



Impacts of increasing temperature due to global warming on key habitat-forming species in the Mediterranean sea: Unveiling negative biotic interactions

Mar Bosch-Belmar^{a,b,*}, Mario Francesco Tantillo^{a,**}, Gianluca Sarà^{a,b}

^a Department of Earth and Marine Science (DiSTeM), University of Palermo, Palermo, Italy

^b NBFC, National Biodiversity Future Center, Palermo, Italy

ARTICLE INFO

Keywords:

Biotic interactions
Stressor
Warming
Predation
Metabolism
Behavior

ABSTRACT

Temperature plays a pivotal role in prey-predator interactions, acting as a potent source of disturbance that can reshape the strengths of interactions between prey and predators. This alteration can subsequently destabilize populations and trigger shifts in the dynamics of ecosystems and food webs. The rising temperatures are exerting significant impacts on Mediterranean biodiversity and community structure. These changes have the potential to influence predation dynamics among co-occurring species, each with distinct responses to the changing climate. Here, we present a case study that delves into the impact of temperature on the biotic interaction between a thermophilic predator polychaete (*Hermodice carunculata*) and a threatened, key structuring coral species (*Astroides calycularis*). Through manipulative laboratory experiments, we explored three main aspects: i) polychaete Prey Preference: the prey preference of *H. carunculata*, revealing that it indeed displays a distinct preference for feeding on *A. calycularis* over other options. ii) Temperature Effect on Predator Ingestion Rate: we examined how temperature influences the ingestion rate of the predator. Notably, we found that the predator's predation performance peaks at a temperature of 25.6 °C, which is in close proximity to the upper thermal limit of the coral. iii) Prey Metabolic Response: when exploring the metabolic response of the prey to contact with the predator, we observed an immediate reaction from the prey. This response led to a decline in the coral's feeding capability and an alteration in its metabolic functioning, effectively worsening the coral's overall performance. These findings underscore that *H. carunculata* not only displays a preference for consuming *A. calycularis* but also exhibits optimal predation performance at a temperature near the coral's upper thermal threshold. Furthermore, the prey's response to the presence of the predator has rapid and detrimental consequences, negatively impacting the coral's metabolic function. Comprehending the repercussions of environmental change on biotic interactions holds paramount importance. It allows us to forecast and manage the trajectory and conservation efforts of biodiversity under current and projected climate change conditions.

* Corresponding author at: Department of Earth and Marine Science (DiSTeM), University of Palermo, Palermo, Italy.

** Corresponding author.

E-mail addresses: mariadelmar.boschbelmar@unipa.it (M. Bosch-Belmar), mariofrancesco.tantillo@unipa.it (M.F. Tantillo).

<https://doi.org/10.1016/j.gecco.2024.e02844>

Received 29 November 2023; Received in revised form 8 February 2024; Accepted 9 February 2024

Available online 13 February 2024

2351-9894/Â© 2024 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).



eEblab
www.unipa.it/gsaralab
courtesy copy
not for commercial use

1. Introduction

Competition and predation stand as pivotal forces shaping ecosystems, exerting considerable influence over community structure encompassing factors like species biomass, composition, and taxonomic as well as functional biodiversity (Freestone et al., 2020; López and Freestone, 2021). Biotic interactions, when intensified or prompted by new species introductions, can act as sources of disturbance. Such biological relationships, when heightened, contribute to novel interactions. Consequently, this may transpire when new species arrive on the scene. In this context, stressors often compound and interact, ultimately molding the responses of organisms and communities to the effects of multiple disturbances. The outcome of these interactions largely hinges on the magnitude and the relative timing of each stressor (Gunderson et al., 2016; Jackson et al., 2021). For instance, the interplay between climatic stressors and the dispersal capability of certain species can profoundly influence the organization of native communities. This synergy can pave the way for the emergence of novel ecological communities, characterized by unique arrangements and ecological interactions. When multiple stressors converge, their effects produce non-linear outcomes that may either be more pronounced (synergistic) or milder (antagonistic) than the combined effects of individual stressors (Darling and Côté, 2008; Gunderson et al., 2016). The potential for interactive effects hinges on the identity and quantity of stressors involved, as well as the trophic position and life-history stage of the organisms affected (Lyons et al., 2016).

At higher levels of the ecological hierarchy, such as populations and communities, biotic interactions can serve as direct stressors (e.g., ecological stressors like competition, predation, and density effects; Power, 1997; Darling and Côté 2008), or they can indirectly disrupt the availability of resources or local environmental conditions (Bruder et al., 2017). Present endeavors to forecast the ramifications of global change predominantly center around the ecological prerequisites of individual species (Kordas et al., 2015). However, an increasing awareness underscores the alteration of biological interactions due to stressors associated with global climate change (Bennett et al., 2015; Bulleri et al., 2016). Given that interactions are inherently dynamic, an imperative exists to comprehend the mechanisms governing the dynamics between prey and predators in the face of unexpected alterations induced by abiotic factors, especially those linked to climate change, such as rising temperatures (Van Der Putten et al., 2004). Rising temperatures and recent marine heatwaves in the Mediterranean Sea have begun to significantly alter the composition and structure of communities (Garrabou et al., 2009; Gómez-Gras et al., 2019). Habitat formers, particularly those found in shallow rocky environments like the vulnerable endemic coral *Astroides calycularis*, have faced severe consequences due to thermal stressors over the past few decades. These stressors have led to substantial mass mortalities in populations, particularly during the more frequent thermal anomalies that occur in the warmer months (Gambi et al., 2018, 2010; Garrabou et al., 2022). Despite the evident negative effect of climate change on the coral performance, there is no scientific evidence regarding the conservation of the species. Because stressors seldom act in isolation, various disturbances, including local factors like biotic interactions, may interact synergistically, impeding species performance and community functions in habitats that are already strained and vulnerable. Against the backdrop of ongoing climate change, particularly in the Mediterranean Sea, rising temperatures have facilitated the expansion and higher densities of non-native and thermophilic species. Among these is the stinging polychaete *Hermodice carunculata*, which is regarded as a "native invader" and is extending its distribution range (Righi et al., 2020). Given its omnivorous behavior and habitat overlap with *A. calycularis*, this invasive species poses a tangible threat to shallow benthic communities, especially those that are already disrupted by climatic stressors.

In response to these concerns, we conducted manipulative mesocosm experiments to delve into the predatory behavior of the fireworm, *H. carunculata*, toward one of the Mediterranean Sea's most crucial shallow structuring species: the orange coral *A. calycularis*. Additionally, we explored the coral's metabolic response to this biotic stressor in the context of climate change. Our objective was to ascertain whether the heightened frequency of interaction between the fireworm and the coral, within the context of climate change, could impact the habitat former's performance, particularly in terms of metabolic responses and predation pressure. To address this, we undertook three distinct interaction experiments, each under escalating temperatures: i) The first experiment sought to determine whether *H. carunculata* exhibited a preference for feeding on *A. calycularis*. We conducted prey preference experiments involving two different Mediterranean coral species (*A. calycularis* and *Cladocora caespitosa*, the latter being a known prey for fireworms). ii) Once predation on *A. calycularis* was confirmed, a second experiment was designed to investigate the fireworm's predation rate on the coral colonies at varying environmental temperatures, thereby constructing a performance curve and identifying optimal and upper thermal predation thresholds for the polychaetae. iii) Lastly, we conducted short-term interaction experiments between *H. carunculata* and *A. calycularis*, assessing the metabolic response of the threatened coral by measuring its respiration rate as a proxy for coral metabolism at two different temperatures (16 °C and 27 °C). This comprehensive study offers crucial insights into the role of climate change stressors on marine benthic communities and provides a mechanistic framework for predicting the impact of biotic interactions in driving such events, including mass mortalities.

2. Material and methods

2.1. Organisms' sampling and maintenance

To perform all experimental trials a total of 105 colonies of *A. calycularis*, 6 colonies of *Cladocora caespitosa* and 102 individuals of the fireworm *Hermodice carunculata* were collected along the coast of Palermo (Italy) (38°11'12.786"N; 13°21'41.1336"E) with sampling effort limited as much as possible to reduce disturbance to the natural populations while maintaining the robustness of the experimental design. Moreover, all colonies were sampled to have a similar size (when possible) to be easy to manipulate, comparable and suitable for mesocosm experiments. Once in the laboratory all colonies were carefully inspected and when possible, all epibiotic organisms were manually removed by forceps. Coral colonies and fireworms were divided and kept separately in three 60 L tanks (3 for

A. calycularis and *C. caespitosa* and 3 for *H. carunculata* individuals) filled with filtered seawater for 10 days, to allow correct acclimation and limit the potential stress deriving from sampling and manipulation. All aquariums were equipped with a skimmer and filtering system, water pumps, individual heater and temperature controller systems. HOBO temperature (Onset Inc., USA) loggers were employed to record temperatures throughout the trials and set at minute data recording. Corals were fed with *Artemia salina* nauplii every 2 days, while fresh mussels were offered to polychaetes every 5 days.

2.2. Measured fireworm behavioural traits

Preliminary observation period of the interaction between *H. carunculata* and *A. calycularis* was performed and according to what was observed predator behavior was categorised in terms of its structure and consequences, identifying three different behavioural traits to be measured in all three experiments: i) “exploring time”: mean time that the predator employed moving around the experimental aquaria immediately after the trial started (measuring units: minutes); ii) “interaction time”: mean time that the predator physically contacted the prey without feeding on it (measuring units: minutes); and iii) “predation rate”: mean number of preyed calyxes for each prey species per day. Measuring duration varied with the measured trait: “exploring time” was continuously observed by an operator during the first 2 hours after the start of the prey-predator interaction; while “interaction time” and “predation rate” were measured at the beginning of the interaction (as “exploring time” variable) and at 5 different posterior times (once per day during 5 days between 3 and 5 pm, as that is the daily time during which the fireworm shows its maximum activity, Wolf and Nugues, 2013).

2.3. Prey preference trials

Hermodice carunculata is a known corallivorous predator (Wolf et al., 2014), which has been observed actively preying on the Mediterranean scleractinians *Cladocora caespitosa* (Simonini et al., 2018) and *Astroides calycularis* (authors field personal observation). In this experiment, we tested the predator’s preference towards two different corals to investigate behavioral traits of predators in major detail. After laboratory acclimation period (previously described), 12 individuals of *H. carunculata* (13.02 ± 1.35 g, mean \pm s.e.) were fed to satiation and then left starving for 10 days prior to predation experiments (Simonini et al., 2018). Six colonies of *A. calycularis* and six of *C. caespitosa* were sampled and carefully inspected in the laboratory to eliminate any other potential prey. Colonies from both species were put in pairs (1:1 *A. calycularis*-*C. caespitosa* colonies) and acclimated in 6 different aquaria of 3 L during 24 h prior the exposure to the fireworm. Colonies of the two species were placed in opposite sides of the aquarium. After this period, one specimen of *H. carunculata* (11.6 ± 1.81 g, mean \pm se) was put in the center of each experimental aquaria (at the same distance from both colonies of the two colonial corals) and the 3 beforementioned behavioural traits (exploring time, interaction time and predation rate) were measured in each experimental unit over time (once per day during 5 days) (Maselli et al., 2020, Simonini et al., 2018). After each experiment, the polychaetes that did not consume the prey were provided with a control food (pieces of unfrozen mussel) to verify that they were not satiated and unwilling to consume any food.

2.4. Modeling predation curve over temperature

Once predation of *H. carunculata* on *A. calycularis* was experimentally tested, we investigated the predation response of the fireworm under different natural Mediterranean temperature conditions. Seven different temperatures ranging from 10 to 31 °C were decided (10, 15, 20, 24, 27, 29 and 31 °C) based on minimum and maximum temperatures observed in the last 5 years in the areas where the species are present. Six different coral colonies of similar size (between 18 and 20 polyps each) and 6 polychaetes (12.4 ± 1.21 g, mean \pm s.e.), were independently used at each temperature (for interactions) and 3 coral colonies per temperature were used as controls for behavior and morphological traits observations (63 coral colonies and 42 fireworms in total). Organisms were individually kept in 3 L aquaria and temperature was increased/decreased at 1 °C h⁻¹ rate (Bosch-Belmar et al., 2021; Marchessaux et al., 2022). After reaching treatment temperature they were acclimated during 5 days at those conditions that were kept stable by means of a circulated thermal bath (Grant Optima TX150) and additionally monitored throughout the recording period by HOBO Pendant® loggers. In addition to traits measured for predators some behavior and morphological prey traits were assessed at the highest tested temperatures in this specific experiment: tentacle contraction (measured as 0/1 when prey was contacted by the predator) and the presence of necrotic tissue (as the number of calyxes presenting necrose at 27, 29 and 31 °C) to assist us in discriminating between the effect of predation and high temperatures on the scleractinian. After acclimation, one fireworm specimen was put within each treatment coral aquaria and observations on predation were performed as for the prey preference experiment.

2.5. Prey metabolic response to predator contact

A first step consisted in experimentally studying the effect of contact between corals and fireworms to test whether coral metabolic change was significant under fireworm exposure under increasing temperatures. After acclimation period, two experimental sets were created according to temperature factor [T16 °C and T27 °C, n = 18 coral colonies (containing between 18 and 20 polyps) and 12 fireworms; 12.1 ± 1.5 g, mean \pm se] by increasing/decreasing 1 °C h⁻¹ from each sampling temperature. Once each experimental temperatures were reached, 18 coral colonies per each temperature treatment were randomly selected and individually kept in 18 small aquaria (2 L) at the reached experimental conditions for 5 days to allowed correct thermal acclimation (Simonini et al., 2018). Twelve of these aquariums were used for the exposure trials (contact with *H. carunculata*), while 6 of them were used as controls (without interaction with the fireworm). After 24 h, one random selected *H. carunculata* specimen was moved to each “interaction”

aquaria for 6 h period according to Simonini et al., (2017), (2018). Beforehand, four video recording cameras (Go Pro version Hero 8 Black) were employed to record the whole steps of interaction in each tank (Martin and Bateson, 1993). Movies were analyzed by an operator to measure exploring time, interaction time and predation rate of both inter-players during each interaction trial.

Respirometric measurements. This second step consisted in measuring metabolic response as expressed by the oxygen consumption (RR, $\text{mg O}_2 \text{ h}^{-1} \text{ g}^{-1} \text{ DW}$) as described below to estimate if the predation by fireworms was recorded at metabolic level by corals, as a proxy of predation risk. In doing so, the 18 coral colonies from each treatment temperature trial were gently moved to respirometric chambers (volume = 310 ml) containing filtered (Whatman GF/C 0.45 μm) air-saturated kept at 38 psu seawater, which is the commonest salinity usually found in the South Tyrrhenian Sea subtidal range at the depth where both organisms co-occurred. To ensure the constant mixing of the water, each chamber was stirred with a magnet bar and an individual stirring device (Bosch-Belmar et al., 2016). Respirometric chambers were further randomly divided into three temperature-controlled water baths and the concentration of dissolved oxygen was measured simultaneously by means of 6 optical oxygen meters (model: Firesting O2; PyroScience Inc. Germany), each equipped with four optodes (24 optodes in total). Four respirometric chambers were used as control in that they were filled only with filtered seawater. Oxygen concentration measurements were performed in continuum for 1 hour and a half, and data useful to estimate the consumption were extracted from the central hour to avoid edge effects. Temperatures in chambers were kept stable by means of a circulated thermal bath (Optima TX150, Grant Inc., UK) and additionally monitored throughout the recording period by HOBO. Respiration rate (RR, $\text{mg O}_2 \text{ h}^{-1} \text{ g}^{-1} \text{ DW}$) was calculated according to Sarà et al. (2013). After the measurements, colonies were kept undisturbed in the respirometric chambers with aerated water for 1 hour (to increase the available recovery time for the treated organisms) and then, each replicate was dried at 90 °C for 24 h and the dry weight (DW, g) was determined (Goffredo et al., 2011) relationship. The same procedure was followed for *H. carunculata* individuals.

2.6. Data analysis

To test if the fireworm predated preferentially on the two offered coral species a GLM with zero inflated Poisson family distribution was used, as our dataset presented a huge amount of zero. Moreover, “colony id” has been added to the model as random variable in order to remove or reduce a source of variance linked with a single colony, and to handle also with non-independence condition among polyps belonging to the same colony. Data regarding *H. carunculata* predation rate on *A. calycularis* were fitted through a non-linear model by using nlsLM and rTPC packages in R (Padfield & O’Sullivan 2020). Accordingly, a total of 21 non-linear least squares performance models were launched and compared, and this allowed us to identify the Briere (Briere et al., 1999) as the “best” fitting model for predation data (i.e. presenting the lowest AICc score). After checking for data normality and homoscedasticity respiration rate data from the “prey metabolic response to predator contact” experiment was analyzed through a Generalized Linear Model (GLM) with “time of interaction” as weighted factor. After each model was run, a check was made on the residuals to ensure that no particular trends were present and that they were normally distributed.

3. Results

3.1. Prey preference trial

Initially, fireworms showed an exploring behavior (18 ± 6.3 min, mean \pm s.e.) moving around the aquarium. Once the prey was

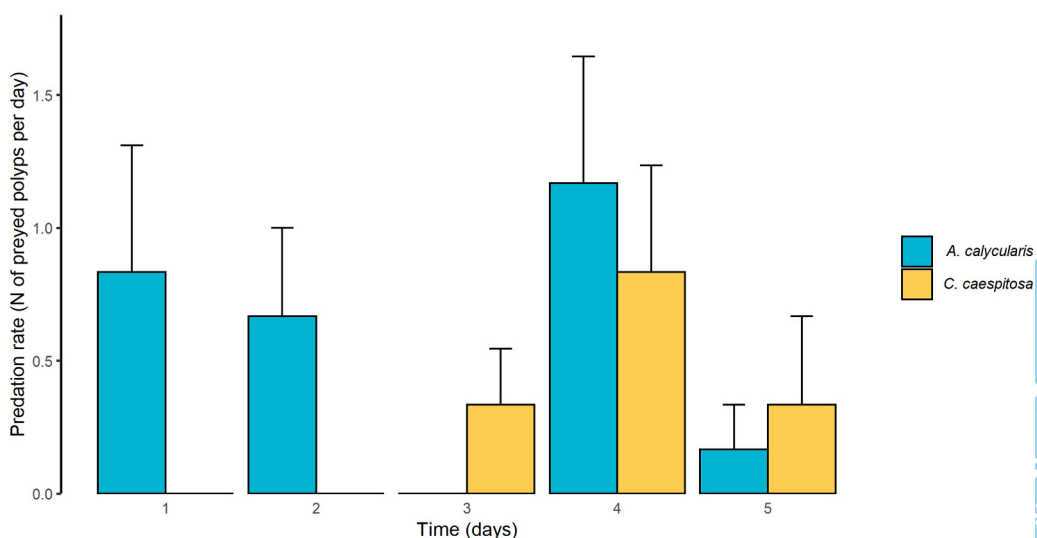


Fig. 1. *Hermodice carunculata* predation rate (mean number of preyed polyps per day) on *A. calycularis* and *C. caespitosa* colonies over time (5 days of observations).

encountered, the predators passed over them with a “prey inspection” behaviour (measured as “interaction time”) and “walk around” during 14 ± 7.7 min, mean \pm s.e.), but no predation was observed during the day of initial interaction. When predation attacks were recorded during the subsequently observation days, fireworm behaviour consisted in everting the pharynx and preyed on corals through suction movements exerted by the pharyngeal musculature. Colonies of both species were partially consumed during the 5 observation days, firstly leaving bared the edge of coenosarc and then the complete calyx. Statistical analysis showed not significant difference between the predation rate (mean number of preyed polyps per day) of the fireworm *H. carunculata* on both coral species ($t= 1.458$, $p > 0.05$), therefore, *H. carunculata* showed higher preference to prey on *A. calycularis* during the first exposure days exclusively feeding on the orange coral. Overall, a higher predation rate was observed on *A. calycularis* than to *C. cespitosa*, being the total number of consumed polyps and the percentage of consumed prey during the 5 days of observations 17 and 9, and 12.86 ± 5.25 and 3.48 ± 1.42 respectively (Fig. 1). This potential preference may be due to the calyx morphology of *A. calycularis* polyps which present a more accessible structure for the feeding strategy employed by *H. carunculata*.

3.2. Modeling predation curve over temperature

Significant differences in *H. carunculata* interaction time and predation rate on *A. calycularis* were observed at different temperatures and over time ($p < 0.05$ for both). The highest interaction time between the fireworm and the coral was recorded at 24 and 27 °C (21.7 ± 2.9 min, 28.3 ± 1.1 min respectively, mean \pm s.e., Fig. 2a), but in agreement with the previous experiments, no predation was observed in the day of starting interaction. The highest predation rate over the tested temperature range was observed at 24 and 27 °C, especially in the second and fourth day of experiment (Fig. 2b).

Modeling approach showed that Brier model was identified as the best fitting model for predation data (Appendix S1: Figure S1), showing an optimum (the highest predatory performance) at 25.6 °C and a critical upper threshold (temperature where predatory performance drastically decreases) of 30.9 °C (Fig. 3).

Behavior corroborated the model predictions, in that we observed reduced mobility in the fireworm individuals at 29 °C and the absence of movement and predation at 31 °C (Fig. 3). Experimental corals (those exposed to *H. carunculata* and controls) showed tentacle contraction at 27 °C, 29 °C and 31 °C, and necrotic tissue was observed at the highest temperature, highlighting the negative effect of high temperatures on the coral performance.

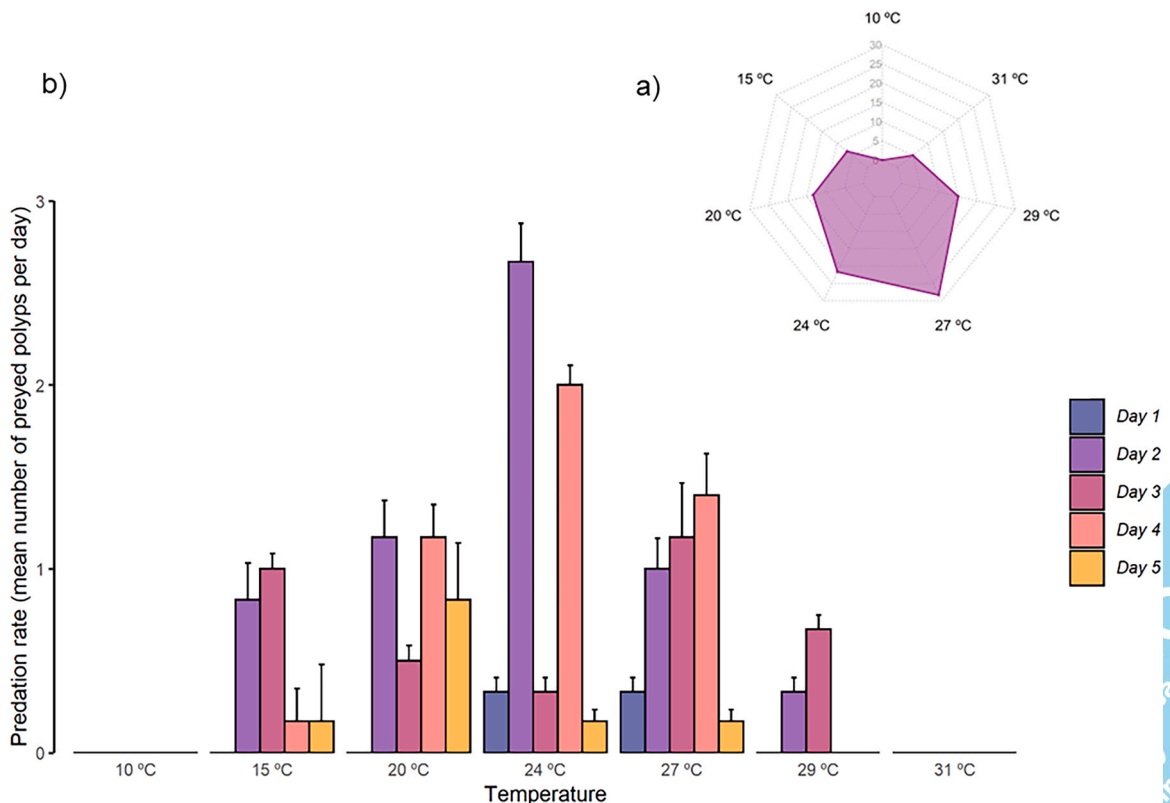


Fig. 2. Measured behavioral traits on *H. carunculata* and *A. calycularis* interactions over temperature: a) “interaction time” between fireworm and orange coral at different temperatures. Light grey numbers in the grid refer to interaction minutes (ranging from 0 to 30 min); b) “predation rate” (mean number of preyed polyps per day) at different temperatures and over time (5 observation days).

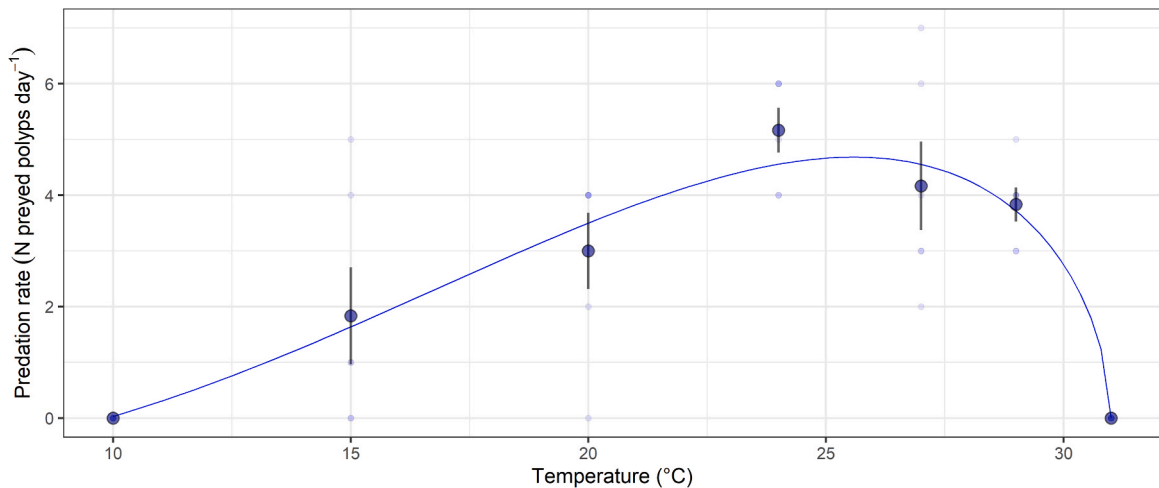


Fig. 3. Predation curve of *Hermodice carunculata*, presenting the maximum predation performance (optimum) at 25.9 °C and the upper critical threshold at 30.9 °C.

3.3. Prey metabolic response to predator contact

Recorded contact time between the fireworms and the experimental coral colonies was slightly lower at low temperature treatment, even if there were not significant differences between 16 and 27 °C. Increasing temperature and contact with the stinging polychaete affected the metabolic response of the coral ($t = 6.95$, $p < 0.05$; $n = 12$). Respiration rate was significantly different at the two temperatures and when the fireworm was present (Fig. 4). At lower temperature (16 °C), the coral presented low respiration rate values, that has more than significantly doubled when it was exposed to the fireworm. The higher temperature led to increased coral oxygen consumption rate, while the combined effects of high temperature and fireworm contact caused a significant increasing rate of oxygen uptake respect to separate effect of either factor, likely presenting a synergistic effect (Fig. 4). Once the contact took place, coral polyps showed tentacle contraction, behaviour that was maintained during the whole experiment and after the end of the interaction. On the contrary, fireworms did not showed significant differences in respiration rate between temperatures, highlighting the potential

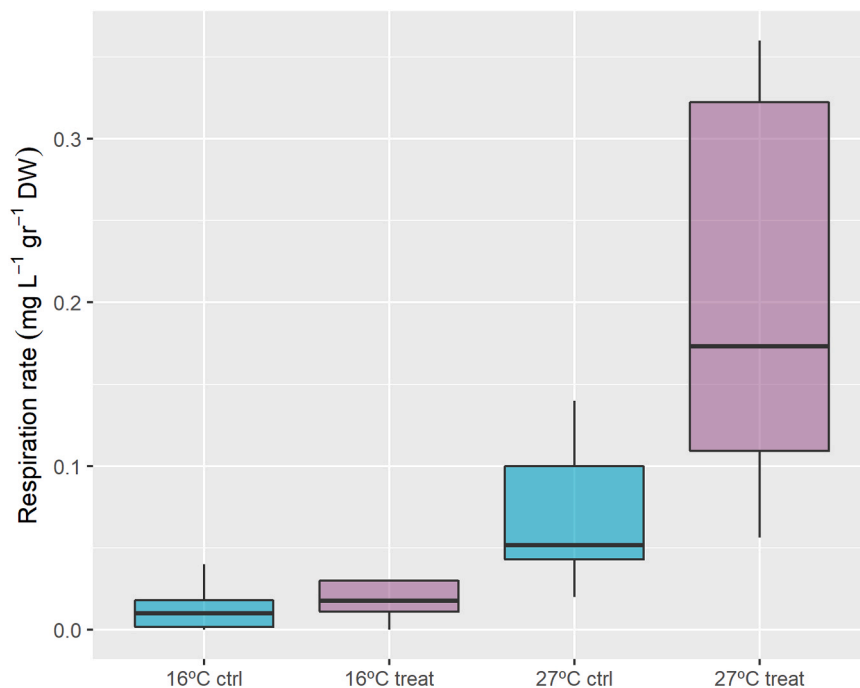


Fig. 4. Metabolic response (respiration rate, $\text{mg L}^{-1} \text{gr}^{-1} \text{DW}$) of treated (fireworm interaction; purple bars) and control (no-interaction; green bars) *A. calycularis* experimental colonies at two different temperature treatments (16° C and 27 °C).

polychaete ability to cope with changing temperature conditions.

4. Discussions

The interplay between temperature-dependent predator-prey interactions assumes significance in shaping ecosystem stability as temperatures rise. The advent of rapid temperature fluctuations and extreme events, such as heatwaves, introduces perturbations that challenge the intricate equilibrium between predators and prey. These disruptions hold the potential to induce unpredictable oscillations in population sizes, consequently heightening the risk of biodiversity loss. The loss of biodiversity can result in the disappearance of biotic interactions associated with local extinct species, along with the ecological services they provide, leading to direct consequences for human well-being (Valiente-Banuet et al., 2015).

Within this context, this study brings to the forefront the role of *Hermodice carunculata*, an endemic benthic infralittoral predator prevalent in the Mediterranean Sea. The predator-prey narrative intertwines with the impending challenges posed by future temperature alterations. While the adaptability of *H. carunculata* grants it a remarkable presence, its implications extend to the well-being of its prey. The predator demonstrates a propensity not only to predate upon *A. calycularis* colonies but also to elicit a stress-induced metabolic response upon physical contact with the coral. Geographically, the ranges of these two species overlap, particularly along the Mediterranean's southern coasts, where the coral plays a pivotal role in shaping shallow infralittoral rocky habitats, hosting more than 80 different species of invertebrates (Terrón-Sigler et al., 2016). The interaction between abiotic (increasing temperatures) and biotic (predation risk by the polychaete) stressors may result in synergistic effects impairing with consequences at population level. Decreasing local populations of this habitat-forming species may suppose significant biodiversity loss and ecosystem services.

Meanwhile, *H. carunculata* has demonstrated a notable surge in both population density and distribution over the past decade (Righi et al., 2020; Terrón-Sigler et al., 2016). The consequences of fireworm predation extend beyond immediate impact, encompassing direct targeting of coral polyps and larvae and, consequently, the compromise of coral fitness. This disruption holds the potential to trigger far-reaching consequences at the population level (Schulze et al., 2017), orchestrated through the intricate channels of non-consumptive predation. Non-consumptive predation, a nuanced force, operates as an underlying architect of biotic interactions, sculpting the contours of prey morphology, physiology, behavior, growth, and reproduction (Truong et al., 2022). In alignment with this insight, our findings underscore that even a mere physical encounter with the fireworm prompts the retraction of coral polyp tentacles, a response that persists beyond the interaction itself. Brief exposure to the stinging polychaete manifests in a palpable decline in coral performance, evidenced by metabolic alterations and potential diminished feeding efficiency. This phenomenon highlights *Hermodice carunculata*'s opportunistic feeding behavior and adept predatory strategies, particularly evident in its interactions with cnidarians and starfish (Barroso et al., 2016; Kudenov et al., 2017; Simonini et al., 2018). This observation concurs with the proposition that Mediterranean fireworm populations may sustain their resilience despite fluctuations in prey community composition (Simonini et al., 2018). Furthermore, this predator exhibits a notable capacity to navigate anthropogenic environmental changes, capitalizing on rising temperatures that fuel both poleward expansion and heightened population densities (Righi et al., 2020).

Temperature, a central effector of biological phenomena, drives the change in the dynamics of predator-prey interactions. As temperatures rise, the intricate relationship undergoes a transformation, reshaping the equilibrium of populations and inducing sweeping alterations in the delicate interplay of ecosystems and food webs (Bjorn et al., 2010). Elevated temperatures trigger an upsurge in metabolism, prompting organisms to augment their food consumption to meet the heightened demands of increased energy expenditure.

The predation response of *H. carunculata* to temperature fluctuations unveils a skewed curve, characterized by a negative skewness. The predator's performance diminishes at lower temperatures, culminating in an apex at approximately 25.6 °C, where the predation rate on the coral reaches its zenith. However, as temperatures transcend this threshold, a cascade of decline ensues, marked by a decline in mobility and reduced pursuit of prey at 29 °C. Feeding ceases altogether at temperatures ranging between 29 and 31 °C. Remarkably, this aligns with model predictions, pinpointing the upper critical temperature for feeding at an exacting 30.9 °C. The variability in consumption rate with temperature hinges on the evolutionary response of both predator and prey to temperature alterations (Dell et al., 2014).

Thus, our results can be seen within the context of a phenological mismatch, particularly considering current and future ocean warming conditions (Renner and Zohner, 2018). Indeed, this polychaete which responds to the mechanistic rules of temperature controlling biotic interactions, when living over certain thermal thresholds will have a negative impact on its ability to prey as predators and prey respond differently to temperature changes. It could result in a phenological mismatches, where peak prey availability no longer coincides with peak predator demand. This finally could have effects of predator reproduction and on its overall population dynamics. Thus introducing mechanisms into the prey-predator relationship makes visible the double side of the coin. On one hand, the predator's inclination towards optimal feeding may disrupt prey populations, already stressed due to abiotic conditions (high temperature), casting a shadow of non-consumptive predator impact up to a certain threshold (in this case, 25.6 °C). On the other hand, as this threshold is approached and surpassed, a decline in predation pressure is anticipated, carrying implications for biodiversity loss on both fronts. This underscores the duality inherent in this complex relationship. Nevertheless, we need to increase our effort in the modelling area for instance adopting ensemble of ecological niche models based on key organisms functional traits and downscaled climate change projections to predict the magnitude of interactive effects among stressors of different nature and properties. This advancement would enhance our mechanistic understanding of ecosystems, particularly the nature of the links that connect biotic interactions within the ambit of increasing temperatures, providing greater realism to the model predictions assisting risk assessment and management strategies. The outcome, in turn, offers a habitat-dependent framework to enrich our comprehension of the mechanisms that underlie community structure and functioning (Enquist et al., 2015) in the face of human-induced environmental

changes. This strategic understanding equips us to effectively anticipate and mitigate potential implications for local biodiversity and would efficiently assist management and conservation plans for vulnerable species and habitats to current and future changing climatic conditions.

5. Conclusions

In conclusion, this study underscores the significance of temperature-dependent predator-prey interactions, particularly the role of a native-invader in shaping ecosystem stability amid rising temperatures. The emergence of rapid temperature fluctuations and extreme events may introduce perturbations that challenge the equilibrium of the ecosystem. The multiple stressor condition, resulting from increasing temperatures and the intensification of negative biotic interactions, pose a significant threat to endemic key habitat forming species in the Mediterranean Sea. Such understanding is crucial for anticipating and mitigating potential implications for local biodiversity, informing management and conservation actions for vulnerable species and habitats in the current and future changing climatic scenarios.

CRedit authorship contribution statement

Sarà Gianluca: Writing – review & editing, Supervision, Resources, Funding acquisition, Conceptualization. **Tantillo Mario Francesco:** Writing – original draft, Methodology, Investigation, Formal analysis. **Bosch Belmar Mar:** Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Mar Bosch-Belmar reports financial support was provided by Italian Ministry of Education, University and Research and by the National Recovery and Resilience Plan. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

We are grateful to Julie Guilleraut and Nicoletta Marsiglia for their kind assistance during the laboratory experiments. This study received funding from the Italian University and Research Minister (MUR) through the PRIN MAHRES project (cod. 2017MHHWBN) and from the PNRR National Biodiversity Future Center Project - NBFC (Cod. CN_00000033).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2024.e02844](https://doi.org/10.1016/j.gecco.2024.e02844).

References

- Barroso, R., Almeida, D., Contins, M., Filgueiras, D., Dias, R., 2016. *Hermodice carunculata* (Pallas, 1766) (Polychaeta: Amphinomididae) preying on starfishes. *Mar. Biodivers.* 46, 333–334. <https://doi.org/10.1007/s12526-015-0394-9>.
- Bennett, S., Wernberg, T., Joy, B.A., De Bettignies, T., Campbell, A.H., 2015. Central and rear-edge populations can be equally vulnerable to warming. *Nat. Commun.* 6, 1–7. <https://doi.org/10.1038/ncomms10280>.
- Bjorn, C.R., Vucic-Pestic, O., Roswitha, B.E., Mark, E., Brose, U., 2010. Temperature, predator-prey interaction strength and population stability. *Glob. Chang Biol.* 16, 2145–2157. <https://doi.org/10.1111/j.1365-2486.2009.02124.x>.
- Bosch-Belmar, M., Giomi, F., Rinaldi, A., Mandich, A., Fuentes, V., Mirto, S., Sarà, G., Piraino, S., 2016. Concurrent environmental stressors and jellyfish stings impair caged European sea bass (*Dicentrarchus labrax*) physiological performances. *Sci. Rep.* 6 <https://doi.org/10.1038/srep27929>.
- Bosch-Belmar, M., Giommi, C., Milisenda, G., Abbruzzo, A., Sarà, G., 2021. Integrating functional traits into correlative species distribution models to investigate the vulnerability of marine human activities to climate change. *Sci. Total Environ.* 799, 149351 <https://doi.org/10.1016/j.scitotenv.2021.149351>.
- Brière, J.F., Pracros, P., Le Roux, A.Y., Pierre, J.S., 1999. A novel rate model of temperature-dependent development for arthropods. *Environmental Entomology* 28, 22–29.
- Bruder, A., Salis, R.K., Jones, P.E., Matthaehi, C.D., 2017. Biotic interactions modify multiple-stressor effects on juvenile brown trout in an experimental stream food web. *Glob. Chang Biol.* 23, 3882–3894. <https://doi.org/10.1111/gcb.13696>.
- Bulleri, F., Bruno, J.F., Silliman, B.R., Stachowicz, J.J., 2016. Facilitation and the niche: implications for coexistence, range shifts and ecosystem functioning. *Funct. Ecol.* 30, 70–78. <https://doi.org/10.1111/1365-2435.12528>.
- Darling, E.S., Côté, I.M., 2008. Quantifying the evidence for ecological synergies. *Ecol. Lett.* 11, 1278–1286. <https://doi.org/10.1111/j.1461-0248.2008.01243.x>.
- Dell, A.I., Pawar, S., Savage, V.M., 2014. Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. *J. Anim. Ecol.* 83, 70–84. <https://doi.org/10.1111/1365-2656.12081>.

- Enquist, B.J., Norberg, J., Bonser, S.P., Violle, C., Webb, C.T., Henderson, A., Sloat, L.L., Savage, V.M., 2015. Scaling from Traits to Ecosystems: Developing a General Trait Driver Theory via Integrating Trait-Based and Metabolic Scaling Theories, 1st ed. *Advances in Ecological Research*. Elsevier Ltd. <https://doi.org/10.1016/bs.aecr.2015.02.001>.
- Freestone, A.L., Carroll, E.W., Papacostas, K.J., Ruiz, G.M., Torchin, M.E., Sewall, B.J., 2020. Predation shapes invertebrate diversity in tropical but not temperate seagrass communities. *J. Anim. Ecol.* 89, 323–333. <https://doi.org/10.1111/1365-2656.13133>.
- Gambi, M.C., Barbieri, F., Signorelli, S., Saggiomo, V., Relazioni, E., Le, C., Termiche, C., 2010. Mortality events along the campania coast (Tyrrhenian Sea) in summers 2008 and 2009 and relation to thermal conditions. *Biol. Mar. Mediterr.* 17, 126–127.
- Gambi, M.C., Sorvino, P., Tiberti, L., Teixidó, N., 2018. Mortality events of benthic organisms along the coast of ischia in summer 2017. *Biol. Mar. Mediterr.* 25, 212–213.
- Garrabou, J., Coma, R., Bensoussan, N., Bally, M., Chevaldonné, P., Cigliano, M., Diaz, D., Harmelin, J.G., Gambi, M.C., Kersting, D.K., Ledoux, J.B., Lejeune, C., Linares, C., Marschal, C., Pérez, T., Ribes, M., Romano, J.C., Serrano, E., Teixido, N., Torrents, O., Zabala, M., Zuberer, F., Cerrano, C., 2009. Mass mortality in northwestern mediterranean rocky benthic communities: effects of the 2003 heat wave. *Glob. Chang Biol.* 15, 1090–1103. <https://doi.org/10.1111/j.1365-2486.2008.01823.x>.
- Garrabou, J., Gómez-Gras, D., Medrano, A., Cerrano, C., Ponti, M., Schlegel, R., Bensoussan, N., Turicchia, E., Sini, M., Gerovasileiou, V., Teixido, N., Mirasole, A., Tamburello, L., Cebrian, E., Rilov, G., Ledoux, J.B., Souissi, J.B., Khamassi, F., Ghanem, R., Benabdi, M., Grimes, S., Ocaña, O., Bazairi, H., Hereu, B., Linares, C., Kersting, D.K., la Rovira, G., Ortega, J., Casals, D., Pagès-Escolà, M., Margarit, N., Capdevila, P., Verdura, J., Ramos, A., Izquierdo, A., Barbera, C., Rubio-Portillo, E., Anton, I., López-Sendino, P., Díaz, D., Vázquez-Luis, M., Duarte, C., Marbà, N., Aspíllaga, E., Espinosa, F., Grech, D., Guala, I., Azzurro, E., Farina, S., Cristina Gambi, M., Chimienti, G., Montefalcone, M., Azzola, A., Mantas, T.P., Frascchetti, S., Ceccherelli, G., Kipson, S., Bakran-Petricioli, T., Petricioli, D., Jimenez, C., Katsanevakis, S., Kizilkaya, I.T., Kizilkaya, Z., Sartoretto, S., Elodie, R., Ruitton, S., Comeau, S., Comeau, S., Harmelin, J.G., 2022. Marine heatwaves drive recurrent mass mortalities in the Mediterranean Sea. *Glob. Chang Biol.* 5708–5725. <https://doi.org/10.1111/gcb.16301>.
- Goffredo, S., Caroselli, E., Gasparini, G., Marconi, G., Putignano, M.T., Pazzini, C., Zaccanti, F., 2011. Colony and polyp biometry and size structure in the orange coral *Astroides calycularis* (Scleractinia: Dendrophylliidae). *Mar. Biol.* Res. 7, 272–280. <https://doi.org/10.1080/17451000.2010.492222>.
- Gómez-Gras, D., Linares, C., de Caralt, S., Cebrian, E., Frlata-Valić, M., Montero-Serra, I., Pagès-Escolà, M., López-Sendino, P., Garrabou, J., 2019. Response diversity in Mediterranean coralligenous assemblages facing climate change: insights from a multispecific thermotolerance experiment. *Ecol. Evol.* 9, 4168–4180. <https://doi.org/10.1002/ece3.5045>.
- Gunderson, A.R., Armstrong, E.J., Stillman, J.H., 2016. Multiple stressors in a changing world: the need for an improved perspective on physiological responses to the dynamic marine environment. *Ann. Rev. Mar. Sci.* 8, 357–378. <https://doi.org/10.1146/annurev-marine-122414-033953>.
- Jackson, M.C., Pawar, S., Woodward, G., 2021. The temporal dynamics of multiple stressor effects: from individuals to ecosystems. *Trends Ecol. Evol.* 36, 402–410. <https://doi.org/10.1016/j.tree.2021.01.005>.
- Kordas, R.L., Dudgeon, S., Storey, S., Harley, C.D.G., 2015. Intertidal community responses to field-based experimental warming. *Oikos* 124, 888–898. <https://doi.org/10.1111/oik.00806>.
- Kudenov, J.D., Barroso, R., Filgueiras, D., Contins, M., Kudenov, J., 2017. First report of the fireworm *Hermodice carunculata* (Annelida: Amphinomidae) preying on a Sea Cucumber SEE PROFILE First report of the fireworm *Hermodice carunculata* (Annelida: Amphinomidae) preying on a Sea Cucumber. *Int. J. Aquat. Biol.* 5, 282–285.
- López, D.P., Freestone, A.L., 2021. History of co-occurrence shapes predation effects on functional diversity and structure at low latitudes. *Funct. Ecol.* 35, 535–545. <https://doi.org/10.1111/1365-2435.13725>.
- Lyons, S.K., Amatangelo, K.L., Behrensmeier, A.K., Bercovici, A., Blois, J.L., Davis, M., Dimichele, W.A., Du, A., Eronen, J.T., Tyler Faith, J., Graves, G.R., Jud, N., Labandeira, C., Looy, C.V., McGill, B., Miller, J.H., Patterson, D., Pineda-Munoz, S., Potts, R., Riddle, B., Terry, R., Tóth, A., Ulrich, W., Villaseñor, A., Wing, S., Anderson, H., Anderson, J., Waller, D., Gotelli, N.J., 2016. Holocene shifts in the assembly of plant and animal communities implicate human impacts. *Nature* 529, 80–83. <https://doi.org/10.1038/nature16447>.
- Marchessaux, G., Bosch-Belmar, M., Cilenti, L., Lago, N., Mangano, M.C., Marsiglia, N., Sarà, G., 2022. The invasive blue crab *Callinectes sapidus* thermal response: predicting metabolic suitability maps under future warming Mediterranean scenarios. *Front. Mar. Sci.* 9, 1055404. <https://doi.org/10.3389/fmars.2022.1055404>.
- Martin, P., Bateson, P.P.G., 1993. *Measuring behaviour: An introductory guide*, 2nd ed., *Measuring behaviour: An introductory guide*, 2nd ed. Cambridge University Press, New York, NY, US. <https://doi.org/10.1017/CBO9781139168342>.
- Maselli, V., Al-Soudy, A.S., Buglione, M., Aria, M., Polese, G., Di Cosmo, A., 2020. Sensorial hierarchy in octopus vulgaris's food choice: chemical vs. visual (Mar). *Animals* 10 (3), 457. <https://doi.org/10.3390/ani10030457>.
- Power, M., 1997. Assessing the effects of environmental stressors on fish populations. *Aquat. Toxicol.* 39, 151–169. [https://doi.org/10.1016/S0166-445X\(97\)00020-9](https://doi.org/10.1016/S0166-445X(97)00020-9).
- Renner, S.S., Zohner, C.M., 2018. Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. *Annu. Rev. Ecol. Evol. Syst.* 49, 165–182. <https://doi.org/10.1146/annurev-ecolsys-110617-062535>.
- Righi, S., Prevedelli, D., Simonini, R., 2020. Ecology, distribution and expansion of a Mediterranean native invader, the fireworm *Hermodice carunculata* (Annelida). *Mediterr. Mar. Sci.* 3, 558–574.
- Sarà, G., Palmeri, V., Montalto, V., Rinaldi, A., Widdows, J., 2013. Parameterisation of bivalve functional traits for mechanistic eco-physiological dynamic energy budget (DEB) models. *Mar. Ecol. Prog. Ser.* 480, 99–117. <https://doi.org/10.3354/meps10195>.
- Schulze, A., Grimes, C.J., Rudek, T.E., 2017. Tough, armed and omnivorous: *Hermodice carunculata* (Annelida: Amphinomidae) is prepared for ecological challenges. *J. Mar. Biol. Assoc. U. Kingd.* 97, 1075–1080. <https://doi.org/10.1017/S0025315417000091>.
- Simonini, R., Righi, S., Maletti, I., Fai, S., Prevedelli, D., 2017. Bearded versus thorny: the fireworm *Hermodice carunculata* preys on the sea urchin *Paracentrotus lividus*. *Ecology* 98, 2730–2732. <https://doi.org/10.1002/ecy.1919>.
- Simonini, R., Maletti, I., Righi, S., Fai, S., Prevedelli, D., 2018. Laboratory observations on predator–prey interactions between the bearded fireworm (*Hermodice carunculata*) and Mediterranean benthic invertebrates. *Mar. Freshw. Behav. Physiol.* 51, 145–158. <https://doi.org/10.1080/10236244.2018.1502031>.
- Terrón-Sigler, A., León-Muez, D., Peñalver-Duque, P., Gálvez-César, R., Espinosa Torre, F., 2016. Geographic distribution of *Astroides calycularis* (Scleractinia: Dendrophylliidae) as a baseline to assess future human impacts on the Southern Iberian Peninsula. *J. Mar. Biol. Assoc. U. Kingd.* 96, 1181–1189. <https://doi.org/10.1017/S0025315415001113>.
- Truong, K.N., Vu, N.A., Doan, N.X., Bui, C.V., Le, M.H., Vu, M.T.T., Dinh, K.V., 2022. Transgenerational exposure to marine heatwaves ameliorates the lethal effect on tropical copepods regardless of predation stress. *Ecol. Evol.* 12, 1–15. <https://doi.org/10.1002/ece3.9149>.
- Valiente-Banuet, A., Aizen, M.A., Alcántara, J.M., Arroyo, J., Cocucci, A., Galetti, M., García, M.B., García, D., Gómez, J.M., Jordano, P., Medel, R., Navarro, L., Obeso, J.R., Oviedo, R., Ramírez, N., Rey, P.J., Traveset, A., Verdú, M., Zamora, R., 2015. Beyond species loss: the extinction of ecological interactions in a changing world. *Funct. Ecol.* 29, 299–307. <https://doi.org/10.1111/1365-2435.12356>.
- Van Der Putten, W.H., De Ruiter, P.C., Bezemer, T.M., Harvey, J.A., Wassen, M., Wolters, V., 2004. Trophic interactions in a changing world. *Basic Appl. Ecol.* 5, 487–494. <https://doi.org/10.1016/j.baec.2004.09.003>.
- Wolf, A.T., Nugues, M.M., 2013. Predation on coral settlers by the corallivorous fireworm *Hermodice carunculata*. *Coral Reefs* 32, 227–231. <https://doi.org/10.1007/s00338-012-0969-x>.
- Wolf, A.T., Nugues, M.M., Wild, C., 2014. Distribution, food preference, and trophic position of the corallivorous fireworm *Hermodice carunculata* in a Caribbean coral reef. *Coral Reefs* 33, 1153–1163. <https://doi.org/10.1007/s00338-014-1184-8>.