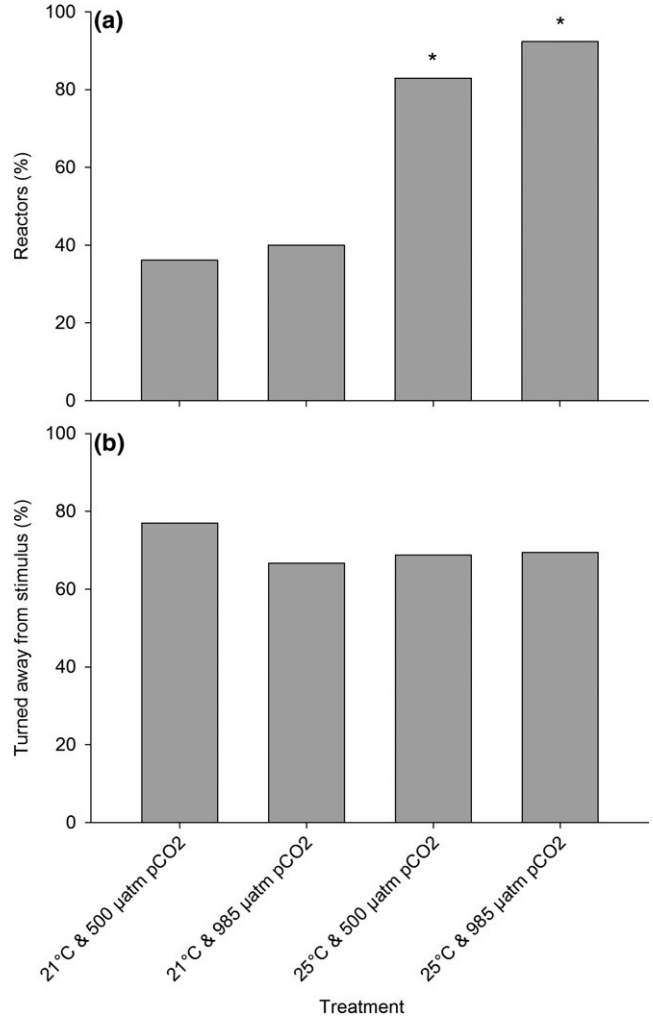

FIGURE 8 Escape performance, (a) percentage of responders and (b) for individuals that responded, the percentage of those that turned away from the stimulus. Asterisk (*) denotes a significant difference from the control treatment

$p = 0.5947$). Larger fish moved further, and fish reared in control pCO_2 conditions moved further than those reared in elevated pCO_2 (Figure 9a). Average speed was affected by fish mass ($t_{73} = 4.477$, $p < 0.001$) and pCO_2 ($t_{20} = -2.225$, $p = 0.0387$), but not temperature ($t_{20} = -0.575$, $p = 0.5719$). Maximum speed during escape responses was influenced by fish mass (t_{73}=4.497, $p < 0.001$) and temperature ($t_{20} = -2.121$, $p = 0.0466$), but not pCO_2 ($t_{20} = -1.540$, $p = 0.1393$). Kingfish reared at 21°C had a comparatively greater maximum response speed for their body weight than those reared at 25°C (Figure 9b). Latency in response to the stimulus was affected by the distance of the fish from the stimulus ($t_{73} = 8.240$, $p < 0.001$) and temperature ($t_{20} = -2.294$, $p = 0.0327$), but not pCO_2 ($t_{20} = 0.054$, $p = 0.957$). Fish reared at 21°C had a longer latency than those reared at 25°C (Figure 9c).

4 | DISCUSSION

While an increasing number of studies have investigated the effects of multiple global change stressors on marine fish (Flynn, Bjelde, Miller, & Todgham, 2015; Gobler, Merlo, Morrell, & Griffith, 2018; Pimentel et al., 2016), little is known about the independent and combined effects of ocean acidification and warming on large pelagic fishes. Our results show that elevated temperature has a greater effect than ocean acidification conditions on survival, growth, development and swimming performance of yellowtail kingfish during their early life history. Larvae and juveniles in the elevated temperature treatments (25°C) had lower survivorship, but faster growth and development than fish reared at the average summer temperature for the study population (21°C). Elevated temperature also increased U_{crit} swimming performance and increased the proportion of individuals that responded to a startle stimulus, reduced the latency to respond, and increased the maximum escape speed. By contrast, elevated pCO_2 did not affect survivorship, and while it increased size at 1 dph, there was no effect of elevated pCO_2 on size or development at 11 and 21 dph. However, elevated pCO_2 had a negative effect on swimming performance. Contrary to elevated temperature, elevated pCO_2 reduced U_{crit} swimming performance and reduced the distance moved and average speed in response to a startle stimulus. Therefore, while temperature had the greatest impact on key life history

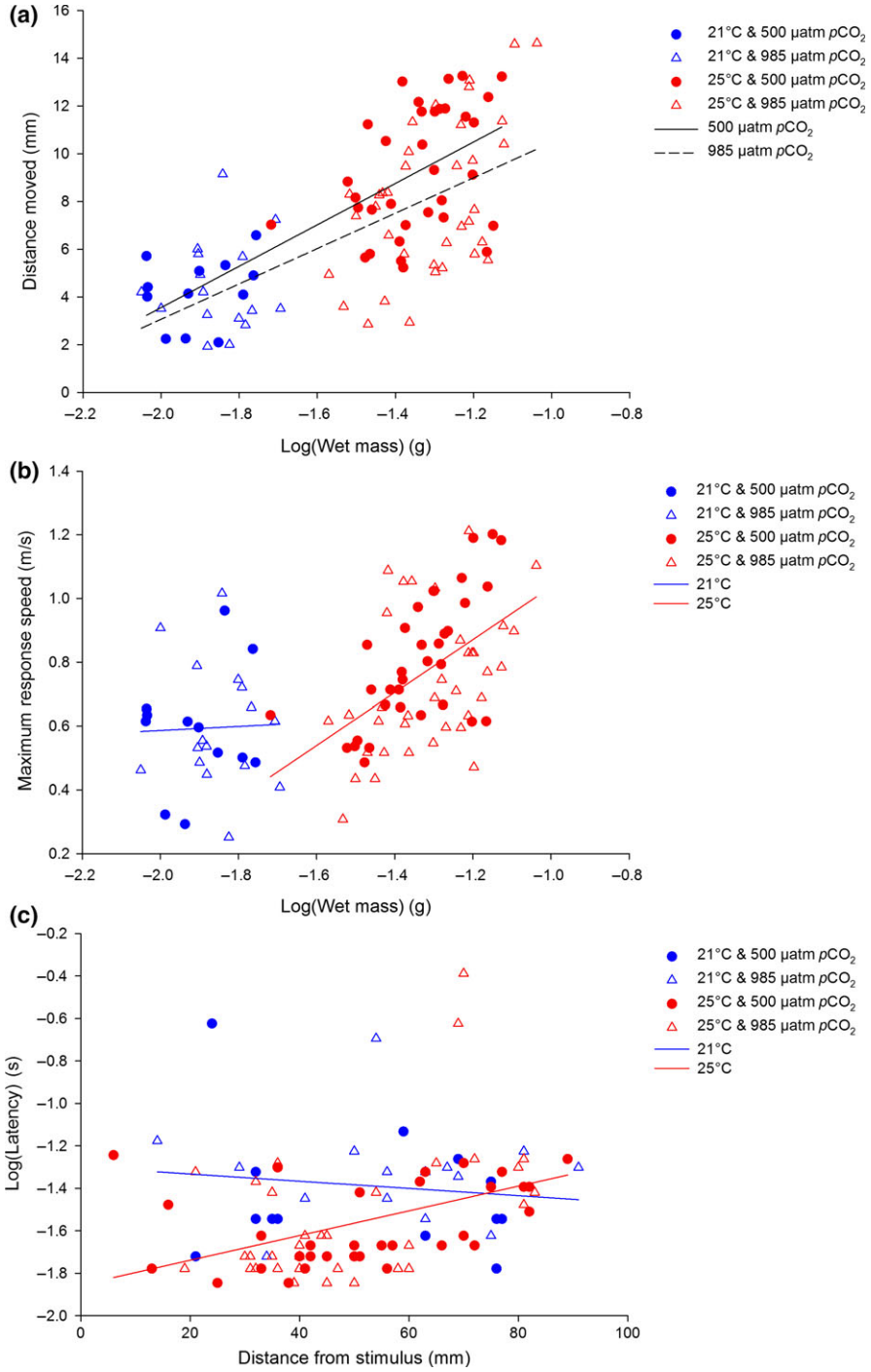

FIGURE 9 Escape performance traits, (a) distance moved, (b) maximum speed, (c) latency

traits such as survival and growth, elevated pCO_2 can still affect individual performance. Overall, elevated pCO_2 tended to act antagonistically to the effects of elevated temperature and pCO_2, with no evidence for additive or interactive effects.

Larval and juvenile kingfish reared at 25°C had reduced survivorship, but faster growth and development compared with fish reared at 21°C. A similar pattern of reduced survival at 25°C has been reported for a population of yellowtail kingfish from China (Yu et al., 2017), suggesting that 25°C is above the optimal temperature for this species. This is also consistent with a peak distribution of adult kingfish at 22.5°C in Australian waters and a strong seasonal shift in distribution to avoid warmer temperatures (Brodie et al., 2015). Larval and juvenile mortality are important drivers of population dynamics in populations of pelagic fishes (Chambers & Trippel, 1997; Houde, 1989) and even small changes in the mortality rate can affect recruitment into the adult population. An increase of 4°C compared with the average summer temperature for the study population resulted in an approximately twofold reduction in survivorship. Such a reduction in survival could have significant ramifications for the population were it to occur in nature. Importantly, 25°C is already within 2°C of the maximum

ocean temperatures that can be experienced during summer in northern New Zealand, even if the warming effects of climate change are not as strong here as they are in other marine systems around the world (Shears & Bowen, 2017). This suggests that the recruitment dynamics of the study population are already influenced by temperature variation within and among years.

An important caveat to our observation that larval and juvenile kingfish had reduced survivorship, but increased rates of growth and development at 25°C, is that the fish in our experiment had a continuous supply of high density food. Food supply is much more unreliable and patchy in nature. Consequently, survivorship at 25°C could be even lower in nature if individuals are unable to meet the energetic demands of faster growth and development in a warmer environment (Llopiz et al., 2014; Pepin, 1991). However, faster growing larvae may also be more efficient at foraging and escaping predators (Chambers & Trippel, 1997; Sogard, 1997), which is consistent with our observations of increased U_{crit} and burst swimming performance at the higher temperature. Therefore, the effect of higher temperatures on mortality rates in nature will likely depend on the distribution of predators and prey, which are also likely to be affected by warming (Llopiz et al., 2014). Whether the reduced survivorship of kingfish exposed to higher temperature is also related to the selection of certain genotypes is unknown, but a potentially important future investigation as it would provide insight about the adaptive potential of kingfish populations to warming.

In contrast to temperature, there was no effect of elevated pCO_2 on survival, growth or development of larval and juvenile yellowtail kingfish, apart from an increase in the length of larvae at 1 dph. End of century pCO_2 levels, similar to those used in the current study, have been found to increase mortality of larval Atlantic silverside (Baumann, Talmage, & Gobler, 2012), Atlantic cod (Stiasny et al., 2016), gilthead seabream and meagre (Pimentel et al., 2016). In cod, elevated pCO_2 caused the mortality rate to double, which was projected to reduce recruitment to the adult population to just 8–24% of current-day recruitment in two separate populations (Stiasny et al., 2016). However, other species appear much more tolerant to the direct lethal effect of elevated pCO_2, with no effect on larval survivorship reported in Baltic cod (Frommel, Schubert, Piatkowski, & Clemmesen, 2013), Atlantic herring (Franke & Clemmesen, 2011) and walleye pollock (Hurst, Fernandez, & Mathis, 2013). Survivorship even increased at 1,000 μatm pCO_2 in European sea bass (Pope et al., 2014). In winter flounder, there was a strong effect of elevated pCO_2 (≥1,800 μatm) on prehatching survival, but no effect on survivorship after hatching (Chambers et al., 2014). While increased larval mortality was reported in yellowfin tuna larvae reared at very high pCO_2 levels (>4,000 μatm), there was no effect of a more moderate pCO_2 level (2,100 μatm) on larval survivorship in either yellowfin tuna (Bromhead et al., 2015) or cobia (Bignami et al., 2013), the only other large pelagic species for which larval mortality rates have been estimated. In combination with our results here, these findings suggest that near-future pCO_2 levels (≤1,000 μatm) are unlikely to have direct lethal effects on pelagic fishes, probably because they are physiologically adapted to dealing with high levels of metabolic CO_2 due to their active lifestyle.

The effects of elevated pCO_2 on fish early life history growth and development are highly variable. Elevated pCO_2 has been observed to reduce (Baumann et al., 2012; Bignami et al., 2017; Frommel et al., 2016; Pimentel et al., 2016), increase (Bignami et al., 2014; Chambers et al., 2014; Munday, Donelson et al., 2009; Pimentel et al., 2016; Pope et al., 2014) or have no effect (Bignami et al., 2013; Frommel et al., 2013; Hurst et al., 2013; Munday, Gagliano, Donelson, Dixson, & Thorrold, 2011) on larval and juvenile growth in a variety of species. Here, pCO_2 had no effect on growth or morphological development, except at 1 dph, when fish were longer (SL, TL, BL) at elevated pCO_2 compared with control pCO_2. However, our results show that larger size in newly hatched fish is not necessarily maintained at older life stage as there was no difference in size of fish between pCO_2 treatments at 11 or 21 dph. Furthermore, elevated pCO_2 did not influence the number of fish that had entered flexion at 11 dph. Similarly, Bignami et al. (2014) found that dolphinfish were longer at 5 dph under elevated pCO_2 compared with current-day controls, yet this did not affect the number of individuals entering flexion. Why newly hatched fish are longer under elevated pCO_2 is unclear, but it indicates that the patterns of energy allocation in the very early life history can be altered by elevated pCO_2 (Heuer & Grosell, 2014; Pimentel et al., 2014; Strobel, Leo, Portner, & Mark, 2013).

The only previous study on the effects of ocean acidification on yellowtail kingfish used a similar elevated pCO_2 level to this study, 880 μatm pCO_2, and also a higher pCO_2 level of 1,700 μatm to determine the effects of ocean acidification on kingfish survival and growth during the prefeeding stage to 3 dph (Munday, Watson et al., 2016). As observed here, the earlier study found no effect of elevated pCO_2 on survival, and although oil globule size was reduced by the highest pCO_2 level (1,700 μatm), it was not affected by 880 μatm pCO_2 level at 3 dph. These results are similar to the current study to 1 dph. The previously reported effect of elevated pCO_2 on growth of unfed larvae at 6 dph (Munday, Watson et al., 2016) was not present in fed larvae or juveniles at 11 or 21 dph in the current study, indicating that although elevated pCO_2 might increase energetic demands during early life history, this can be countered when food is available ad libitum. However, food is not always abundant in nature, and consequently, there could still potentially be effects of elevated pCO_2 on larval growth if they are unable to acquire sufficient food resources to offset the additional costs of living in a high pCO_2 environment. Indeed, Bignami et al. (2017) observed reduced starvation resistance in larval cobia at 1,700 μatm pCO_2, indicating that increased energetic demands of living in a high CO_2 environment could potentially affect survival if food availability is patchy in nature.

In contrast to elevated pCO_2, higher temperature had very clear and highly significant effects on growth and morphological development. At 1 dph, elevated temperature reduced body size (SL, TL, BL) and energy reserves (YL, YA, OGD) but increased mandible length (ML). However, differences between 21 and 25°C at 1 dph may primarily be related to the extra time that fish in the 21°C treatment took to hatch, which was 1 day more than at 25°C. By 11 dph, fish at 25°C were heavier and longer than fish at 21°C

and differed in the majority of morphological traits. Furthermore, a greater proportion of individuals had entered flexion at 25°C, demonstrating that they were more developmentally advanced than fish at 21°C. The differences in growth and development were even more prominent at 21 dph, where all morphological measures differed between the temperature treatments and where the 25°C fish were visibly much more advanced than the 21°C fish. These results are consistent with the generally positive effects of temperature on the growth and development of fish early life history stages (Munday, Leis et al., 2009; Pepin, 1991; Rombough, 1997) although there are exceptions.

Kingfish are powerful swimmers and had better swimming performance at 25°C, measured by U_{crit}, than their 21°C counterparts. This is not surprising because swimming performance can increase in warmer water due to the combined effects of reduced viscosity and increased muscle efficiency (Fuiman & Batty, 1997; Wieser & Kaufmann, 1998). By contrast, we found that elevated pCO_2 reduced U_{crit} in 21 dph juvenile kingfish. Similarly, Bignami et al. (2014) found a trend towards decreasing U_{crit} with increasing pCO_2 in 20 dph dolphinfish, although there was no effect of elevated CO_2 on U_{crit} in cobia (Bignami et al., 2017). Reduced U_{crit} of kingfish at elevated pCO_2 could either be due to reduced physiological performance, such as reduced aerobic capacity, or a reduced motivation to swim. Indeed, a combination of both factors may occur since elevated pCO_2 has been observed to reduce oxygen consumption rate in larval dolphinfish (Pimentel et al., 2014) and can also affect a wide range of behaviours in larval fishes (Nagelkerken & Munday, 2016). Reduced U_{crit} could be ecologically important, particularly for juveniles of pelagic fish where continuous swimming is an essential mode of life. Reduced swimming performance could affect foraging ability, dispersal and vulnerability to predators (Munday, Leis et al., 2009). In larval seabream and meagre, elevated pCO_2 has been found to reduce swimming activity and cause reduced attacks on prey and capture success (Pimentel et al., 2016). In the current study, the reduction in swimming performance with elevated pCO_2 appeared to be driven by a greater incidence of low-performing individuals at elevated pCO_2, whereas other individuals reared at elevated pCO_2 maintained a U_{crit} equivalent to control fish. Growth rate may also play a role in swimming performance at elevated pCO_2, since larger individuals appeared more affected by elevated pCO_2. If variation in performance has a genetic basis, then selection for greater swimming speed might enable U_{crit} to be maintained with rising pCO_2 (Sunday et al., 2014).

Enhanced escape performance was observed at 25°C, likely due to the advanced developmental stage of these individuals. More individuals reacted to the startle stimulus at 25°C compared with 21°C, although there was no difference in the proportion of individuals that turned away from rather than towards the stimulus. Elevated pCO_2 had no effect on the proportion of individuals that reacted to the startle stimulus or the direction turned; however, it reduced the distance moved and average speed in response to the startle stimulus. Conversely, temperature did not affect the distance moved, but increased the maximum speed and reduced latency, potentially linked to the advanced developmental stage of fish at 25°C, even when the greater size of the fish at 25°C was accounted for. Similar results have been found recently in coral reef fish, where escape responses in predator–prey interactions were affected more by elevated temperature than elevated pCO_2 (Allan, Domenici, Watson, Munday, & McCormick, 2017). These results show that elevated temperature and pCO_2 can interact in complex ways to alter the escape responses of larval fishes.

Elevated temperature and pCO_2 had both prominent and subtle effects that may affect the early life history survivorship, growth and swimming performance of this large pelagic fish. The effects of elevated temperature and pCO_2 appear to function antagonistically, as we found no evidence for interactive effects of these drivers. Overall, our results suggest that elevated temperature has a greater effect on larval and juvenile performance of kingfish than the corresponding elevated pCO_2 levels. As warming occurs, it is likely that kingfish populations will shift their distributions poleward to avoid higher temperatures and maintain their preferred temperature range, and this may confer fitness benefits to their larvae. Poleward range shifts in response to rising temperatures have already been documented in many marine species (Poloczanska et al., 2013) and are likely to be especially prevalent for large mobile species, such as pelagic fishes. By contrast, marine species will not be able to escape rising pCO_2 levels through migration. For kingfish populations, this means that even with southward migration to avoid higher temperatures, there may still be effects on swimming performance caused by higher pCO_2 levels, unless populations can adapt to this stressor. Importantly, we observed substantial variation among individuals in their swimming performance at elevated pCO_2 and this could be the basis for adaptive responses (Sunday et al., 2014). However, further studies are required to test if variation in swimming performance at elevated pCO_2 is heritable, and thus could adapt. Furthermore, there could be genetic correlations with other climate change drivers, or effects of fishing, that could constrain the pace of adaptation (Munday, Warner, Monro, Pandolfi, & Marshall, 2013). Therefore, future assessments of evolutionary potential to climate change in kingfish should consider responses to multiple environmental drivers. Finally, our results will be useful in parameterising ocean-biophysical population-dynamics models in order to test the sensitivity of fish populations to future warming and acidification and how these environmental drivers may affect the distribution and abundance of large pelagic fishes.

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