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LETTER

Anomalous sea temperatures can impair coral reef fish recruitment

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Abstract

Understanding how temperature affects coral reef fish recruitment success is crucial for assessing impacts of ocean warming on coral reef resilience. We utilized a long-term fish survey dataset along the west coast of Hawai'i Island to investigate the role of sea surface temperature (SST) in influencing recruitment timing and density. The dataset consisted of 17 years of surveys, with 25 sites annually surveyed in the months of May, July, September and November. We found that peak recruitment, i.e. the maximum number of recruits recorded across all surveys per year, usually occurred during July surveys. For sites where peak recruitment for that year occurred outside July, there were significantly fewer fish recruits than for sites whose peak recruitment occurred in July. In addition, the timing of peak recruitment is influenced by anomalously warm or cool years prior to spawning. The decrease in recruit density outside these times is likely influenced by recruits being exposed to temperatures warmer and cooler than their optimum. Our results show that climate variability is having an impact on the timing of peak recruitment, creating a mismatch between the thermal optimum of developing recruits and the thermal environment they develop in, negatively affecting recruit density in critical coral reef habitats. Altered and reduced recruitment has the potential to disrupt reef community structure and long-term fisheries sustainability in Hawai'i, with important management implications for coral reefs in the future.

1. Introduction

Recruiting new individuals is a fundamental component of fish population dynamics, where a consistent supply of recruiting fish is essential for the maintenance of coral reef fish populations [1]. Recruits represent juvenile fishes that have settled onto the reef within the past few months, which are usually smaller than 5 cm [2]. For coral reef fishes, peak recruitment driven by seasonal spawning normally occurs during warmer months [3] in line with peaks in primary production [4] and optimal temperatures for growth [5]. At high latitude reefs, recruitment is seasonal [6], often occurring during summer with discrete pulses of recruitment [7, 8]. Minor changes in temperature can have negative impacts on developing fish, decreasing performance and survival [7, 8], and thus temperature is one of the most important determinants of growth during early life history [9]. As a result, early life stages of fish are the most sensitive to impacts of climate change [9].

Temperature has been found to impact the entire reproductive biology of fishes, from gametogenesis to spawning (reviewed in [10]). The response to temperature also changes with environmental history and the magnitude of thermal exposure. Gonadal development often commences after a post-spawning resting period, where the thermal environment of gamete development between annual spawning events can impact gamete maturation, sperm and oocyte quality, and ultimately spawning time [10–12].

Shifts in phenology in response to climate warming have been well-documented [13]. For commercially important fish such as Atlantic croaker (*Micropogonias undulatus*) and the walleye pollock (*Gadus chalcogrammus*), spawning is very sensitive to changes in ambient temperature [14, 15]. Warmer temperatures can result in both earlier spawning as seen in the Atlantic cod (*Gadus morhua*) [16], or delayed spawning through differential effects on gonad development as seen for the North Sea lesser sandeel (*Ammodytes marinus*) [17]. For coral reef fish like the grouper *Epinephelus striatus*, warming is causing a contraction in spawning season duration [18].

Changes in seasonal spawning patterns are critically important as they determine the conditions that early life stages, such as recruits, will encounter. The period between spawning and settlement lasts several months (e.g. a minimum of two months in the family *Acanthuridae*, or surgeonfish), and is associated with extremely high mortality during both the pre-settlement, planktonic phase and immediately after settlement [19, 20]. A major cause of mortality is predation, which may be affected by ocean warming. In several previous experiments, increased temperature led to higher maximal attack speeds by predators and reduced escape speeds, escape distances, and sensory performance in prey, increasing prey mortality overall [21, 22]. Recruits may therefore be highly vulnerable to temperature-mediated predation until they reach maturity, e.g. 0.73–1.21 years in *Ctenochaetus strigosus* (Kole) [23]. Climate warming, however, can benefit some species of temperate ectotherms by increasing their summer growing season [24]. Warmer winter temperatures have also been linked to increases in tropical fish diversity and abundance [25] with similar results seen on West Hawaiʻi reefs [26].

Recruits in Hawaiʻi also face non-climatic threats; for example, the aquarium fishery targets smaller size classes of fish and have caused significant reductions in fish abundances across collection sites in West Hawaiʻi [27]. In the Hawaiʻian Islands, which represents over 60% of coral reefs in the United States [28], young-of-the-year (YOY) fish are highly variable, with some years experiencing very low recruitment rates that subsequently influence overall fish communities [2]. YOY refers to the juvenile fishes that have hatched recently, i.e. recruit fish, typically ranging from a few millimeters to a few centimeters in length. YOY are often behaviorally distinct from the adults and provide important insights into recruitment and population health. YOY populations are often monitored to understand the reproductive success of a species, and to inform whether current fishing practices are sustainable [4, 29, 30].

The main goal of this study was to investigate whether ocean warming impacts recruitment success. In particular, we aimed to assess: (1) if and when during the year a significant peak in recruitment occurs, (2) Whether sea surface temperature (SST) anomalies influence the annual timing of peak recruitment for tropical reef fish, (3) If there is a cost to recruiting outside normal timing, i.e. does development under a different SST regime affect recruit density, and (4) What the optimal temperatures for developing recruits are. Ocean warming and heatwaves represent the most imminent stressors on Hawaiian coral reefs, where average monthly SST are projected to be ∼1 °C warmer than present-day [31]. Understanding whether recruits are impacted by temperature variability in Hawaiʻi will help show whether recruit survival will be affected by warm anomalies and heatwaves. An understanding of how ocean warming has influenced recruitment in Hawaiʻi is essential to conservation and management efforts in a continually changing climate [32].

2. Methods

2.1. Study region and recruit fish data collection

The dataset utilized in this study was part of the long-term, daytime monitoring program of coral reefs in West Hawaiʻi conducted by the Hawaiʻi Division of Aquatic Resources (DAR) at 25 permanent sites from 2003 to 2019, which span over 140 km of the West Hawaiʻi coastline (figure 1). While DAR conducts multiple rounds of surveys each year, we considered the surveys targeting recruits, which were conducted at four separate rounds per year from 2003–2019 during the months of May, July, September and November. Surveys are usually not conducted between November—May due to dangerous ocean conditions. Therefore, each site was surveyed four times per year.

At each site per round, four replicate transects were surveyed and averaged for the final data point per site (individuals m^{-2}). Each transect was 25 m long by 4 m wide, with the first two transects placed in opposing directions from a central pin, and the second two transects placed 10 m inshore and approximately parallel to the first two. Transects were located in coral reef habitats at depths ranging from 5–15 m, with a mean of 11.6 m. At each site, two divers each surveyed a 25 m × 2 m belt on either side of the transect line with counts combined to generate the full transect width. The divers first performed a ‘high’ swim, swimming down the transect and recording larger mobile species, mid-water species and uncommon species. On return, the divers performed a ‘low’ swim quantifying the remaining fishes, including cryptic species and recruits. While all species of fish and selected invertebrates were recorded along the transects, only recruits were considered in our analyses (table S1). Recruits were enumerated as such in the field based on size relative to known or estimated maximum sizes for YOY of each species [33].

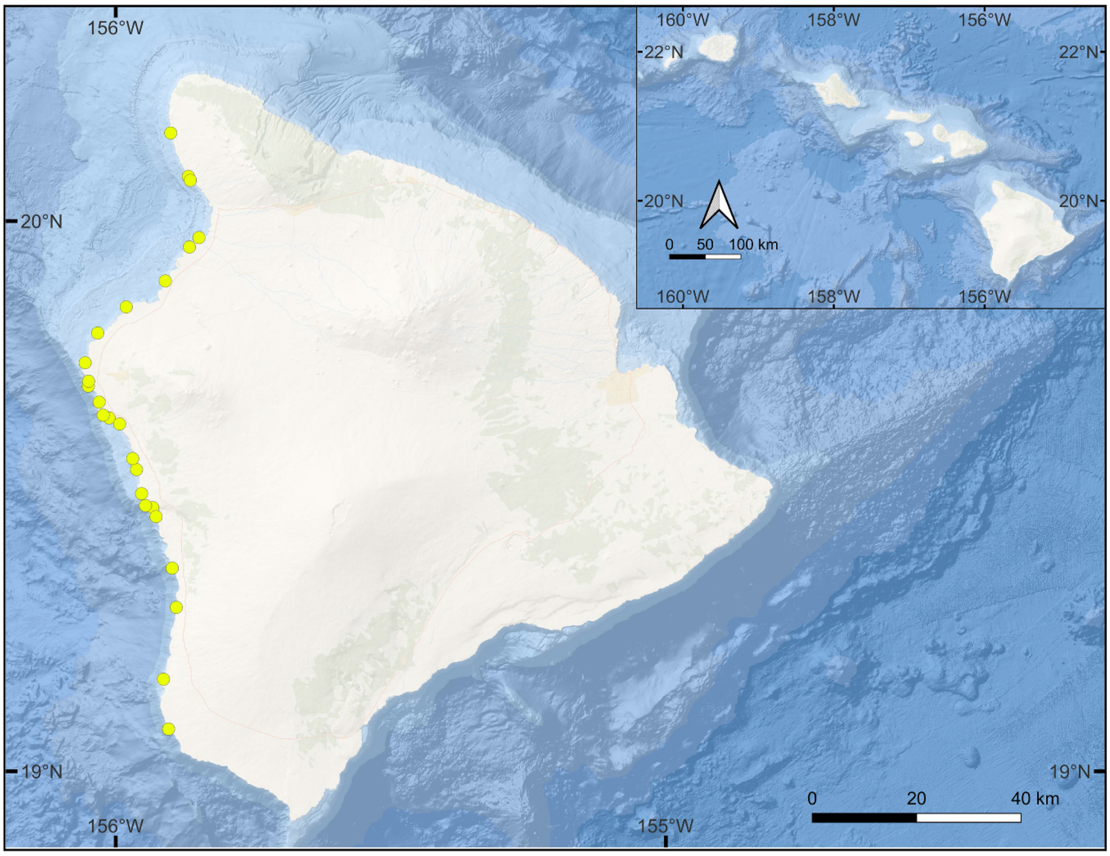

Figure 1. Locations of the Hawai'i Division of Aquatic Resources' 25 monitoring sites in West Hawai'i. The inset displays the Main Hawaiian Islands. The 25 permanent sites are indicated by the yellow circles. The map is based on QGIS basemap 'ESRI Ocean'.

2.2. SST data collection

We paired each individual fish survey across each site, round and year with remotely sensed measurements of SST and SST anomalies (SSTA) to assess how changes in the thermal regime affect the timing and density of fish recruitment. Hawai'i has experienced multiple heatwaves in the past decade, including heatwaves that induced coral bleaching in 2015 and 2019 [34, 35], providing sufficient temperature variation to analyse climatic effects on recruits. While we conducted a preliminary assessment of a range of oceanographic drivers beyond SST, including particulate organic carbon, salinity and currents, high-resolution data were lacking for our study sites and could not therefore be considered.

The U.S. National Oceanic and Atmosphere Administration Coral Reef Watch program (CRW) generates daily, satellite-derived global 5 km resolution SST dating back to 1985 [36]. SST and SST anomaly (SSTA, the difference between the current SST and the long-term average) data were extracted for each round of the 25 survey sites from 2003–2019 (Figures S1 and S2), with monthly SST and SSTA means derived as the mean of the daily measurements. CRW temperature data were accessed at https://coralreefwatch.noaa.gov/satellite/hdf/index.php and extracted for the pixel containing each survey location and date when the survey was conducted using ERDDAP [37] and the *sf* package in R [38].

2.3. Data analyses

All statistical procedures were performed in R software (v 4.2.1). Species-specific analyses were investigated but not included for several reasons: (1) recruit density is generally low in Hawai'i and we aimed to track broad recruitment patterns, (2) while recruit density was low due to high mortality at this stage [19], a range of recruit species were encountered across all surveys (table S1), but the majority of recruits recorded were represented by *Zebrasoma flavescens* (Yellow Tang) and *Ctenochaetus strigosus* (Kole) [2]. Therefore, all species were considered together for the analyses.

To assess when peak recruitment across the survey periods (May, July, September, November) occurred, we used bootstrapping to compare recruitment in May, July, September, and November at each site. Bootstrapping used 10 000 iterations drawing on 17 years of data (four rounds per year; $n = 1596$) to generate 95% confidence intervals (CI) for mean recruitment. Non-overlapping 95% CI was an indication that recruit means were significantly different [39] between survey periods. This analysis showed that the majority of recruitment occurred in July.

We then further statistically validated that peak recruitment, the survey month where recruit density was significantly higher than other months, was more likely to happen in July. To do this, we first identified the surveys that represented 'peak recruitment', i.e. the main peak in density of recruits of the year at each site, where each survey was assigned a binary value of 'peak recruitment' or 'not peak'. Peak recruit density was calculated by extracting the field survey round (i.e. May, July, September or November) which had the maximum recruit density across the four rounds for each site per year, removing any site that recorded exclusively low values for that year, i.e. less than the mean recruits recorded across the 25 sites for that year, because some sites had very low recruit density throughout the whole year and no true peak. This resulted in 245 observations of peak recruit density out of the total of 1596 surveys. We then used a chi-squared test to determine whether there was a link between the survey month and whether the survey showed peak recruitment (table S2). This test again indicated that a survey month of July was linked to peak recruitment (see Results), and we hereafter refer to July as the 'peak recruitment season.'

We then subset the recruit dataset to consider only peak recruitment counts, i.e. the main peak in density of recruits of the year ($n = 245$). To assess whether peak recruit density differed if the peak occurred outside the 'peak recruitment season' (identified from analysis above), we divided the peak recruit density surveys into two groups, where peaks occurred inside and outside of the 'peak recruitment season' and used bootstrapping with 10 000 iterations to generate 95% CI for mean peak recruitment inside and outside the 'peak recruitment season.'

As the thermal environment between annual spawning events and therefore peak recruitment, can impact spawning time [10], we extracted mean SSTA (°C) for the year prior to each survey year (e.g. if the survey was conducted in May 2018, the mean SSTA for 2017 was calculated) to investigate whether SSTA impacted peak recruitment timing in our surveys. The surveys were then divided into 'warm' (positive anomalies >0.1 °C), 'normal' (minor anomalies >-0.1 and <0.1 °C) and 'cool' (negative anomalies <-0.1 °C) depending on the SSTA of the year prior to the survey, and plotted as boxplots showing the mean SSTA of the prior year for each survey month when peak recruitment was observed. We used a fisher's exact test (appropriate when sample sizes are small [40]) to determine whether 'warm', 'normal', or 'cool' years impacted the timing of peak recruitment (i.e. May, July, September, November) from peak recruit density surveys ($n = 245$). Fisher's exact test is used to determine if the proportions of categories across groups significantly differ from each other, and if the counts observed differ from what is expected.

We used a generalized additive model (GAM) to quantify the relationship between SST and peak recruit density to understand optimal temperatures for developing recruits. As recruit survival is variable month to month [2, 19], we considered the mean SST of the month that the survey was conducted. GAMs are appropriate when fitting non-linear relationships as determined through model testing. For the GAM, we used peak recruitment data ($n = 245$) co-located with the mean SST during the month and year of each survey. Using the *mgcv* package in R, a model was developed where we included SST as a variable, incorporating 'site' as a random effect in our model to account for possible spatial autocorrelation of sites and population sample bias [41, 42]. Several models were fitted as suitable for count data with the best model (determined by assessing the heterogeneity of the error distribution and histograms of the residuals) fitted with a negative binomial distribution, appropriate for overdispersed count data. We limited the number of knots to four to prevent overfitting of the model. We then used this model to predict the peak recruit density across different SSTs using the predict procedure from the *mgvc* R package.

3. Results

3.1. Temporal patterns of recruit density

When considering all survey data ($n = 1596$), bootstrapped estimates of CI for mean recruitment across survey months indicated a significantly greater density of fish recruits in July. There were significantly fewer recruits in other survey months (May, September and November) (figure 2(A)). A chi-squared test of independence showed that a significantly higher number of peak recruitment surveys occurred in July (65%) than in other survey months (table S2), X^2 $(1, n = 1596) = 205.92, p < 2.2\times10^{-16}$. Therefore, July was determined as the normal peak recruitment season where recruit density was significantly higher than other months, and the month where peak recruitment was more likely to occur.

When the dataset was subset to only those surveys that logged peak recruitment per site for that year ($n = 245$), bootstrapped estimates show that when peaks occur outside of the 'peak recruitment season' of July, there were significantly lower densities of peak recruits (figure 2(B)).

3.2. SST anomalies and timing of peak recruitment

For those surveys that captured peak recruitment per site and per year ($n = 245$), the mean SSTA for the entire year prior to the survey were extracted, with surveys classified as 'warm', 'normal' and 'cool' (see *Data analyses*). Table 1 shows the frequency of surveys per month (May, July, September, and November) from this dataset, organized by whether the previous year was 'warm', 'normal' or 'cool' where fisher's exact test showed these were significantly different ($p = 0.0005$), i.e. the SSTA of the previous year affects when the month of peak recruitment occurs.

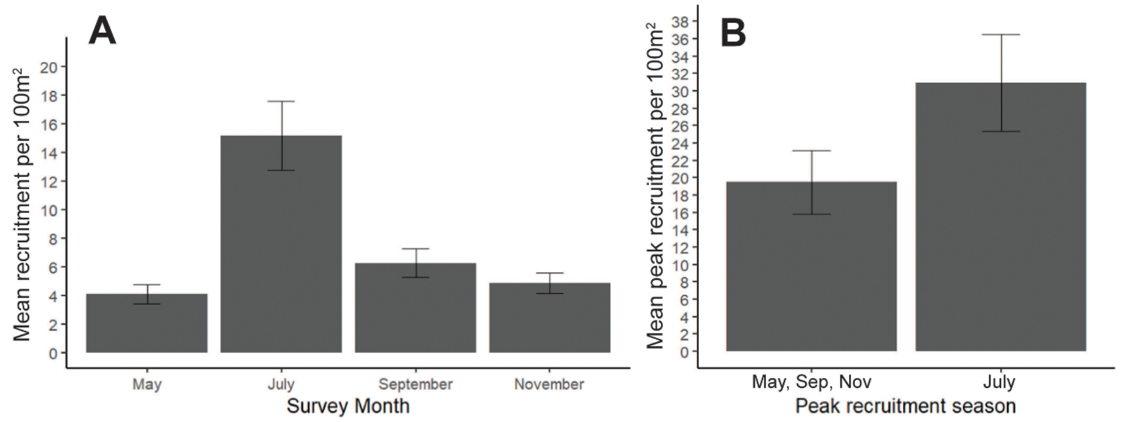

Figure 2. Patterns of fish recruitment. When considering all surveys ($n = 1596$), mean recruitment with 95% confidence intervals across survey months (A) show that the greatest number of recruits occur in July. When considering peak recruit surveys only ($n = 245$), mean peak recruitment with 95% confidence intervals inside (July) and outside (May, September and November) the peak recruitment season (B) show that peak recruitment is significantly less when it occurs outside July. Non-overlapping error bars indicate significant differences between groups.

Table 1. Counts of peak recruitment surveys per month categorized by sea surface temperature anomalies for the previous year. Fisher's exact test shows that the timing of peak recruitments depends on whether the SSTA of the previous year was warm, normal or cool.

SSTA of previous year	Warm >0.1 °C	Normal >−0.1 and <0.1 °C	Cool <−0.1 °C
May	18	1	5
July	67	43	49
September	9	2	24
November	11	0	16

To explore this relationship further, boxplots of mean SSTA of the year prior to each survey with the month of peak recruitment show that the timing of peak recruitment in July is associated with minimal SST anomalies (figure 3). Warm previous years (i.e. SSTA > 0.1 °C) are associated with peak recruitment occurring in May, with cooler previous years (i.e. SSTA < -0.1 °C) associated with peak recruitment occurring in September and November (figure 3).

3.3. Impacts of SST on peak recruit density

A GAM was used to explore the relationship between SST and peak recruit density ($n = 245$) revealing a non-linear relationship (figure 4). While the results are quite variable due to differences between sites, SST is significantly related to recruit density (figure 4 and table S3). The thermal performance curve indicates that the greatest number of recruits occur when SST is ~26 °C–27 °C, which is close to the mean July SST and also the November SST (figures 4 and S1). Peak recruit density was less when SST was cooler or hotter than 26.5 °C. Recruits, however, seem more heat tolerant than cool tolerant due to a much steeper decrease seen in recruitment with cooler SST in comparison to warmer SST.

4. Discussion

We utilized a long-term dataset on reef fish recruits to investigate whether SSTA impacts recruitment timing and whether SST impacts recruit density, processes critical to reef fish populations, community structure and ecosystem processes. When considering all survey data, a clear peak in recruitment occurs in July in comparison to other survey months. In years when peak recruitment occurs before or after July, there are significantly fewer recruits per site, showing that there is a cost when recruitment occurs outside the normal time.

Considering there is a negative impact of recruiting outside of the month of July (i.e. it leads to fewer recruits), we sought to understand why peak recruitment timing may change across years. As shifts in phenology in response to temperature are well documented [13], we investigated whether SSTA of the year prior to recruitment would affect when the timing of peak recruitment occurs. We find that anomalously warm years prior to recruitment are related to peak fish recruitment occurring earlier in the year, i.e. in May rather than July. When an anomalously cool year occurs prior to recruitment, we see the opposite pattern, with peak recruitment occur-

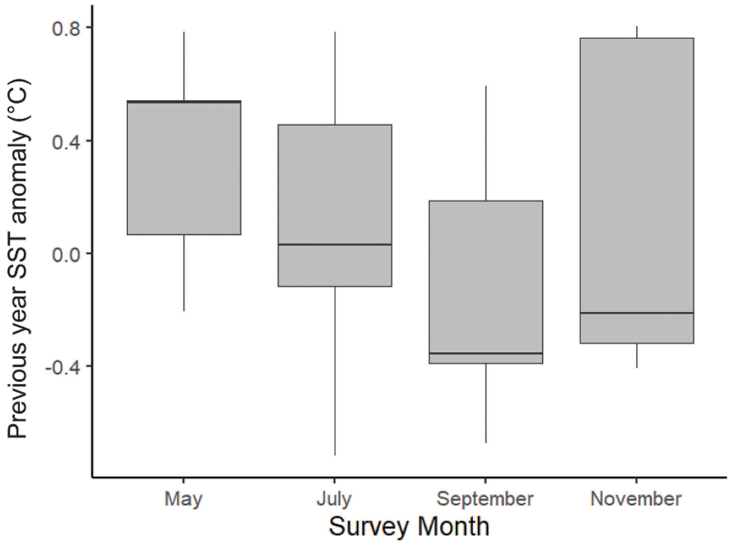

Figure 3. Boxplots of the mean SSTA of the year prior to maximum recruitment, by month. Surveys are only included in this boxplot if peak annual recruitment was observed in the stated month. The figure shows that when the previous year is warmer than expected, i.e. a higher SST anomaly, peak recruitment more frequently occurs in May, with the opposite seen for cool anomalies.

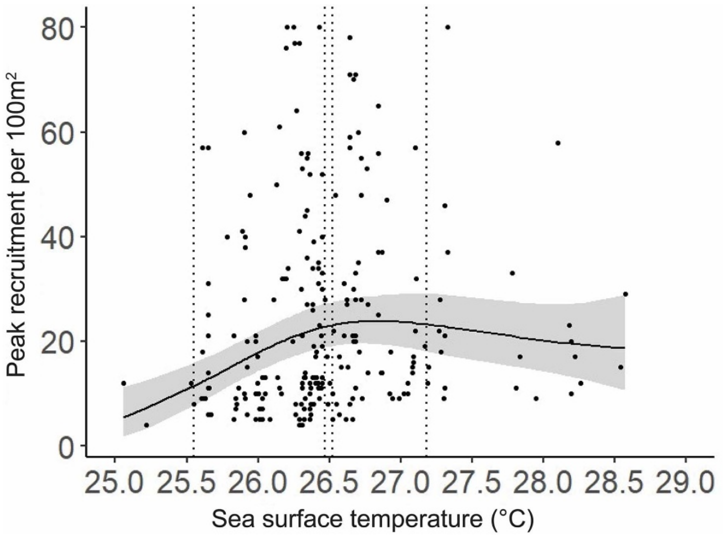

Figure 4. Thermal performance curve of peak recruit density, modeled by GAM with 95% prediction intervals. The dotted lines represent the mean SST of May, November, July and September from L–R. Raw values show the average number of individuals per 100 m^2 recorded at each site and round from 2003–2019 matched with mean SST during the month that the survey was conducted.

ring later in the year, i.e. in September and November. With minimal anomalies, we see that peak recruitment is more likely to occur in July, in line with the normal peak recruitment period. Therefore, in years of anomalous SST, atypical temperature conditions over the previous year have the ability to impact the timing of peak recruitment.

This change in recruitment timing could be due to negative impacts on gonad development and oocyte quality [43, 44]. As ectotherms, fish metabolism increases with greater SST, thus increasing the demand for food. Increased SST could be diverting the energy required for developing gonads thus negatively impacting both larvae and recruitment success. Additionally, there are other stresses induced by increased SST such as generation of heat-shock proteins, further diverting energy away from reproductive strategies [44]. Cool temperature anomalies can be similarly problematic and gonad degeneration, decreased egg size, and reduced fertility have been observed in cooling reservoirs [45].

The timing of recruitment, in turn, determines the temperature conditions under which recruits continue to develop. Recruiting before or after July shifts the normal temperature regime that fish recruits encounter. While recruit density is known to be variable, likely due to year-to-year fluctuations and site variability [46], the GAM model shows patterns of recruit density with SST. The greatest peak recruit density occurs ∼26 °C–27 °C, which is also closest to the long-term mean SST of July that young recruits would normally encounter. From the model, we see that peak recruitment density decreases either side of ∼26 °C–27 °C, with a steeper decrease observed with cooler SST than warmer SST. Increased temperature has been shown to influence fish growth, reproduction and metabolism up to a thermal limit [47], which could help explain why recruits appear to be more heat tolerant than cool tolerant. The change in timing of peak recruitment is causing a misalignment in temperature regimes and is exposing recruits to temperatures outside their performance optimum. Increasing temperatures cue reproduction and spawning in summer [44], thus anomalously warm years and heatwaves late in the year could be cueing summer spawners to start earlier than normal. It appears that recruiting in early summer, before July, is not beneficial for recruits as they are exposed to SST below the thermal optimum. While the long-term mean SST of November is similar to July, and could provide recruits the optimal temperature to develop in, recruiting after July is more likely to expose the recruits to SST that are warmer than optimal, where heatwaves tend to occur during September onwards in Hawai‘i [26, 48].

Our results show that changes in ocean temperature can adversely affect fish recruits in Hawai‘i through multiple processes, by decoupling the predictable timing of peak recruitment and exposing them to thermal regimes that are sub-optimal for recruit development. This has the potential to negatively impacting recruit survival. This study, however, only investigated general trends; to better inform possible management strategies, conducting recruit surveys equally across all seasons and months as in [2] would help to improve the prediction accuracy of SST impacts on recruits, particularly important for fish that mainly recruit in winter in Hawai‘i, such as *Thalassoma duperrey* (Saddle wrasse), since responses to global warming could differ between summer- and winter-growing fish species. Further, for *Z. flavescens* and *C. strigosus*, which represent the dominant species of recruits detected in these surveys and are also some of the key species targeted in the aquarium industry [8, 27, 49], investigation into sustainable catch limits will be important to understand, especially during heatwave years. Photoperiod and temperature are the key factors in phasing reproductive seasonality, but other environmental cues include nutritional status [50], lunar cycle [51] and precipitation [52]. Such data, if collected during the time of the surveys, could help provide a more detailed understanding of local conditions driving recruitment and how they interact with temperature.

Cool years followed by heatwave years may pose a large threat to recruits as our results show that anomalously cool years influence delays in peak recruitment timing (i.e. recruitment delayed until after July). This, in turn, increases the likelihood that recruits are exposed to high temperatures which typically occur in late summer in Hawai‘i; for example, heatwaves in the region usually occur during September [48]. Management strategies that focus on protecting recruits, such as minimum size limits or bans on aquarium fishing, will be essential to preventing significant declines in coral reef fish in Hawai‘i.

Data availability statement

Fish data are available to download from NOAA's NCEI data repository.

The data that support the findings of this study are openly available at the following URL/DOI: www.ncei.noaa.gov/access/metadata/landing-page/bin/iso?id=gov.noaa.nodc:0164965. The most current data can be requested from the Hawai‘i Division of Aquatic Resources team in Kailua–Kona.

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