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# Consequences of temperature and temperature variability on swimming activity, group structure, and predation of endangered delta smelt

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## Abstract

1. The effects of water temperature on individual and group movement behaviour in prey fish can affect ecological interactions such as competition and predation, but how variability in temperature influence fish behaviour is less understood. Of particular concern is how increased warming in tidally fluctuating estuaries may impact the native and endangered delta smelt (*Hypomesus transpacificus*, Osmeridae).

2. To help address this issue, we tested the effects of increased water temperature (fluctuating [17–21°C] and warm [21°C] acclimated treatments) on juvenile delta smelt individual and group behaviour, response to chemical alarm and predator cues, as well as capacity to evade predation. In addition, predation of delta smelt was tested in the presence of a dominant invasive competitor, Mississippi silversides (*Menidia beryllina*, Atherinopsidae), as well as comparative predation mortality on Mississippi silversides when isolated.

3. After 7 days of increased temperature treatments, delta smelt in the warm treatment increased swimming velocity, decreased turning angle, and altered group structure with larger inter-individual distances compared to fish in the control (17°C) and fluctuating temperature treatments. Following conspecific and predator chemical alarm cues, delta smelt showed anti-predator responses. Control and fluctuating treatment fish responded to conspecific cues with increased swimming speeds, decreased inter-individual distances and near-neighbour distances, and, after 15 min, fish recovered back to baseline behaviours. In contrast, fish in the warm treatment had not recovered after 15 min, and swimming speeds were maintained at roughly 25 cm/s, close to maximum capabilities. Fish in control and fluctuating treatments showed minimal responses to predator cues, whereas delta smelt exposed to warm conditions significantly increased swimming speeds and decreased turning angle.

4. Predation of delta smelt by largemouth bass (*Micropterus salmoides*, Centrarchidae) was greatest under the warm treatment, correlating with altered behaviours of

delta smelt; however, predation of Mississippi silversides was greater than delta smelt, independent of temperature.

5. This study provides novel insight into the group behaviour of delta smelt, their response to predation, and how prolonged exposure to elevated temperature may induce negative individual and group behaviours causing alterations in predator–prey dynamics. This work highlights the importance of testing ecologically realistic temperature fluctuations in experiments as delta smelt had significantly altered responses to elevated temperature, dependent on variability of warming.

## 1 | INTRODUCTION

Temperature can influence ecological patterns of fish populations by altering habitat selection, range distributions, and ecosystem functioning (Pörtner & Peck, 2010). Changing population patterns are driven largely by temperature effects on individual physiology and behaviour (Killen, Marras, Metcalfe, McKenzie, & Domenici, 2013; Peck, Clark, Morley, Massey, & Rossetti, 2009), including growth rate, metabolism, reproduction, and swimming activity (Brett & Groves, 1979). For animals that live in groups, individual movement behaviour (determined by integrated physiological signals) scales up to affect group structure, such as shoaling and social behaviour, because individuals tend to update their spatial position in response to that of near-neighbours (Cooper, Adriaenssens, & Killen, 2018; Ward, Krause, & Sumpter, 2012). This process represents the spread of information between individuals, and is essential in establishing the biotic interactions of group-living species within a community (Berdahl, Torney, Ioannou, Faria, & Couzin, 2013). The outcomes of biotic interactions such as inter- and intra-specific competition for space and food resources as well as predator–prey relationships ultimately determine survivorship of the group, and the distribution and abundance of the population (Ward & Webster, 2016).

Many of the benefits individuals receive through shoaling, such as increased foraging efficiency (Clark & Mangel, 1986; Morgan, 1988; Pitcher, 1986; Pitcher, Magurran, & Winfield, 1982), reduced predation risk (Ioannou, Bartumeus, Krause, & Ruxton, 2011), and group decision making (Ward et al., 2012) rely on the group remaining cohesive. As inter-individual interactions within fish shoals are strongly determined by energetic requirements (Hansen, Schaerf, Krause, & Ward, 2016), temperature is an important factor to consider when understanding the structure and movement behaviour of fish shoals. Bartolini, Butail, and Porfiri (2015) found that increasing temperature increased swimming activity in *Devario auquipinnatus* and that this correlated positively with social behaviour, with more active fish tending to have larger nearest-neighbour distances (NNDs) and lower polarisation (i.e. similar orientation). Temperature-driven reductions in cohesiveness of the group can subsequently affect ecological interactions, leading to alterations in competition and susceptibility to predation (Malavasi et al., 2013; Weetman, Atkinson, & Chubb, 1998). Reductions in group cohesion can dilute the social information transfer acquired by individuals via altered visual and olfactory information. The reduced transfer of social information may make individuals more susceptible to predation or competition for resources (Ioannou, Couzin, James, Croft, & Krause, 2011). While several studies have found swimming speed, activity (Green & Fisher, 2004; Peck, Buckley, & Bengtson, 2006; Pritchard, Lawrence, Butlin, & Krause, 2001), and inter-individual distances (Hurst, 2007) also increase with temperature, others have found contrasting results (Colchen, Teletchea, Fontaine, & Pasquet, 2017; Weetman et al., 1998). Activity often will increase with temperature but then decrease after it reaches the upper thermal limit of physiological performance (Claireaux, Couturier, & Groison, 2006; Claireaux & Lefrancois, 2007; Colchen et al., 2017). Temperature universally affects metabolic rate of fishes, but it does not do so uniformly across populations or species, as responses to temperature are dependent on specific thermal tolerances and plasticity (Fangue, Hofmeister, & Schulte, 2006). Populations can also behaviourally respond differently to temperature changes due to differences in their local environment, such as the availability of food, shelter, mates and predation threat (Weetman, Atkinson, & Chubb, 1999).

While most of the studies characterising the effects of temperature on fish behaviours test realistic environmentally stressful temperatures (Bartolini et al., 2015), they do not always fluctuate temperature in a natural way. More commonly, a consistent and homogenous temperature is maintained throughout the experiment. In nature, temperature varies throughout the day due to factors including changing air temperature, tides, water depth, and human activities. Given that the degree of variability in water temperature has been shown to affect individual physiological responses (Todgham, Iwama, & Schulte, 2006), it is important to take this aspect of environmental complexity into consideration when testing for predicted responses of animals to warming. For example, metabolic rates of Atlantic salmon parr (*Salmo salar*; Salmonidae) acclimated to fluctuating temperature conditions (with a mean of 20°C) were 25–32% higher than parr held stable at 20°C (Beauregard, Enders, & Boisclair, 2013). In contrast to salmon, juvenile green sturgeon (*Acipenser*

*medirostris*; Acipenseridae) acclimated to fluctuating temperature conditions (narrow or widely variable) demonstrated no change in upper temperature tolerance. Furthermore, swimming performance was insensitive to a wide range of temperatures, suggesting that sturgeon were responding to the mean temperatures and not the daily peaks (Rodgers, Cocherell, Nguyen, Todgham, & Fangue, 2018). Understanding species-specific responses to increased temperatures as experienced in nature may better inform ecological responses.

To date, there have been few studies describing the behaviour of critically endangered delta smelt (*Hypomesus transpacificus*), a planktivorous pelagic fish endemic to the San Francisco Estuary (SFE) in California (Moyle, Herbold, Stevens, & Miller, 1992). Delta smelt were once relatively abundant in the SFE until the 1980s, after which the population has rapidly declined to near extinction (Hobbs, Moyle, Fangue, & Connon, 2017; Sommer et al., 2007). Delta smelt are relatively sensitive to increases in water temperature, as demonstrated by their range compression (Brown et al., 2016), and elevated physiological costs to increased water temperature (Jeffries et al., 2016; Komoroske, Connon, Jeffries, & Fangue, 2015); however, less is known about the influence of elevated temperature on their behaviour and temperature sensitivity of anti-predator behaviour (similar to physiology) that may increase vulnerability to predation. Previous behaviour studies demonstrate delta smelt maximum swimming speed (Ucrit; 28 ± 4 cm/s) was independent of temperature acclimation (Swanson, Young, & Cech, 1998) and exhibited three types of swimming modalities: (1) stroke and glide, (2) continuous, and (3) burst and glide (Young, Swanson, & Cech, 2004), which may correlate to predation susceptibility. Providing a better understanding of effects of elevated water temperature on delta smelt behaviour and susceptibility to predation can provide needed information for restoration habitat requirements, thereby providing more information for decisions surrounding water management for fish conservation strategies and economic uses in California.

The overall goal of this study was to characterise individual and group movement behaviour of delta smelt and determine if high temperature increases predation vulnerability. Testable study questions included: (1) what are basic individual movement behaviours of delta smelt and how does elevated temperature and variability of warming alter these behaviours? (2) do delta smelt exhibit group behaviours and how does elevated temperature alter group structure? (3) how do delta smelt respond to predation cues (conspecific alarm and predator water cues), and how does elevated temperature interfere with these anti-predator responses? and (4) how does increased temperature affect predation mortality rates by largemouth bass (*Micropterus salmoides*)? Because delta smelt live in habitats with a high abundance of non-native species (Mahardja, Farruggia, Schreier, & Sommer, 2017) we also tested how predation of delta smelt may be altered if they are in the presence of Mississippi silversides (*Menidia beryllina*), a non-native forage species in mixed shoals. Lastly, we determined predation morality on the non-native Mississippi silversides when isolated. Mississippi silversides are often caught in delta smelt habitats (Enhanced Delta Smelt Monitoring

[EDSM-USFWS], 2019; Mahardja, Conrad, Lusher, & Schreier, 2016; Schreier, Baerwald, Conrad, Schumer, & May, 2016) and may compete for similar resources; therefore, Mississippi silversides are likely to be susceptible to similar predation pressures as delta smelt. The present study tested chronic and acute exposures to 21°C, a moderate thermal challenge well within tolerance limits (Davis et al., 2019; Jeffries et al., 2016; Komoroske et al., 2014) of fishes that will provide relevant information to current and future habitat conditions. Given that many of the species of conservation concern inhabit environments with fluctuating environmental tidal conditions, factoring in this level of environmental complexity (i.e. fluctuating conditions) into conservation physiology and behaviour research is critical for realistically projecting how anthropogenic change will affect species interactions that form the foundation of assemblage structure.

## 2 | METHODS

### 2.1 | Fish species and maintenance

Juvenile delta smelt were acquired from University of California Davis Fish Conservation and Culture Laboratory (FCCL) in Bryon, CA in late August 2017. Delta smelt were F10 generation, and FCCL has standard procedures for maintaining genetic diversity (Lindberg et al., 2013). It should be noted that recent evidence indicates that domestication is taking place in hatchery delta smelt as demonstrated by differential survival and genetics across level of hatchery ancestry (Finger et al., 2018); however, due to dire wild population numbers the FCCL is the only source of fish for experimental purposes. Physiological and behavioural effects of domestication are uncertain but should be considered in the interpretation of study results. Delta smelt were transferred from FCCL to the Putah Creek Aquaculture Facility in Davis, CA at 159 days post-hatch (5.9 ± 0.4 cm standard length, 1.4 ± 0.4 g; mean ± *SD*). Juvenile Mississippi silversides (estimated F3 generation) were transported from Aquatic BioSystems at 130 days post-hatch (3.6 ± 0.3 cm fork length, 0.4 ± 0.1 g, mean ± *SD*) in August 2017. Delta smelt and Mississippi silversides were acclimated to the laboratory conditions of 16.5–17°C and 0.4 ppt for a minimum of 2 weeks in four black replicate tanks (533 L) for each species prior to the experiment starting the beginning of September 2017. Each tank was on a flow-through system with roughly 2 L/min water exchange and only a subtle directional flow. Fish were fed a mix of BioVita starter (#1 crumble, Bio-Oregon) and Hikari plankton (semi-float, Kyorin Co., Ltd.) at 3% body weight per day (calculated from the average wet mass for each species). Largemouth bass predators were donated from The Fishery in Galt, CA in 2016 and held in the laboratory at 17–18°C and 0.4 ppt for 6 months prior to the experiment (28.9 ± 2 cm total length, 383.3 ± 92 g). Largemouth bass were fed a pellet diet (2 mm, 1% body weight per day, Skretting) until 1 week prior to the experimental trial. Twenty-four bass were moved to a pre-exposure tank and fed fathead minnows (*Pimephales promelas*; Cyprinidae; 2 fish/bass) every other day until being moved to experimental tanks, where they continued being fed live food for 1 week and experienced the same temperature treatments and

acclimation time-course as prey species (described in the next section). Fish care and experimental protocols were approved by the University of California Davis Institutional Animal Care and Use Committee (protocol no. 19372).

## 2.2 | Temperature treatments

To assess the effects of variable versus stable increased water temperature exposures on delta smelt behaviour and determine if warming increased susceptibility to predation, three treatments were used, two with a peak temperature of 21°C (see Figure 1). Temperature for treatment 1 (*control*) was held at roughly 17.1 ± 0.8 (mean ± *SD*) for the entire 7-day exposure. For treatment 2 (*fluctuating),* water temperature increased to 20°C and decreased to 18°C on day 1, after which temperature increased from 18 to 21°C daily at a rate of 1°C per 2 hr for the remainder of the experimental time course (6 days), simulating a natural warming–cooling cycle (Figure S1). Daily temperature ramping to 19°C started at 10:00, to 20°C at 12:00, and hit a peak 21°C from 14:00 to 16:00, and began to decrease again after 16:00 towards 18°C (at 1°C per 2 hr). Ambient temperature of the fluctuating treatment ranged between 17 and 18°C due to cooling of the system during the night, driving the set temperature of 18°C. Treatment 3 (*warm*) water temperature was increased to 21°C on day 1 at a rate of 1°C per 2 hr and held stable at 21°C for 7 days of warm-water treatment (21.4 ± 0.4, mean ± *SD*). Tank temperatures were checked twice daily with a hand-held thermocouple,

and a minimum of 2 replicate tanks per treatment were monitored every 5 min throughout the experiment using submerged HOBO data loggers (Onset) suspended in the tank outflow standpipes (see Figure S2 for examples of recorded temperature treatments). All experimental tanks were held at the Center for Aquatic Biology and Aquaculture (CABA) at the University of California Davis and consisted of flow-through water sourced from a non-chlorinated agricultural well designated to the CABA facility (with adequate control of nitrates, pH [7.8–8.2] and conductivity [750–850 micromhos]). Slight fluctuations in daily temperatures (*c.* 0.5–1°C) for the control and warm treatments seen in Figure 1 and Figure S2 were an artefact of natural temperature variability of the water source used during experimentation. Tank water exchange was 2.4 L/min and a mesh screen diffused water inputs, eliminating any directional water cues and disturbance to the water surface.

The study included three species assemblages: (1) delta smelt (*n* = 12 individuals/tank); (2) Mississippi silverside (*n* = 12/tank); and (3) mixed species shoals (*n* = 6 delta smelt + *n* = 6 Mississippi silverside [*n* = 12 total/tank])—each assemblage was introduced into 6 of 18 different individual circular grey tanks (103.6 L, 93 cm in diameter, 15.25 cm water depth) all within a single aquaculture building (see Figure S3 for conceptual diagram) at CABA. Pilot observations of shoal density and behaviour are detailed in the Methods section of the Supporting Information. After introduction of fish to tanks (day 0) fish were given the day to recover from handling before temperature treatments (as described above) and behavioural monitoring began
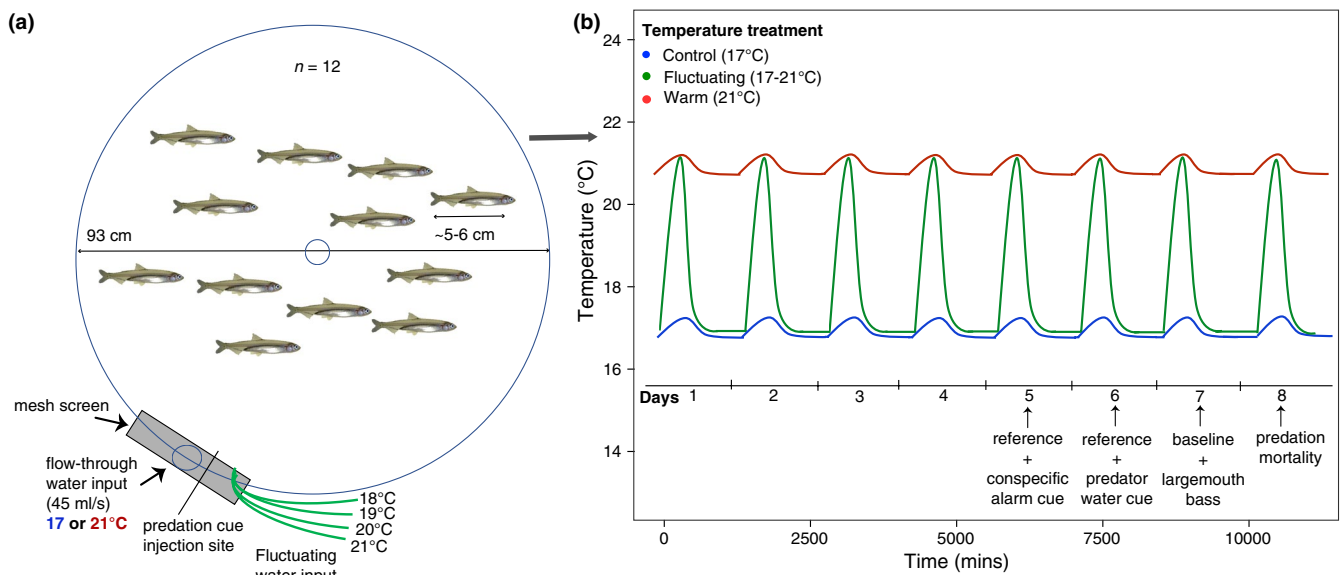


**FIGURE 1** Behaviour tank arenas for delta smelt and three experimental temperature treatments. Delta smelt (*n* = 12) were held in flow-through arenas (a) for the entire experiment (8 days) where temperatures and predation cues were introduced and behaviour responses were recorded and measured across time. The mesh screen diffused water inputs eliminating any directional water cues. Several temperature traces are shown (b) representing a control temperature treatment (17°C, blue scale), a fluctuating warm treatment (green scale), where temperatures increased from *c.* 17 to 21°C and then decreased back to *c.* 17°C daily, and a warm-acclimation treatment (red scale), where temperature was increased to 21°C the first day and held at 21°C for the remainder of the experiment. Throughout the temperature treatments, behavioural assessments were conducted including the response to a conspecific alarm cue (day 5), response to a predator water cue (day 6), as well as actual predation by largemouth bass and mortality counts (days 7–8). Before each cue, a collection of *reference* behaviours were recorded, whereas before the last predator event on day 7 an overall *baseline* of behaviours was recorded to determine the influence of a week of increased temperature. See Figure S2 for measured experimental temperatures

(day 1) and continued for 8 days. Of the six tanks for a particular species assemblage, tanks were divided into two replicates for each of the three temperature regimes (i.e. control, fluctuating, warm). The experiment was repeated 4 times in total, resulting in eight replicate tanks for each treatment by species combination. Each week, control and warm treatment tanks were randomised, while fluctuating tanks remained in place due to fixed experimental set-up limitations. Species assemblages were also randomised within each treatment (including the fluctuating) each week. During each experimental week, largemouth bass from the pre-exposure tank (i.e. a live-feeding tank outside the behaviour trial building) were transferred to three separate experimental tanks (n = 6/tank), each reflective of the temperature treatments (control, fluctuating, warm). Not randomising the location of the fluctuating treatment is not ideal experimentally; however, it should be noted that comparative behaviour analysis of delta smelt under the control and fluctuating treatments (as described later in this study) showed no differences under baseline conditions and in response to cues suggesting the lack of randomisation of the fluctuating treatment probably had no effect.

Each tank was affixed with a video camera overhead (QSEE 1080 p with night vision) that was connected to one of three DVR systems (QSEE, 8-channel, 2 TB, Heritage security systems) and monitored for real-time observations. Each tank was surrounded by a white shower curtain, eliminating external visual disturbance while also creating more consistent lighting (lux = 275 ± 70 lumen/m$^2$ [mean ± SD]). Daily, each tank was siphoned for food and faeces prior to 08:00, allowing for undisturbed tanks prior to video recording. At 09:30, 12:30, and 15:30 delta smelt, mixed species shoals, and Mississippi silversides were fed 3% body weight/day of Hikari plankton (0.2 g [delta smelt and mixed shoals], and 0.08 g per feeding [Mississippi silversides]). On days 5 and 6, the last feeding occurred after the cue trials at 16:30. Food was delivered through a small opening in the curtain just below the camera. Largemouth bass were fed 12 fathead minnows (2 prey/bass) at days 0, 2 and 4 until satiation. Leftover fatheads not eaten were removed the following morning.

## 2.3 | Baseline behaviour

To establish a collective baseline of delta smelt individual and group behaviour following a week exposure to temperature treatments, 15 min of video was recorded after 7 days. Pilot analysis of behaviour across time demonstrated similar behaviour across a 30-min period and therefore 15- and 20-min clips for analysis were selected. From the video recordings, individual movement variables (average velocity and turning angle) were calculated, as well as group structure variables (average inter-individual distance [IID] and NND [see below Section 3.1 for details]). All recordings took place at 15:00, when temperature was at the maximum in the fluctuating warm treatment.

## 2.4 | Behavioural responses to predation cues

To characterise anti-predator responses and the influence of temperature, following an initial recording of reference behaviour at 15:00 across each temperature treatment, a variety of experimental treatments were presented individually to each tank after 5 and 6 days (see Figure 1 for experimental timeline). These treatments included a conspecific alarm cue (day 5) and a predator water cue (day 6). All anti-predator trials were conducted between 15:20 and 16:20. It should be noted that reference behaviour recorded prior to the anti-predation cues (days 5 and 6) showed no difference to the baseline behaviour recorded after 7 days of exposures.

Conspecific alarm cues were prepared as in Davis et al. (2018), with slight modifications. Delta smelt cues were prepared by dorso-ventrally scoring the skin of sacrificed, non-experimental fish 5 times (not piercing any organs), and rinsing those scores with 10 ml of water three times collecting the cue in a beaker (30 ml). The same protocol was repeated on the other side of the fish collecting a total of 60 ml of alarm cue from one sacrificed fish for each tank. To avoid disturbance, cues were injected through airline tubing that was affixed 1 cm below the tank water level in each individual tank. Using a two-outlet syringe coupler, 60 ml water was first drawn from the tank priming the airline tubing, then 60 ml alarm cue was pushed into the tubing and tank, and lastly 60 ml of tank water was pushed into the tubing ensuring all of the cue entered the tank and no air bubbles were introduced that could alarm the fish. Video of the fish (and shoal) behaviour across all temperature treatments was then recorded for a 20-min period and compared to the 20 min of reference behaviour recorded before the cue injection. This protocol generated a 40-min total behaviour response curve to determine if delta smelt exhibited anti-predator responses, and if so, to determine if recovery from responses was evident over a 20-min period. Compared to 15 min of baseline behaviours (collected at 7-days) mentioned above we extended the measured time of behaviour to 20 min in effort to observe and quantify recovery behaviours in relation to the pre-cue reference behaviour at each day. Since each tank was flow-through with the cue injection site just beside the incoming water, a sham was not included prior to the alarm cue; however, a separate sham cue (well water) was conducted on a series of tanks (n = 4 replicates/treatment) using the same alarm cue protocol, and behaviour recordings showed no response to the sham (Figure S4).

Delta smelt response to a predator-borne water cue was tested after 6 days of exposure to each temperature treatment. The predator water cues were prepared by placing a largemouth bass in an aerated, insulated cooler (50 ml water/g of bass) for 24 hr prior to the time of the cue injection (Ferrari, Messier, & Chivers, 2008). The surrounding predator water (60 ml) was then injected in the same manner as the alarm cue and fish behaviour recorded similarly to comparative pre-cue reference behaviour and post-cue response behaviours.

## 2.5 | Predation trials

After 7 days of temperature exposures, predation trials took place on each species assemblage including a single species shoal of delta smelt, mixed species shoals of delta smelt and Mississippi silversides, and a single species shoal of Mississippi silversides. Largemouth bass were

gently collected in a grey bucket (11 L) submerged within the tank to ensure no air exposure occurred. Buckets with individual largemouth bass were then quickly carried to all 18 prey tanks with the same temperature treatment and gently released. Following 15 min of initial video recording of baseline behaviour (beginning at 15:00), recording continued through the introduction of predators and lasted for 18 hr, after which prey survival was assessed (morning of day 8). Predation mortality was quantified as the total number of prey that were consumed, whereas predation-related mortality was counted as the number of prey left critically injured, dead in the tank, or that experienced loss of equilibrium (LOE). The total sum of these counts were considered as *ecologically dead* (sum of all fish predated upon [consumed + injured + dead in the tank + LOE]). Largemouth bass and remaining prey in tanks were removed and measured for fork length (cm) and mass (g). Each bass was only used once during the experiment. A linear regression analysis determined predation of delta smelt was independent of largemouth bass size (see Figure S5). Interpretation of the predation results of the species assemblages should also consider that Mississippi silversides were smaller than delta smelt (see Figure S6).

## 2.6 | Behaviour data collection

Video tracks of delta smelt behaviour were analysed using EthoVision behaviour software with the Social Interaction Module (v.13, Noldus Information Technology). We initially planned to individually track the movements of Mississippi silversides, but due to their observed tendency to school tightly and reduced pigmentation EthoVision could not reliably track individuals and therefore Mississippi silverside behaviour could not be analysed. Fish tracks and movement data, recorded as *x* and *y* coordinates per frame, were collected at 30 frames/s for the entire 15 min (baseline videos) and 40 min (pre/post predation cue) videos to maximise precision. Individual delta smelt variables of swimming velocity (cm/s) and turning angle (the angle between the *x* and *y* coordinates of a fish between two successive frames [degrees/s]) were calculated for each of the 12 delta smelt within a tank at each frame using EthoVision (similar to endpoints used in Colchen et al., 2017). An average of each metric (speed or turning angle) was then calculated for the group at each frame, and then averaged for each 1 s (30 frames) for a final output of a mean group response for each tank, thus resulting in a total of eight tank replicate responses for each temperature treatment across time (detailed steps of behaviour tacking and processing are provided in the Supplementary Material). To characterise variables of group structure of delta smelt shoals, indices including NND, IID, and variance of the IID (VID) were collected (Colchen et al., 2017; Parrish, Viscido, & Grunbaum, 2002). Nearest-neighbour distance indicates if the shoal is aggregated or randomly dispersed, whereas IID provides an estimate of shoal cohesion, and VID is the variation or change in cohesiveness (Colchen et al., 2017). At each tracked frame, EthoVision calculated the distance from a given focal fish to all other 11 fish in the shoal, and was repeated for each and every fish in the group. Nearest-neighbour distance was then determined by selecting the distance (cm) from each focal fish to its closest

single neighbour in every frame. Inter-individual distance was determined by taking the distance (cm) from one focal fish to all other fish in the shoal, and calculating the average of all the distances at each frame. Nearest-neighbour distance and IID were calculated for all 12 fish in the group at each frame, and then averaged across all 12 fish for a single NND and IID value at each frame, then averaged for each 1 s (30 frames). This was done for each tank (*n* = 8 tanks/ temperature treatment). Lastly, VID was calculated as the variance around each individual fish's distances to other fish and averaged for each temperature. Raw data behaviour responses at each 1 s are shown in supplementary materials (Figures S7–S9).

Statistical analyses were conducted in R (ver. 2.15.0, R Development Core Team 2013). Due to non-linear behaviour responses and repeated measures across time, polynomial generalised additive mixed modelling (*gamm*, *mgcv* package; Wood, 2011) was used (modified from Bjelde, Miller, Stillman, & Todgham, 2015; Flynn & Todgham, 2018). *Gamm* uses a smoothing function to link the behaviour metrics (dependent variable) as a function of time (continuous independent variable) and tests differential responses by temperature (fixed independent variable; Angilletta, Zelic, Adrian, Hurliman, & Smith, 2013; Zuur, Leno, Walker, Saveliev, & Smith, 2009). To account for repeated measures of group behaviour across time within each tank, the identity of each tank replicate was included as a random factor in the *gamm* model. To test treatment-specific differences in response curve parametric estimates (height) and smoothing (shape), as in Flynn and Todgham (2018), the control treatment (17°C) was set as the reference curve and the warm treatment curves for fluctuating (17–21°C) and warm (21°C) were compared by how much they deviated from the control treatment. The curve height (i.e. intercept) was the overall mean of the behavioural response across time for each temperature treatment. A *summary* of the model indicated if the height of the response curves was significantly affected by temperature and if treatments deviated from the control, whereas an ANOVA of the model tested deviation in behavioural responses (shape) as a function of time. *Gamm* model assumptions were checked using *gam.check* as in Flynn and Todgham (2018). *Gamm* analyses were conducted for behaviour responses of velocity, turning angle, NND, IID, and VID at the 7-day baseline, and during predation experimental treatment cues (conspecific alarm and predator cues). To determine if delta smelt exhibited different recovery responses from the predation cues, 5 min of behaviour from the before (0–5 min, reference period) and after (35–40 min, response period) the cue injections were tested with an ANOVA with temperature treatment and trial period (start or end) as fixed independent variables and tank replicate nested within each trial period. Multiple comparisons of recovery responses within trial period and temperature treatments were conducted with *lsmeans* using Tukey. All behavioural responses are presented as *gamm* fitted models with *SE* of the fit.

Comparative predation on delta smelt, Mississippi silversides and mixed species shoals of delta smelt and Mississippi silversides were analysed with a generalised linear model (*glm*) using a *poisson* for non-normal count data. Counts of fish ecologically dead (i.e. total morbidity; the sum of fish consumed, injured, and LOE) was the dependent variable with species assemblage and temperature treatments as
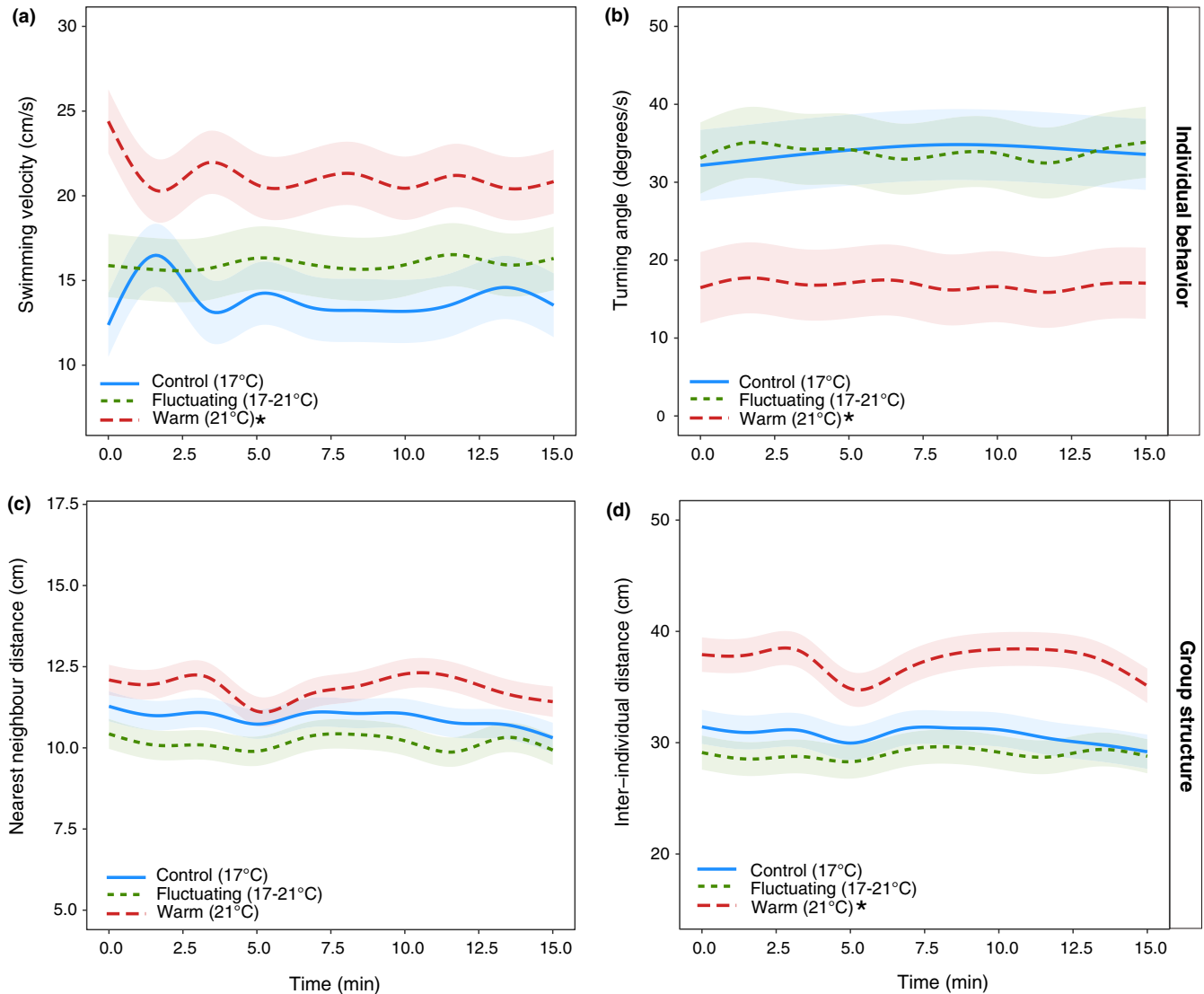
**FIGURE 2** Delta smelt behaviour after 7 days of exposure to one of three different temperature treatments. Individual behaviour is shown as (a) swimming velocity and (b) absolute turning angle, whereas group structure is shown as (c) nearest-neighbour distance and (d) inter-individual distances. The fitted line in each panel is the behaviour response as a function of time (sampled every second), generated using generalised additive mixed modelling (*gamm*), with the shaded region the *SE* of the fit (n = 8 curves replicates per treatment). Each temperature treatment is indicated by colour for the control (17°C, blue), fluctuating (17–21°C, green), and warm- (21°C, red) acclimation treatments. Asterisks indicate as significant difference (*p* < 0.05) in the height (intercept estimate from *gamm*) of the behavioural response compared to the control treatment. The shape of each curve was significantly different for each treatment and behaviour combination (*p* < 0.0001, see statistical results see Table 1) [Colour figure can be viewed at wileyonlinelibrary.com]

fixed factors. An ANOVA was then run on the *glm*, providing $\chi^2$ differences, and *lsmeans* was then used for multiple comparisons. To test additional impacts of increased temperature on predation vulnerability of delta smelt separate *glms* were conducted on delta smelt actually consumed versus predation-related mortality (i.e. injured/LOE).

## 3 | RESULTS

### 3.1 | Individual behaviours—swimming velocity

Average swimming velocity (i.e. speed) of delta smelt in the control treatment at 17°C was 13.9 ± 1.8 cm/s (mean ± *SE*; Figure 2a).

Following 7-days of exposure to warming, speed was not altered by fluctuating warming (17–21°C, *p* = 0.447), but significantly increased to 21.0 ± 2.6 cm/s in delta smelt groups under warm-acclimation (21°C, *p* = 0.007; see *gamm* curve heights in Table 1). In response to a conspecific alarm cue, fish in the control temperature treatment rapidly increased swimming speed by roughly 8–10 cm/s compared to pre-alarm cue/reference speeds (Figure 3a), followed by recovery to reference speeds by 15 min past the cue injection (*p* = 0.497, ANOVA Table S1, *lsmeans* Table 3). Response curves of fish in the fluctuating treatment were similar to the control treatment curves marked by curve height (*p* = 0.785, Table 2) and recovery; however, speed alterations in delta smelt under the warm

**TABLE 1** Evaluations of generalised additive mixed models (*gamm*) of delta smelt behaviours as a function of time (*fT*), with the fluctuating (17–21°C) and warm (21°C) acclimation treatments referenced to the control response curves (17°C)

| Behaviour parameter and fixed temperature effects | Parametric (curve height) | | | | Smooth (curve shape) | | |
|---|---|---|---|---|---|---|---|
| | Intercept | SE | T | p | edf | F | p |
| Individual behaviours | | | | | | | |
| Swimming velocity (cm/s) | | | | | | | |
| *f*(T) for control | 13.96 | 1.86 | 7.50 | <0.0001 | 8.85 | 41.41 | <0.0001 |
| Deviance from *f*(T) for fluctuating | 2.00 | 2.63 | 0.76 | 0.447 | 8.70 | 25.64 | <0.0001 |
| Deviance from *f*(T) for warm | 7.05 | 2.63 | 2.68 | 0.007 | 8.89 | 42.01 | <0.0001 |
| Turning angle (degrees/s) | | | | | | | |
| *f*(T) for control | 34.00 | 4.55 | 7.47 | <0.0001 | 3.92 | 22.23 | <0.0001 |
| Deviance from *f*(T) for fluctuating | −0.14 | 6.44 | −0.02 | 0.982 | 8.24 | 23.33 | <0.0001 |
| Deviance from *f*(T) for warm | −17.17 | 6.44 | −2.67 | 0.008 | 6.97 | 14.85 | <0.0001 |
| Group structure | | | | | | | |
| Nearest neighbour distance (cm) | | | | | | | |
| *f*(T) for control | 10.92 | 0.45 | 24.22 | <0.0001 | 8.17 | 12.79 | <0.0001 |
| Deviance from *f*(T) for fluctuating | −0.76 | 0.64 | −2.00 | 0.231 | 6.51 | 6.63 | <0.0001 |
| Deviance from *f*(T) for warm | 0.93 | 0.64 | 1.46 | 0.143 | 7.78 | 14.31 | <0.0001 |
| Inter-individual distance (cm) | | | | | | | |
| *f*(T) for control | 30.69 | 1.52 | 20.22 | <0.0001 | 8.25 | 21.48 | <0.0001 |
| Deviance from *f*(T) for fluctuating | −1.73 | 2.15 | −0.80 | 0.421 | 5.09 | 13.55 | <0.0001 |
| Deviance from *f*(T) for warm | 6.67 | 2.15 | 3.11 | 0.002 | 7.95 | 27.90 | <0.0001 |
| Variance of inter-individual distance | | | | | | | |
| *f*(T) for control | 165.21 | 21.72 | 7.61 | <0.0001 | 6.65 | 14.69 | <0.0001 |
| Deviance from *f*(T) for fluctuating | −13.33 | 30.72 | −0.43 | 0.664 | 3.10 | 6.82 | <0.0001 |
| Deviance from *f*(T) for warm | 116.02 | 30.72 | 3.777 | <0.001 | 8.25 | 36.23 | <0.0001 |

*Note:* The parametric effects test the significance of temperature treatment on height of the behavioural response curve (estimated intercept, standard error [SE], T-value [T], and p-value [p]). The estimated intercept is the overall mean of the behavioural response across time for each temperature treatment. The smooth determines the significance of temperature treatment on the shape of the behavioural response curve. Effective degrees of freedom (*edf*) indicates the amount of smoothing, and the F-statistic (F) and p-value (p) are provided.

treatment differed from the control treatment by curve height (magnitude; $p = 0.007$), shape (change in response across time; $p < 0.0001$, Table 2), and lacked a recovery response (return to reference; $p < 0.0001$, Table 3). Swimming speed of delta smelt in the control treatment showed a subtle increase following the predator (i.e. largemouth bass) water cue as the response curve was slightly non-linear ($p < 0.0001$), and the fluctuating treatment showed a similar response to the control (curve height $p = 0.759$, Table 2). The warm-acclimation treatment response to the predator cue significantly deviated from the control (curve height [$p = 0.006$] and shape $p < 0.0001$) as swimming speed continuously increased following delivery of the cue, and showed no recovery ($p < 0.0001$, Table 3 and Figure 3).

## 3.2 | Individual behaviours—turning angle

Turning angle (degrees/s), reflective of turning speed under normal control conditions, was 34.0 ± 4.6 degrees/s (Figure 2b). Turning angle was not affected by the fluctuating warm treatment (17–21°C;

curve height, $p = 0.982$, Table 1) but significantly decreased to 16.83 ± 6.4 degrees in the warm (21°C) treatment ($p = 0.008$). In response to a conspecific alarm cue, fish under control temperature decreased turning angle by c. 10–15 degrees/s (Figure 3c) followed by a significant recovery response to reference conditions (*lsmeans*, $p = 0.290$, see Table 3 for multiple comparisons). Fish in the fluctuating warm treatment (17–21°C) had similar turning angle response curves by height ($p = 0.881$, see Table 2 for all statistical results), whereas fish response curves under warm temperature differed in curve height ($p = 0.006$) and shape ($p < 0.0001$), as turning angle steadily decreased across time following delivery of the alarm cue (Figure 3c). Turning angle curves in response to the predator cue for fish in the control treatment was non-linear in shape ($p < 0.0001$), even though visually it appeared relatively linear (Figure 3d). Fish in the fluctuating warm treatment showed similar responses in turning angle to the control fish with matched curve height ($p = 0.934$), whereas the warm treatment curve deviated from the control in curve height ($p = 0.004$) and shape ($p < 0.0001$, Table 2), as turning angle significantly decreased across time following delivery of the predator cue (Figure 3d).
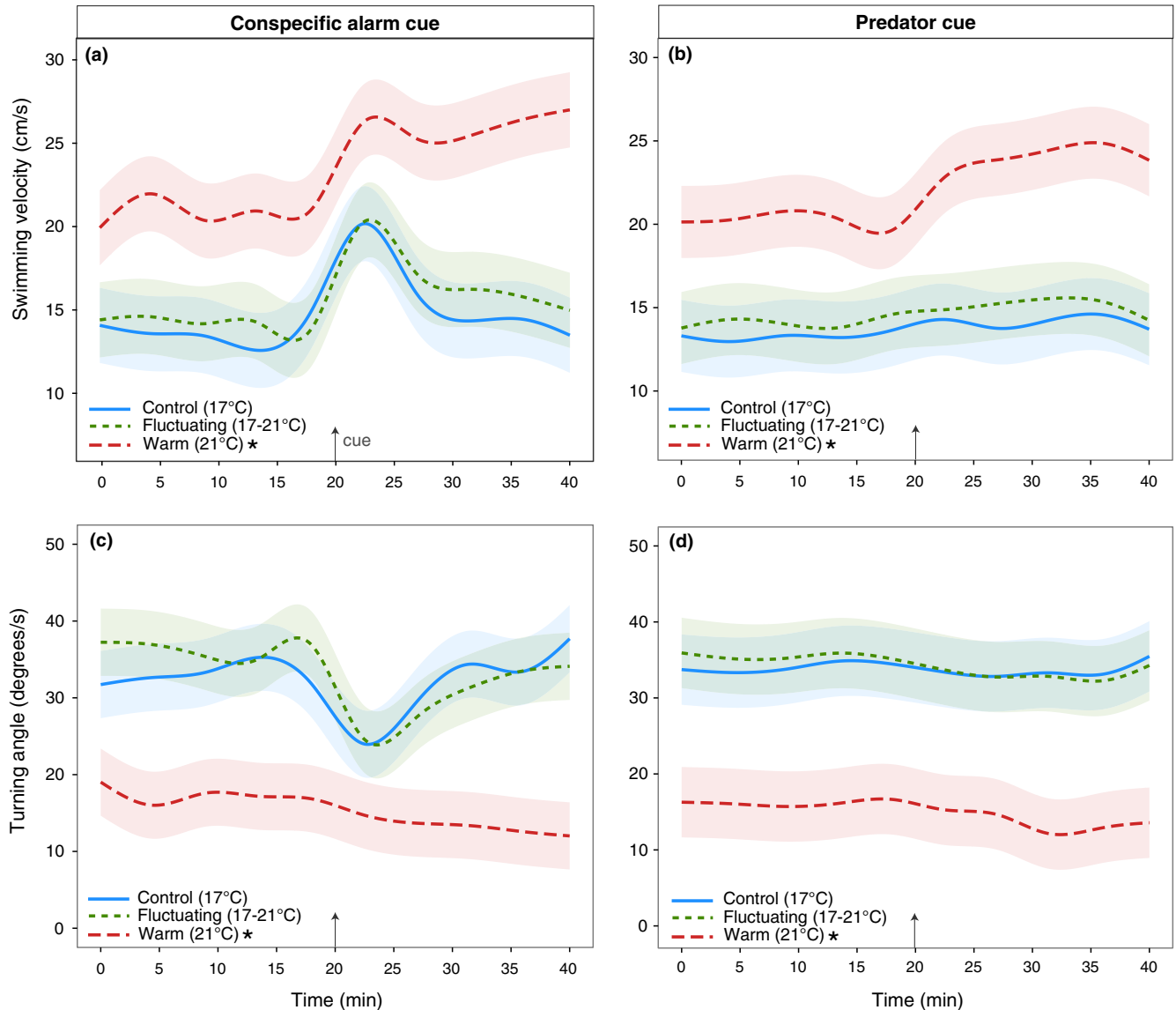
**FIGURE 3** Individual behavioural response curves of delta smelt in response to a conspecific alarm cue and predator cue under control (17°C, blue), fluctuating (17–21°C, green), and warm- (21°C, red) acclimation treatments. Responses curves are shown as (a and b) swimming velocity and (c and d) turning angle for fitted generalised additive mixed models (*gamm*) with the fitted line of *n* = 8 replicate responses per treatment (sampled every second) with the shaded regions the *SE* of the fit. The significant behavioural responses observed prior to the cue injection is an artefact of the *gamm* smoothing (see Figure S8 for raw data). *Gamms* tested the deviation in curve height and shape of the warming treatments in reference to the control. Asterisks indicate the height of the response curves of delta smelt in the fluctuating and warm treatments were significantly different than the control response (*p* < 0.05). The shape of each curve was significantly different for each treatment and behaviour combination (*p* < 0.0001). Statistical results for *gamm* are in Table 2 [Colour figure can be viewed at wileyonlinelibrary.com]

## 3.3 | Group structure

Average NND of delta smelt was 10.9 ± 0.5 cm (roughly 1.8 body lengths) after the 7-day acclimation in the control treatment (Figure 2c), with no significant changes by fluctuating or warm-acclimation treatments (*gamm* curve heights, *p* > 0.05, Table 1). In response to a conspecific alarm cue, NND changed as a function of time in all treatments (*gamm* curve shapes, *p* < 0.0001, Table 2). Nearest-neighbour distance in the control treatment decreased by *c.* 5 cm (*c.* 1 body length, Figure 4a) in response to the alarm

cue, with similar decreases seen in the fluctuating and warm treatments (*p* > 0.05, *gamm* curve heights, Table 2). Recovery of NND following the alarm cue was dependent on temperature treatment (ANOVA, significant interaction *p* < 0.05, Table S1). Fish in the control treatment and warm treatment maintained lower NND following the delivery of the alarm cue at the end of the trial compared to the starting reference behaviour (*lsmeans*, *p* < 0.01, Table 3). In contrast, NND returned to initial distances in fish in the fluctuating warm treatment (*p* = 0.321, Figure 4a). Nearest-neighbour distance changed across time following the predator water cue for fish in

**TABLE 2** Comparisons of generalised additive mixed models (*gamm*) of delta smelt behaviours as a function of time (*f*T) during predation water cue trials, with temperature treatment (fluctuating and warm) responses referenced to the control treatment response curves

| Behaviour parameter and fixed temperature effects | Parametric (curve height) | | | | Smooth (curve shape) | | |
|---|---|---|---|---|---|---|---|
| | Intercept | SE | T | p | edf | F | p |
| Conspecific alarm cue | | | | | | | |
| Individual behaviour | | | | | | | |
| Swimming velocity (cm/s) | | | | | | | |
| *f*(T) for control | 14.721 | 2.241 | 6.568 | <0.0001 | 8.95 | 581.99 | <0.0001 |
| Deviance from *f*(T) for fluctuating | 0.8643 | 3.169 | 0.273 | 0.785 | 8.71 | 44.97 | <0.0001 |
| Deviance from *f*(T) for warm | 8.595 | 3.169 | 2.712 | 0.007 | 8.831 | 320.75 | <0.0001 |
| Turning angle (degrees/s) | | | | | | | |
| *f*(T) for control | 32.031 | 4.337 | 7.385 | <0.0001 | 8.927 | 401.4 | <0.0001 |
| Deviance from *f*(T) for fluctuating | 0.92 | 6.134 | 0.15 | 0.881 | 8.861 | 140.8 | <0.0001 |
| Deviance from *f*(T) for warm | -16.751 | 6.134 | -2.731 | 0.006 | 8.851 | 253.9 | <0.0001 |
| Group structure | | | | | | | |
| Nearest-neighbour distance (cm) | | | | | | | |
| *f*(T) for control | 10.281 | 0.462 | 22.233 | <0.0001 | 8.961 | 703.98 | <0.0001 |
| Deviance from *f*(T) for fluctuating | -1.045 | 0.654 | -1.598 | 0.11 | 8.573 | 67.87 | <0.0001 |
| Deviance from *f*(T) for warm | 0.679 | 0.654 | 1.038 | 0.299 | 8.593 | 60.91 | <0.0001 |
| Inter-individual distance (cm) | | | | | | | |
| *f*(T) for control | 29.1 | 1.513 | 19.227 | <0.0001 | 8.97 | 765.78 | <0.0001 |
| Deviance from *f*(T) for fluctuating | -2.755 | 2.14 | -1.287 | 0.198 | 8.538 | 65.68 | <0.0001 |
| Deviance from *f*(T) for warm | 4.334 | 2.14 | 2.025 | 0.043 | 8.287 | 52.26 | <0.0001 |
| Variance of inter-individual distance | | | | | | | |
| *f*(T) for control | 153.44 | 20.16 | 7.612 | <0.0001 | 8.944 | 231.440 | <0.0001 |
| Deviance from *f*(T) for fluctuating | -22.71 | 28.51 | -0.797 | 0.451 | 8.335 | 23.31 | <0.0001 |
| Deviance from *f*(T) for warm | 78.61 | 28.51 | 2.757 | 0.008 | 6.467 | 66.81 | <0.0001 |
| Predator water cue | | | | | | | |
| Individual behaviour | | | | | | | |
| Swimming velocity (cm/s) | | | | | | | |
| *f*(T) for control | 13.721 | 2.149 | 6.385 | <0.0001 | 8.503 | 54.66 | <0.0001 |
| Deviance from *f*(T) for fluctuating | 0.93 | 3.089 | 0.306 | 0.759 | 8.232 | 11.23 | <0.0001 |
| Deviance from *f*(T) for warm | 8.3603 | 3.089 | 2.751 | 0.006 | 8.696 | 236.48 | <0.0001 |
| Turning angle (degrees/s) | | | | | | | |

(Continues)

**TABLE 2** (Continued)

| Behaviour parameter and fixed temperature effects | Parametric (curve height) | | | | Smooth (curve shape) | | |
|---|---|---|---|---|---|---|---|
| | Intercept | SE | T | p | edf | F | p |
| f(T) for control | 33.853 | 4.59 | 7.376 | <0.0001 | 8.596 | 20.08 | <0.0001 |
| Deviance from f(T) for fluctuating | 0.491 | 6.49 | 0.076 | 0.934 | 8.709 | 57.48 | <0.0001 |
| Deviance from f(T) for warm | −18.614 | 6.49 | −2.868 | 0.004 | 8.468 | 51.59 | <0.0001 |
| Group structure | | | | | | | |
| Nearest-neighbour distance (cm) | | | | | | | |
| f(T) for control | 10.575 | 0.492 | 21.506 | <0.0001 | 8.811 | 82.315 | <0.0001 |
| Deviance from f(T) for fluctuating | −0.898 | 0.695 | −1.291 | 0.197 | 6.456 | 21.098 | <0.0001 |
| Deviance from f(T) for warm | 0.909 | 0.695 | 1.307 | 0.191 | 8.099 | 8.921 | <0.0001 |
| Inter-individual distance (cm) | | | | | | | |
| f(T) for control | 29.814 | 1.545 | 19.299 | <0.0001 | 8.892 | 115.2 | <0.0001 |
| Deviance from f(T) for fluctuating | −2.29 | 2.185 | −1.048 | 0.295 | 6.882 | 16.75 | <0.0001 |
| Deviance from f(T) for warm | 5.588 | 2.185 | 2.558 | 0.011 | 8.71 | 43.08 | <0.0001 |
| Variance of inter-individual distance | | | | | | | |
| f(T) for control | 156.91 | 19.1 | 8.216 | <0.0001 | 8.821 | 59.267 | <0.0001 |
| Deviance from f(T) for fluctuating | −20 | 27.01 | −0.741 | 0.469 | 5.324 | 9.107 | <0.0001 |
| Deviance from f(T) for warm | 9.63 | 27.01 | 3.689 | <0.001 | 8.794 | 89.302 | <0.0001 |

*Note:* Parametric effects test the significance of temperature treatment on height of the behavioural response curve (estimated intercept, standard error [SE], T-value [T], and p-value [p]). The estimated intercept is the overall mean of the behavioural response across time for each temperature treatment. The smooth determines the significance of temperature treatment on the shape of the behavioural response curve. Effective degrees of freedom (edf) indicates the amount of smoothing, and the F-statistic (F) and p-value (p) are provided. *Gamm* model comparisons are given for both predation cues, a conspecific alarm cue and a predator (largemouth bass) water cue.

**TABLE 3** Mean (±SE) behavioural response of delta smelt at the start and end of the predation cue trials under control (17°C), fluctuating (17–21°C), and warm (21°C) treatments

| Behaviour parameter and fixed temperature effects | Conspecific alarm cue | | | Predator water cue | | |
|---|---|---|---|---|---|---|
| | Before (0–5 min) | After (35–40 min) | *p*-value | Before (0–5 min) | After (35–40 min) | *p*-value |
| Individual behaviour | | | | | | |
| Swimming velocity (cm/s) | | | | | | |
| Control | 13.558 ± 1.22 a | 14.10 ± 1.19 a | 0.497 | 13.03 ± 1.13 a | 14.30 ± 1.39 a | 0.04 |
| Fluctuating | 14.30 ± 1.75 a | 15.46 ± 1.73 a | 0.132 | 14.02 ± 1.35 a | 15.00 ± 1.44 a | 0.108 |
| Warm | 21.13 ± 1.64 b | 26.15 ± 1.56 b | <0.0001 | 20.19 ± 1.46 a | 24.44 ± 1.61 b | <0.0001 |
| Turning angle (degrees/s) | | | | | | |
| Control | 32.42 ± 3.45 a | 34.79 ± 3.46 ab | 0.29 | 33.73 ± 3.47 a | 33.20 ± 3.76 a | 0.684 |
| Fluctuating | 36.90 ± 3.71 a | 33.96 ± 3.37 a | 0.194 | 35.76 ± 3.37 a | 33.77 ± 23.09 a | 0.136 |
| Warm | 17.06 ± 2.26 b | 12.68 ± 1.26 b | 0.058 | 16.47 ± 1.74 b | 12.82 ± 1.32 b | 0.01 |
| Group structure | | | | | | |
| Nearest-neighbour distance (cm) | | | | | | |
| Control | 11.39 ± 0.31 a | 10.13 ± 0.37 a | <0.001 | 10.89 ± 0.37 ab | 10.45 ± 0.31 ab | 0.031 |
| Fluctuating | 9.63 ± 0.33 b | 9.36 ± 0.40 b | 0.321 | 9.88 ± 0.37 | 9.77 ± 0.32 a | 0.538 |
| Warm | 11.56 ± 0.24 a | 10.55 ± 0.17 a | 0.001 | 11.91 ± 0.22 b | 11.51 ± 0.25 b | 0.045 |
| Inter-individual distance (cm) | | | | | | |
| Control | 31.79 ± 0.92 a | 29.11 ± 1.24 ab | 0.005 | 30.68 ± 1.09 ab | 29.71 ± 0.95 a | 0.183 |
| Fluctuating | 27.48 ± 1.12 a | 27.34 ± 1.36 a | 0.869 | 28.13 ± 1.16 a | 27.74 ± 0.95 a | 0.586 |
| Warm | 34.43 ± 0.85 a | 33.25 ± 0.70 b | 0.176 | 36.11 ± 0.78 b | 36.31 ± 1.04 b | 0.786 |
| Variance of inter-individual distance | | | | | | |
| Control | 171.44 ± 10.28 ab | 157.20 ± 14.71 a | 0.197 | 163.56 ± 11.46 a | 157.73 ± 10.05 a | 0.514 |
| Fluctuating | 139.18 ± 17.73 a | 145.93 ± 18.83 a | 0.534 | 142.26 ± 12.91 a | 138.90 ± 10.61 a | 0.706 |
| Warm | 232.37 ± 14.72 b | 249.77 ± 13.58 b | 0.118 | 251.87 ± 12.44 b | 280.30 ± 14.96 b | 0.004 |

*Note:* Start time was taken from 0 to 5 min as a reference. To assess recovery following the cue, time was taken from 35 to 40 min into the trial (20 min following the cue injection). Lowercase lettering indicates a significant difference within a time period and the *p*-value indicates a significant difference within a single temperature treatment across time periods (before versus after the cue; *lsmeans* Tukey). Non-significance indicates delta smelt behaviour returned/recovered to pre-cue behaviours.

each temperature treatment (*gamm* curve shapes, *p* < 0.0001, Table 2 and Figure 4b); however, the response to the predator cue was subtle compared to the alarm cue, with a decrease of roughly 1–2 cm body lengths.

Inter-individual distance was 30.7 ± 1.5 cm (Figure 2d) after the 7-day acclimation to control conditions. Fish shoals in the fluctuating warm treatment exhibited similar IID to the control treatment (*p* = 0.421, *gamm* curve heights in Table 1); however, IID of fish in the warm treatment was on average 6.7 ± 2.1 cm greater (*p* = 0.002). In response to both the conspecific alarm cue and predator water cue, delta smelt showed significant changes in IID as a function of time (Figure 4c,d) in the control treatment (*p* < 0.0001, *gamm* shape, Table 2). For both cues, both the fluctuating and warm treatment fish had different response curve shapes (*p* < 0.0001, Table 2) compared to the control, but curve height was only significantly greater in the warm treatment (*p* = 0.043 [alarm cue] and *p* = 0.001 [predator cue]), and not the fluctuating warm treatment (*p* = 0.198 [alarm cue] and *p* = 0.295 [predator cue]). Changes in IID following alarm and predator cues were fully recovered and returned to reference conditions in all temperature treatments

(*p* > 0.05), with the exception of fish in the control treatment following delivery of the conspecific alarm cue (*p* = 0.005, Table 3).

Variance of the IID across trial time was 165.2 ± 21.7 after a 7-day acclimation to control conditions (Table 1). Fish in the fluctuating warm treatment had similar VID to the fish in the control treatment (*p* = 0.664), but fish in the warm-acclimation treatment deviated by 116.0 ± 30.7 (*gamm* curve height, *p* < 0.001). In response to both conspecific alarm cues and predator water cues, VID in all treatments changed as a function of time (*gamm* curve shape, *p* < 0.0001); however, only curve height (i.e. intercept) of VID of fish shoals in the warm treatment was significantly greater than the control curve height (*p* < 0.001, Table 2).

## 3.4 | Predation trials

Delta smelt morbidity (i.e. considered ecologically dead) following largemouth bass predation was significantly affected by temperature treatment ($X_2^2$ = 8.43, *p* = 0.014). Specifically, delta smelt in the warm (21°C) treatment were predated on more than the control treatment
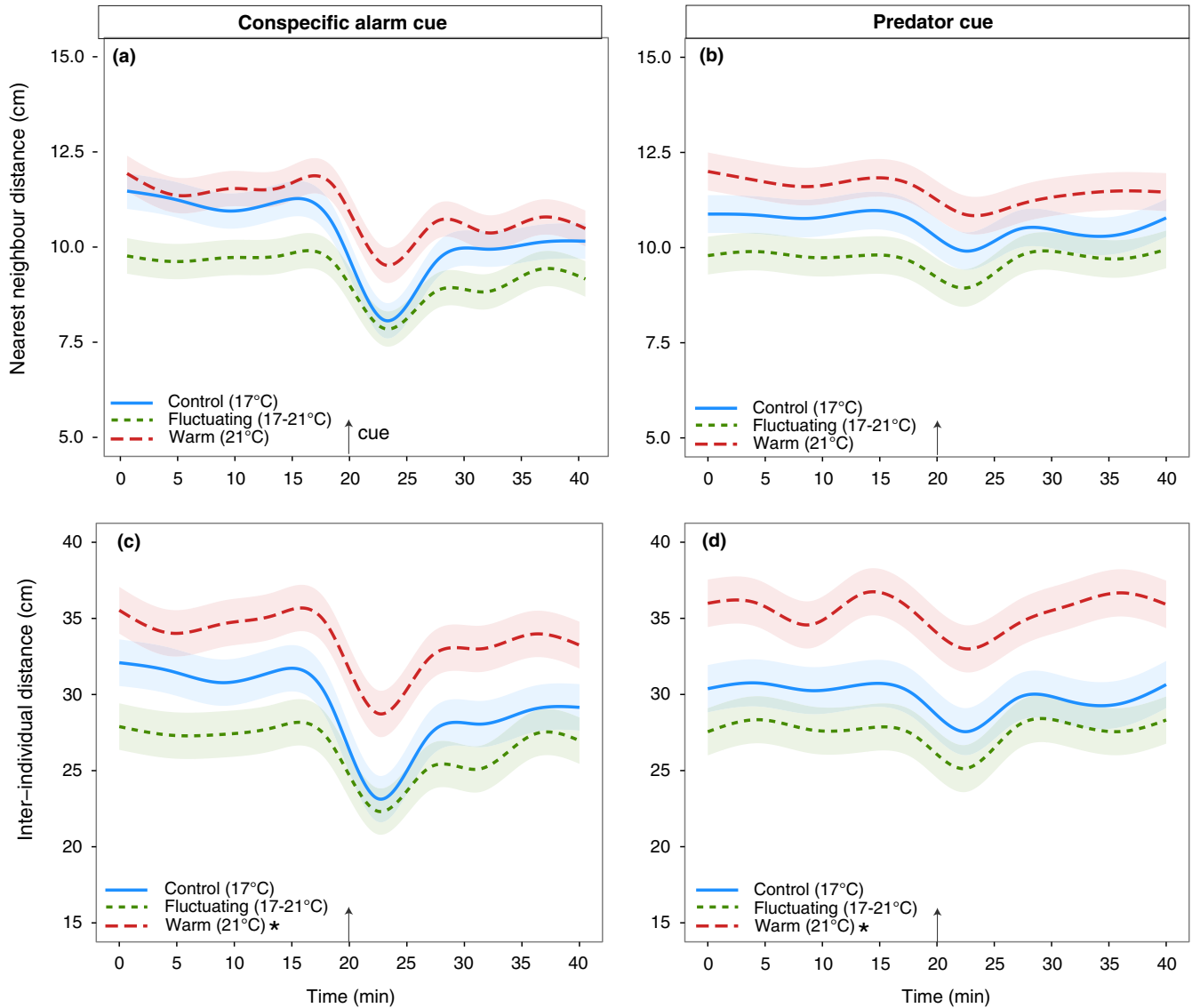
**FIGURE 4** Alterations in group structure of delta smelt in response to a conspecific alarm cue and predator water cue under control (17°C, blue), fluctuating (17–21°C, green) and warm- (21°C, red) acclimation treatments. Group structure responses are shown as (a and b) nearest-neighbour distance and (c and d) inter-individual distance for fitted generalised additive mixed models (*gamm*) with the fitted line of *n* = 8 replicate responses per treatment (sampled every second) with the shaded regions the *SE* of the fit. The significant behavioural responses observed prior to the cue injection is an artefact of *gamm* smoothing (see Figure S9 for raw data). *Gamms* tested the deviation in curve height and shape of the warming treatments in reference to the control. Asterisks indicate the height of the response curves of delta smelt in the fluctuating and warm treatments were significantly different than the control response (*p* < 0.05). The shape of each curve was significantly different for each treatment and behaviour combination (*p* < 0.0001). Statistical results for *gamm* are in Table 2 [Colour figure can be viewed at wileyonlinelibrary.com]

(*p* < 0.05, *lsmeans* Tukey), whereas predation of the fish in the fluctuating warm treatment (17–21°C) was intermediate to both the control and the warm treatments (*p* > 0.05). Actual consumption of delta smelt by largemouth bass was not altered by temperature ($X^2_2$ = 0.87, *p* = 0.645, Figure 5). On average, largemouth bass consumed 2–3 delta smelt by the end of the 18-hr trial. Predation-related mortality of delta smelt (fish not consumed but left critically injured by predator attacks or had experienced loss of equilibrium) was significantly greater in the warm treatment ($X^2_2$ = 12.441, *p* = 0.002).

Predation (ecological death) of delta smelt in mixed species shoals with Mississippi silversides, as well as predation of single species shoals

of Mississippi silversides were compared to the predation of single species shoals of delta smelt (see Figure 6). A significant interaction ($X^2_6$ = 14.039, *p* = 0.029) between species assemblage ($X^2_3$ = 153.306, *df* = 3, *p* < 0.0001) and temperature treatment ($X^2_2$ = 1.009, *p* = 0.603) indicated the effects of temperature on predation were dependent on species assemblage. For example, predation of single species shoals of delta smelt increased under warm-acclimation (*p* < 0.05, *lsmeans* Tukey); however, in mixed species shoals, predation on delta smelt did not significantly increase under the warm treatment (*p* > 0.05). Predation on single species shoals of Mississippi silversides was significantly greater (*p* < 0.05) than predation on single species shoals of
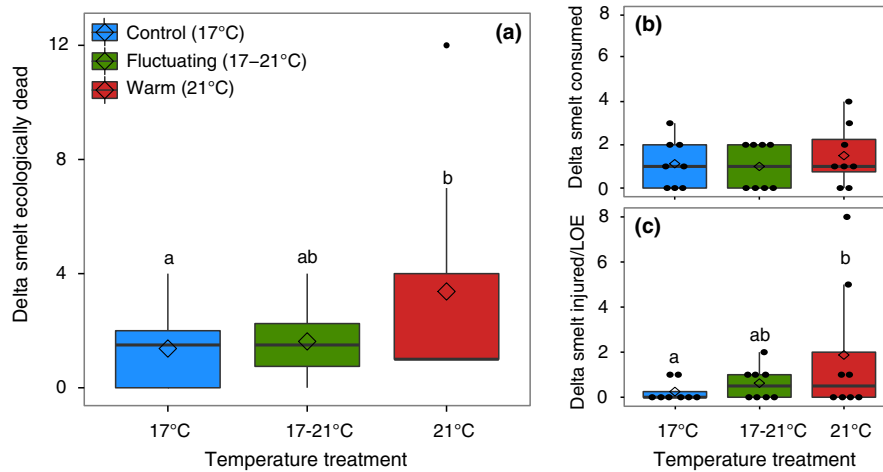
**FIGURE 5** Predation of delta smelt by largemouth bass. Delta smelt determined (a) ecologically dead (i.e. morbid), (b) fish actually consumed by bass, and (c) fish left critically injured or observed having loss of equilibrium (LOE) are plotted by each temperature treatment. Each temperature treatment is indicated by colour for the control (17°C, blue), fluctuating (17–21°C, green), and warm- (21°C, red) acclimation treatments. The box represents the interquartile range (IQR), extended whiskers are 1.5 × IQR, the line is the median, and open diamonds are the mean. Filled circles in (b) and (c) are the actual count values from each predation replicate ($n$ = 8). *Note.* Delta smelt ecologically dead in panel (a) are the sum of values in panels (b) and (c). Statistical lettering indicates a significant difference ($p < 0.05$) between temperature treatments on predation of delta smelt [Colour figure can be viewed at wileyonlinelibrary.com]

delta smelt and mixed species shoals within the control and fluctuating warm treatments, but remained more similar to delta smelt in the warm-acclimation treatment.
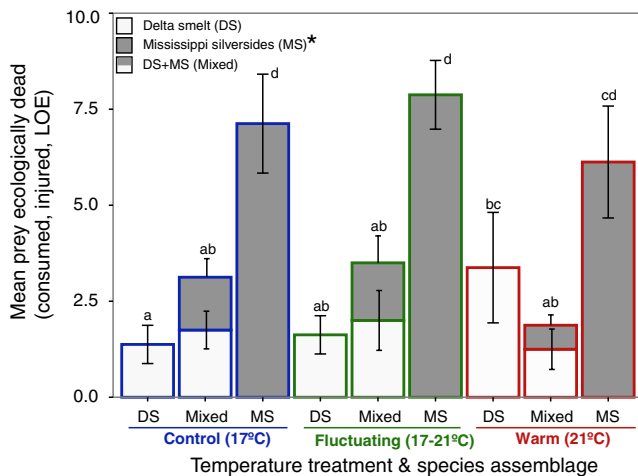


**FIGURE 6** Largemouth bass predation on single species shoals of delta smelt and Mississippi silversides, and mixed species shoals of delta smelt/Mississippi silversides. Bars are mean (±*SE*) for each temperature treatment and species assemblage. Each species assemblage, delta smelt (white), Mississippi silversides (grey), and mixed shoals (split white/grey) are pictured within each temperature treatment (control [blue], fluctuating [green], and warm [red]). Asterisks indicate a difference in species assemblage ($p < 0.0001$; *glm*), independent of temperature treatment, whereas statistical lettering indicates a significant difference ($p < 0.05$; post-hoc Tukey comparisons) between and within temperature treatments and species assemblage on the mean fish ecologically dead fish (i.e. consumed, injured, and loss of equilibrium [LOE]) [Colour figure can be viewed at wileyonlinelibrary.com]

## 4 | DISCUSSION

This study adds to the growing body of literature demonstrating the effect of temperature on the group behaviour of fishes (Colchen et al., 2017; Cooper et al., 2018; Hurst, 2007; Weetman et al., 1998, 1999). This study quantified for the first-time free-swimming characteristics and group structure of California's critically endangered delta smelt (*Hypomesus transpacificus*). Delta smelt demonstrated shoaling behaviour similar to brown trout fry, *Salmo trutta* (Salmonidae; Colchen et al., 2017), remaining on average 2 body lengths from their nearest neighbour and interacting in a social manner. There were significant effects of increased temperature (21°C) on both individual and group structural behaviours; however, if increased temperatures were fluctuated in a manner closely mimicking that of the natural diurnal tidal cycle, delta smelt movement was less affected. Similarly, the responses of delta smelt to conspecific alarm cue, predator cues, and predation were also dependent on the type of temperature treatment (fluctuating versus warm), suggesting that future studies should take care to match temperature treatments more closely with environmentally-realistic daily fluctuations whenever possible.

### 4.1 | Individual and group movement

The current study showed that short-term acclimation to warm conditions (21°C) significantly increased delta smelt swimming speed from *c.* 13 cm/s to roughly 21 cm/s (*c.* 1 body length/s at 6–7 cm fork length), with an observed continuous swimming modality comparable to Young et al. (2004), and speeds at 75% of their maximum swimming capacity (28 ± 4 cm/s; Swanson et al., 1998). Fish in the control and fluctuating warm treatments, however, swam between 13 and 16 cm/s, consistent with more discontinuous stroke and glide

swimming modalities as described previously in delta smelt (Young et al., 2004). Increased swimming speed of delta smelt with increasing temperature concurs with numerous other studies (Bartolini et al., 2015; Green & Fisher, 2004; Peck et al., 2006; Pritchard et al., 2001).

Further increases in swimming activity in response to predation cues were equivalent to maximum swimming capacity of delta smelt (Swanson et al., 1998). Spending long periods or multiple days swimming near maximum velocities could lead to deficiencies in energy balance if energy supply needed to sustain that swimming performance cannot be met by available food resources. Food limitation in delta smelt habitats has been described (Hammock, Hobbs, Slater, Acuña, & Teh, 2015). Surprisingly, the fish did not slow down to reduce energy expenditure after 20 min of responding to different cues. The high sustained swimming speeds of delta smelt in the warm treatment may have been a result of the fish attempting to swim in straight lines to escape harmful conditions, but instead having to conform to the walls of the arena. Alternately, the high sustained swimming speeds of fish may have been an artefact of the arena conditions, where individuals were constantly getting locomotory feedback information from conspecifics. For example, if one fish is following its nearest neighbour who is swimming at a high speed, and that fish is getting speed information from another neighbour, this could create a cycle such that the group never reduces speed. In nature, it could be that fish travelling at such speeds would break away from shoals and reduce their speed upon entering more favourable environmental conditions or the entire group could respond consistently and all slow down. It is also noteworthy that fish in the fluctuating warm treatment never attained the high speeds of the warm treatment, suggesting that periodic respite from elevated temperature conditions (similar to that which delta smelt would experience in nature) was sufficient to maintain individual movement behaviour found at the lower control temperature. Because temperature sensitivity of delta smelt is critically important for management and conservation of the species, this finding is particularly important when considering how delta smelt will be able to cope with warmer temperatures projected under climate change scenarios. It should also be noted that the time-course at which baseline behaviours were measured may have been influenced by the predation cue exposures days prior (days 5 and 6). However, interacting carry-over effects from the cues were unlikely (due to the order of cues, time, and design; see review Brown, 2003), demonstrated by similar reference (pre-stimulus) behaviours seen in the first 20 min prior to the cues to the overall baseline behaviours assessed on day 7.

Activity behaviour of fish is highly mediated through physiological metabolism and environmental conditions (Claireaux & Lefrancois, 2007). Commonly, behavioural trade-offs are observed, such as reduced swimming activity, as an energy conservation mechanism to offset physiological costs (Careau & Garland, 2012; Davis et al., 2017). Delta smelt, however, under the warm treatment did not reduce swimming activity compared to fish in the control and fluctuating treatments (as seen across days 5, 6, and 7), suggesting that the fish may be accruing an energetic debt that without additional food

resources could result in limited energetic resources to cope with additional external perturbations. For example, if a predation event were to be presented in addition to warming (as conducted in the present study), the fish may not have the required energy (aerobic or anaerobic capacity) to respond, thereby decreasing survival from predators. Furthermore, it is important to consider how trade-offs in energy allocation may negatively affect reproduction. The delta smelt is an annual species and reproduce during colder temperature (7–15°C; Bennett, 2005). Alterations in bioenergetics of juveniles and sub-adults such as re-allocation of energy to meet physiological and behavioural costs during warm months may be particularly detrimental to the population if there are carry-over effects on reproduction, including reduced fecundity or skipped spawning due to reduced growth (Donelson, Munday, McCormick, Pankhurst, & Pankhurst, 2010; Pörtner et al., 2001). Delta smelt, however, when exposed to warming in a naturally fluctuating way had similar behaviour to control fish, possibly suggesting that relief from high temperature may offset some of the negative energetic consequences. Alternative explanations for sustained elevated swimming speeds of delta smelt in the warm treatment may present as a behaviour that helps fish find new areas with higher concentrations of food or avoidance behaviour in search of colder temperatures, both of which have been described in salmon (Hunter & Wisby, 1964; Sauter, McMillan, & Dunham, 2001). The underlying mechanism driving the elevated swimming activity of delta smelt remains unknown.

This study is the first to document group movement behaviour of delta smelt. Our results agree with previous studies of other fishes showing that IID increases with increasing temperature (i.e. decreased group cohesion; Hurst, 2007; Colchen et al., 2017). Measures of group behaviour in delta smelt mirrored the individual movement results, in that only the warm treatment differed from the control, and not the fluctuating treatment. It could be hypothesised that the increased IID in the warm treatment was a result of fish at the higher temperatures having greater energetic demands (as described above) and therefore attempting to reduce inter-individual competition by expanding foraging movement (Hoare, Couzin, Godin, & Krause, 2004; Pitcher & Parrish, 1993; Robinson & Pitcher, 1989). However, since fish were fed during the experiment, it is more likely that the increased IID in the warm treatment was a direct result of the increased swimming activity, as fish in this treatment rapidly swam around the perimeter of the tank, close to the walls, in large circles. This pattern would also explain why NND was not different in the warm treatment compared to the fluctuating and control treatments. The control treatment NND was roughly 10–11 cm (c. 1–2 body lengths) with more cohesion marked by IID (roughly 30 cm). Fish in the warm treatment, however, formed smaller clusters of groups (e.g. three small subgroups of four fish), thereby increasing IID of about 40 cm (due to some fish being the entire diameter of the arena away), but NND remained similar due to the smaller clusters of fish each still with a close near-neighbour. Clustering into subgroups has been described previously as *active-sorting* behaviour of fish schools, based on familiarity of size or collective movements towards other fish (Hemelrijk & Kunz, 2004). Delta smelt were all of

similar size, and therefore the cluster formations were probably an artefact of increased individual swimming speeds leading to fragmented subgroups that collectively continued to move towards the group in front of them. Indeed, despite competitive interactions that drive fish to have greater NND, isolation also brings a greater risk of predation and reduces the advantage of the transfer of information (Foster & Treherne, 1981; Magurran, 1990; Major, 1978). Therefore, perhaps it is not surprising fish did not alter their NND from the control.

## 4.2 | Behavioural responses to predation cues

Fish reared under control and fluctuating temperatures demonstrated common adaptive anti-predator behaviours in response to conspecific alarm cues (Chivers & Smith, 1998). For example, alarm and predator-water cues were followed by increased shoal cohesion (i.e. reduced NND and IID) and dashing (elevated swimming speeds) before recovering to pre-stimulus levels (with some exceptions). Visual inspections of shoal cohesion (NND and IID) of the control treatment do indicate a recovery response was present following the alarm cue. Statistical tests indicated, however, that recovery of cohesion to pre-cue levels did not occur but a difference of 1–2 cm (for NND and IID) is probably not biologically significant. In contrast to the fluctuating treatment, swimming speed and turning angle (i.e. tendency to change direction) did not recover to pre-stimulus levels for the warm treatment, even after 20 min, as it did for fish in the control and fluctuating treatments. It was unexpected that swimming characteristics did not recover in the warm treatment. Sustaining unnecessary anti-predator responses has increased energetic costs that could ultimately lead to increased predation vulnerability (Fievet, Lhomme, & Outreman, 2008; Lind & Cresswell, 2005) because fish are energy limited with time and probably would not have the capacity to mount effective predator avoidance behaviours later when needed. Another response to a predation threat, the fright reaction (i.e. freezing time), has been shown to be a more persistent behaviour at colder temperatures in sea bass (Malavasi et al., 2013). Delta smelt showed an opposite pattern in response to predation and instead of freezing, they increased their activity. This is a common strategy for many fission–fusion species (i.e. changes in group splitting and merging) that rely on the confusion effect (Couzin & Laidre, 2009) to escape predation (Kelley, Morrell, Inskip, Krause, & Croft, 2011). Therefore, if responses to conspecific alarm cues are determined by energetics, as predicted, fish should eventually reduce their speeds and recover to normal behaviour, as occurred in the control and fluctuating treatments; however, why individual behaviours of delta smelt did not return to pre-cue levels in the warm-acclimation treatment is unknown. Fish in the warm treatment may suffer confusion in threat perception or even hypersensitivity (Brown, Bongiorno, DiCapua, Ivan, & Roh, 2006; Brown, Rive, Ferrari, & Chivers, 2006) to the alarm cue due to physiological stress (e.g. tank confinement and re-encountering walls).

Only delta smelt in the warm treatment reacted to the predator cue by increasing swimming speed, which may indicate a potential difference in delta smelt risk assessment ability dependent on warming regime. Commonly, prey fish in river and estuary systems live in close proximity to predators and so perhaps it is not surprising that delta smelt under control and fluctuating conditions showed no response in swimming speed to largemouth bass olfactory cues, indicating that visual cues are probably important in anti-predator responses (see review Brown, 2003). Another sensory modality of environmental cues may be utilised to detect and respond to predators. For example, a previous study on guppies, *Poecilia reticulata* (Poeciliidae), demonstrated a sensory response to increased temperature alone (without a predator) may be a learned environmental cue for predation risk (Weetman et al., 1998), as predators often have higher feeding rates in warmer water (Rice, Breck, Bartell, & Kitchell, 1983). Increased swimming velocity in delta smelt in response to predation cues may support this hypothesis of a learned cue. The differential response to predation by delta smelt in the warm treatment may be the result of a cascade of negative stimuli (i.e. warming + bass water). In response to both predation cues (conspecific alarm and predator water), group structure of delta smelt in the warm treatment grew more dispersed with a greater shoal size as seen in NND and IID. These group structure alterations coupled with the individual changes, such as reduced turning angle demonstrating a reduction in the tendency to change the direction of movements (present in more thrashing and erratic behaviour; Blaser & Gerlai, 2006) may create more opportunity for predators to isolate individuals from the group thereby increasing predation vulnerability (Major, 1978).

## 4.3 | Temperature effects on predation

Largemouth bass are less sensitive physiologically and behaviourally to warm temperatures compared to delta smelt. The maximum physiological temperature limit of largemouth bass ranges from *c.* 36 to 40°C (Smith & Scott, 1975) while delta smelt range from *c.* 26 to 29°C, depending on acclimation temperature (Davis et al., 2019; Komoroske et al., 2014; Swanson, Reid, Young, & Cech, 2000). Under the warm temperature treatment at 21°C, delta smelt swimming velocity significantly increased, which may have led to physiological stress. In contrast, largemouth bass feeding efficiency has been shown to increase at 21°C compared to colder temperatures (Rice et al., 1983), suggesting a mismatch in thermal optima. Differences in temperature sensitivity may have led to the increased predation mortality of delta smelt in the warm treatment. Differential effects of temperature on a predator's and a prey's physiology and behaviour have been shown in mosquitofish (prey, *Gambusia holbrooki*, Poeciliidae) and Australian bass (predator, *Macquaria novemaculeata*, Percichthyidae) (Grigaltchik, Ward, & Seebacher, 2012). Warming increased swimming capacity and escape speeds of mosquitofish to a greater extent than bass, thus reducing predation susceptibility (Grigaltchik et al., 2012). Largemouth bass behaviour in the present study was not quantified; however, predator attack speeds have been noted to increase with increased temperatures (Allan, Domenici, Munday, & McCormick, 2015) and largemouth bass do

have specialised eyes adapted for movement perception (Kawamura & Kishimoto, 2002), instinctually attacking prey moving at different speeds (Howick & O'Brien, 1983). The high swimming velocities of delta smelt in the warm treatment may have actually induced an increased predatory response in largemouth bass compared to the other temperature treatments. Evidence of movement induced predation was demonstrated in two of the eight predation trials. In these two trials, only two to four delta smelt were actually consumed, but all other delta smelt in the tank were either attacked at some point and left with apparent injury, or possibly chased to exhaustion leaving the delta smelt exhibiting severe LOE and, hence, ecologically dead.

Comparative predation trials conducted on mixed shoals of native delta smelt and non-native Mississippi silversides, as well as single shoals of Mississippi silversides provided additional insight into predation susceptibility of delta smelt. First, Mississippi silversides were predated on significantly more than delta smelt. Second, mixed species shoals seemed to have greater total counts of fish predated on compared to delta smelt in single species shoals; however, the increased predation of delta smelt under the warm treatment appeared to be reduced if in a mixed species shoal. Mississippi silversides may have experienced increased predation as they shoaled tightly and were half the size of the delta smelt and therefore may have been easier to catch by the largemouth bass, potentially consuming multiple individuals in a given attack (uncertain from video recordings) or were size-preferred by the bass (Hambright, 1991). These results suggest several potential implications for predation: (1) largemouth bass attempt to consume a delta smelt but have taste aversion (supported by the number of observed delta smelt injured or spit out following unsuccessful predation events; Gawlik, 1984; Morais, 2017); (2) the size of the delta smelt was outside of the largemouth bass prey size preference (Nobriga & Feyrer, 2007; Paradis, Pepin, & Brown, 1996); and (3) while the largemouth bass may not particularly like the delta smelt, increased temperatures created behaviours in delta smelt (i.e. increased swimming speed and dispersion), which enhance predator activity.

In conclusion, this study adds to the growing body of literature demonstrating the sensitivity of delta smelt to elevated temperatures (when warming is constant). Additionally, this study demonstrates the need for studies to conduct ecologically realistic experiments to better assess cause and effect of biological responses to environmental change, particularly for species of high concern. If natural temperature variation were not used in this study, the analysis and conclusions may drastically over-estimate the behavioural responses and predation risk. Additionally, this study showed that intra- and inter-specific species interactions and the influence of environmental factors can be complex. Anti-predator responses varied by cue type and predation mortality rates varied by species assemblages. Studies investigating species interactions should consider multi-species assemblages with non-native and native species that compete for similar resources, in addition to native and non-native predators. While this study tested elevated temperatures well within the tolerance limits of delta smelt, climate change warming projections for the SFE (freshwater rivers, estuaries, and bays) indicate that habitat temperature cycles will be altered such that the daily peaks in temperature will last longer, and the daily minimum temperatures (i.e. period of relief) will decrease in duration, thereby reducing delta smelt suitable habitat (Brown et al., 2013, 2016) and further negatively affecting the population. More studies are needed to test the thresholds for behavioural changes in responses to projected temperature cycles under climate change to accurately forecast resiliency of both delta smelt and other fishes to future habitat conditions.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.