

Warmer temperatures reduce the influence of an important keystone predator

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Summary

1. Predator–prey interactions may be strongly influenced by temperature variations in marine ecosystems. Consequently, climate change may alter the importance of predators with repercussions for ecosystem functioning and structure.

2. In North-eastern Pacific kelp forests, the starfish *Pycnopodia helianthoides* is known to be an important predator of the purple sea urchin *Strongylocentrotus purpuratus*. Here we investigated the influence of water temperature on this predator–prey interaction by: (i) assessing the spatial distribution and temporal dynamics of both species across a temperature gradient in the northern Channel Islands, California, and (ii) investigating how the feeding rate of *P. helianthoides* on *S. purpuratus* is affected by temperature in laboratory tests.

3. On average, at sites where mean annual temperatures were < 14 °C, *P. helianthoides* were common, *S. purpuratus* was rare and kelp was persistent, whereas where mean annual temperatures exceeded 14 °C, *P. helianthoides* and kelp were rare and *S. purpuratus* abundant. Temperature was found to be the primary environmental factor influencing *P. helianthoides* abundance, and in turn *P. helianthoides* was the primary determinant of *S. purpuratus* abundance. In the laboratory, temperatures > 16 °C (equivalent to summer temperatures at sites where *P. helianthoides* were rare) reduced predation rates regardless of predator and prey sizes, although larger sea urchins were consumed only by large starfishes.

4. These results clearly demonstrate that the effect of *P. helianthoides* on *S. purpuratus* is strongly mediated by temperature, and that the local abundance and predation rate of *P. helianthoides* on sea urchins will likely decrease with future warming. A reduction in top-down control on sea urchins, combined with other expected impacts of climate change on kelp, poses significant risks for the persistence of kelp forests in the future.

Key-words: ecosystem shift, global climate change, kelp forest, *Pycnopodia helianthoides*, sea urchin barren, *Strongylocentrotus purpuratus*, structural equation modelling, top-down control

Introduction

Changing temperatures drive subsequent variability in many living systems, focusing attention on the possible effects of global warming on individual behaviour, species distribution and community function. Coastal ecosystems have warmed significantly in recent decades and there is a concomitant increase in the frequency and intensity of local temperature anomalies (Lima & Wetthey 2012; Hobday *et al.* 2016). In marine systems, temperature increases may directly lead to changes in species distribution and mass mortalities (Parmesan & Yohe 2003; Harley *et al.*

2006; Garrabou *et al.* 2009; Smale & Wernberg 2013). In addition, global warming and transient temperature anomalies can indirectly influence entire communities by creating novel interactions among species (Galasso *et al.* 2015) or affecting the strength of the existing ones (Sanford 1999; Gianguzza *et al.* 2011; Harley 2011; Nogués-Bravo & Rahbek 2011; Milazzo *et al.* 2013; Wernberg *et al.* 2013; Alexander *et al.* 2016). In this regard, variation in both the local distribution and predation rate of key species are particularly important, due to the large effects on marine communities (Sanford 1999; Harley 2011; Nogués-Bravo & Rahbek 2011). Loss of predator control on prey populations may lead to irreversible shifts in community structure and ecosystem function (Paine

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1980; Paine, Castillo & Cancino 1985; Estes *et al.* 2011), with detrimental effects on ecosystem services and biodiversity (Steneck *et al.* 2002; Graham 2004). Hence, understanding how temperature affects interaction strengths between key predators and their prey is a crucial step to predicting consequences of global warming on the stability of communities and ecosystem processes (Traill *et al.* 2010).

In intertidal rocky systems of the North-eastern Pacific coast, changes in temperature are predicted to influence the role of the starfish *Pisaster ochraceus*, which is a keystone predator in this system. Sanford (1999) found that the abundance of *P. ochraceus* and its rate of predation on mussels decreased when water temperature dropped by 3–5 °C during upwelling events (Sanford 1999). In subtidal systems, starfish can also play important predatory roles (e.g. Duggins 1983; Lafferty 2004; Eckert 2007; Bonaviri *et al.* 2009; Gianguzza *et al.* 2009, 2016; Rassweiler, Schmitt & Holbrook 2010; Lane 2012; Urriago, Himmelman & Gaymer 2012; Galasso *et al.* 2015) that may be modified by temperature variations. For example predation rate of the polar starfish *Odontaster validus* is compromised by high-temperature stress (Peck *et al.* 2008; Kidawa, Potocka & Janecki 2010). Temperate regions routinely undergo wide temperature oscillations, due to seasonal cycles and temperature anomalies (Miller *et al.* 1994; Hobday *et al.* 2016), such as during ENSO events. Such temporary fluctuations and more long-term global warming have the potential to affect the capacity of key predators to control prey populations and, indirectly, community structure.

The sunflower starfish, *Pycnopodia helianthoides*, inhabits temperate subtidal North-eastern Pacific coasts, from the Aleutian Islands, Alaska, to the Channel Islands, California (Duggins 1983; Lafferty 2004; Eckert 2007; Rassweiler, Schmitt & Holbrook 2010). *P. helianthoides* can play a key role in shaping benthic communities by preying upon the purple sea urchin, *Strongylocentrotus purpuratus*, which in the absence of predators can reach high abundances and graze down kelp forests (Watanabe & Harrold 1991; Pearse 2006). *P. helianthoides* may therefore prevent the transition from productive kelp forests to impoverished urchin barrens (Duggins 1983; Lafferty & Kushner 2000; Behrens & Lafferty 2004; Lafferty 2004), especially in areas such as southern California where other predators such as the California sheephead wrasse and the spiny lobster have been excluded by fishing (Lafferty 2004; Hamilton *et al.* 2010). The wide geographic distribution of *P. helianthoides* and its potential role in controlling sea urchin abundance make it a good model species to study the effect of temperature change on the interaction strength between putative keystone predators and their prey.

The northern Channel Islands, the southernmost limit in the distribution of *P. helianthoides*, are characterized by a large temperature gradient (Fig. S1, Supporting Information) due to the confluence of cool waters from the northwest and warmer currents from the southeast. In

summer, the eastern edge of the archipelago is up to 6 °C warmer than its western edge (Eckert 2007; and references therein). These conditions make the archipelago an ideal place to evaluate the effect of sea surface temperature differences on the local abundance of *P. helianthoides* and on its predation pressure on *S. purpuratus*. *Pycnopodia helianthoides* are known to be more abundant in the cooler part of the islands, whereas *S. purpuratus* are more abundant in the warmer part of the island (Lafferty 2004; Shears *et al.* 2012). Given that *S. purpuratus* occurs in much cooler waters to the north (Hammond & Hofmann 2010), we hypothesized that this pattern in *S. purpuratus* abundance was a result of *P. helianthoides* predation, and the higher urchin abundances in warm waters are due to temperature limiting the abundance and predation rate of *Pycnopodia*, rather than a direct effect of temperature on *S. purpuratus*.

In the present work, we combined field observations and laboratory experiments to investigate the effect of temperature variation on the interaction strength between *P. helianthoides* and *S. purpuratus*. We used long-term kelp forest monitoring data to investigate how the density of both species varies in relation to temperature and other environmental variables across the Channel Islands and over time. We used structural equation modelling to test the hypothesis that *S. purpuratus* abundance was indirectly affected by temperature and ultimately mediated by the effects of temperature on *P. helianthoides*. We then carried out laboratory experiments to test whether typical water temperatures observed in summer in the eastern Channel Islands affected predation rates of *P. helianthoides*.

Materials and methods

RELATIONSHIPS BETWEEN WATER TEMPERATURE, *P. HELIANTHOIDES* AND *S. PURPURATUS*

To evaluate the relationship between temperature and abundance of *P. helianthoides* and *S. purpuratus*, we used data from the US National Park Service kelp forest monitoring program at the Channel Islands (Kushner *et al.* 2013). Densities of *P. helianthoides* and *S. purpuratus* have been measured annually at 16 sites located across the Channel Islands since 1982 and at 17 additional sites since 2005 (Fig. S1). The sites are distributed on both the north and south sides of each of the islands, spanning the east-west transition from the Californian to the Oregonian biogeographic provinces. Sites were selected based on the presence of continuous patches of rocky habitat (typically more than 100 m in long-shore extent) that was known to be good habitat for giant kelp forests. Depths ranged from 5 to 16 m depth (Table S1). We excluded two of the 33 sites (Cathedral Cove and Landing Cove) because they were located in a long-term marine reserve and purple urchin density was considerably lower than nearby sites due to the high abundance of spiny lobsters (Lafferty 2004; Shears *et al.* 2012). At each site, *P. helianthoides* were counted in 12 band transects (20 × 3 m²) and *S. purpuratus* were counted in 12 2 m² quadrats (see Kushner *et al.* 2013 for

sampling details and site locations). The size (length of the longest arm from centre of the starfish) of *P. helianthoides* was measured *in situ* at sites where it was present. The number of individuals measured at each site was highly variable ($n = 1\text{--}91$) due to the varying density and availability of starfish.

Mean daily temperature data are available from *in situ* temperature loggers since 1993 at long-term sites and 2005 at all other sites (Kushner *et al.* 2013). These data were used to calculate average temperature over the preceding 3, 7, 14, 28, 56, 84, 180 and 365 days before annual sampling in 2006–2011 at each site. Maximum mean daily temperature was also calculated for the preceding 28, 56, 84, 180 and 365 days. Both *P. helianthoides* and *S. purpuratus* densities were correlated with each of the 13 metrics to determine at what temporal scale temperature best predicted abundance. For both species, densities were most strongly correlated with average daily temperature over the previous 365 days (*P. helianthoides*: $r = -0.36$; *S. purpuratus*: $r = 0.42$). This temperature metric was used for all further analysis.

The mean annual water temperature across sites from 2006 to 2011 ranged from 12.4 °C at the westernmost site at San Miguel Island (WL) to 15.6 °C at Santa Barbara Island (AP) in the east, with mean monthly maxima of 13.9 and 18.7 °C respectively (Table S1). The western-most sites (including all sites at San Miguel and Santa Rosa Island's, and Gull Island at Santa Cruz Island) had mean annual temperatures <14 °C and maximum monthly temperatures <16 °C, whereas the eastern sites had mean annual temperatures >14 °C and maximum monthly temperatures >16 °C (Table S1).

To account for other large-scale physical differences among sites mean depth information was obtained for each site from Kushner *et al.* (2013), and wind fetch was calculated for each site as an index of wave exposure. Wind fetch was calculated as the average distance to land for each 10 degree sector of the compass rose, with a maximum distance of 300 km used for sectors of open sea.

Distance based linear modelling was carried out in Primer v6 (Clarke & Gorley 2006; Anderson, Gorley & Clarke 2008) to explore the relationship between the density of both *P. helianthoides* and *S. purpuratus* across sites from 2006 to 2011, and temperature, depth and fetch. Euclidean distance was used for these analyses. Density data were natural log-transformed ($x + 1$) and environmental data normalized prior to analysis. *Pycnopodia helianthoides* density ($\ln[x + 1]$) was also included as an explanatory variable in the *S. purpuratus* model as it is an important predator of *S. purpuratus* (Duggins 1983; Lafferty & Kushner 2000; Behrens & Lafferty 2004).

Bivariate analyses were carried out in R v 3.3.0 (R Core Team 2016). Loess smoothing curves were used to visualize variation in *P. helianthoides*, *S. purpuratus*, and temperature from west to east across the Channel Islands. Logistic regression was then used to analyse the relationship between the presence of *P. helianthoides* and temperature, and a log-log regression was used to analyse the relationship between *S. purpuratus* and *P. helianthoides*.

Structural equation modelling was used to test the direct and indirect effects of temperature on *S. purpuratus*. A test of mediation was carried out (Grace 2006), where we asked whether the effect of temperature on *S. purpuratus* abundance (natural log ($x + 1$)) could be explained by *P. helianthoides* abundance (natural log ($x + 1$)). We compared three models with AIC: no mediation (i.e. direct effect only: *S. purpuratus* ~ Temperature), complete mediation (i.e. indirect effect only: *S. purpuratus* ~ *P. helianthoides*

and *P. helianthoides* ~ Temperature) and partial mediation (i.e. both direct and indirect effects). All models were fit using the *lavaan* package in R (Rosseel 2012).

Finally we examined how the abundance of *P. helianthoides*, *S. purpuratus* and kelp (*Macrocystis pyrifera*, *Eisenia arborea*, *Pterygophora californica* and *Laminaria farlowii*) co-varied over time (1982–2011) at the 14 long-term monitoring sites (again excluding the Cathedral Cove and Landing Cove data). Sites were divided into two groups based on mean annual maximum temperatures: <14, and >14 °C (Fig. S1, Table S1). This coincides with a division of sites between the western and eastern Channel Islands.

EFFECTS OF TEMPERATURE ON PREDATOR–PREY INTERACTION STRENGTH

To determine the effect of temperature and size on the feeding rate of *P. helianthoides* on *S. purpuratus*, predation experiments in the laboratory were conducted from February to June 2011. Given that the strength of this starfish-urchin interaction may depend on their respective sizes (Freeman 2006), as large prey may reach a size escape (Paine, Castillo & Cancino 1985; Paine & Trimble 2004), and that smaller individuals are potentially less sensitive than larger ones to temperature increases (Peck *et al.* 2009), we considered two size classes for both predator and prey.

Starfishes and urchins were collected by SCUBA diving along the coast of Big Sur (California). In each experimental trial, 10 urchins were placed into a 120 L tank. The number of urchins was chosen considering the natural density in areas where *P. helianthoides* was supposed to exercise an impact on *S. purpuratus* populations (i.e. Channel Island sites with high densities of *P. helianthoides*, data from Channel Island Nation Park monitoring program). A single *P. helianthoides* individual was added to each tank. Starfishes had been starved and acclimatized to the selected temperature for 72 h before the experiment started. The number of surviving *S. purpuratus* individuals was determined every 24 h. Replicate trials used different (independent) individual predators. Each experimental replicate was paired with one control trial in which *S. purpuratus* experienced the temperature used in the experiment without the predator. To test for the effects of size and temperature on predation, we selected two *S. purpuratus* and two *P. helianthoides* size classes, measured as urchin test length (small, 2.5–3.5 cm; large, 4.0–5.0 cm) and starfish 'tip-to-tip' length (small, 20–30 cm; large, 35–45 cm) respectively. The experiments were run at two different temperatures: low (mean \pm SE: 12.67 \pm 0.59 °C) and high (mean \pm SE: 16.60 \pm 0.44 °C). The temperature interval of 4 °C, from 12.7 °C to 16.6 °C, is typically found during summer along the distribution range of *P. helianthoides*. Summer mean water temperatures reach around 14 °C in Alaska and exceed 16 °C in the eastern Channel Islands (www.nodc.noaa.gov, Table S1), the latter being the geographical limit for the *P. helianthoides*. Moreover, higher temperatures are also reached during ENSO events (Eckert 2007), or potentially in other periods of temperature anomalies (Hobday *et al.* 2016).

Temperature in the experimental tanks was maintained by heaters and oxygenation was ensured by air pumps. The treatment at the highest temperature for 6 days (length of the whole experiment) did not harm *P. helianthoides*, since the same individuals used in the experiments intensely fed on *S. purpuratus* when the low temperature was restored.

During the experiments, the predation rate was linear for the first 48 h in all experiments, but in some trials predation rate

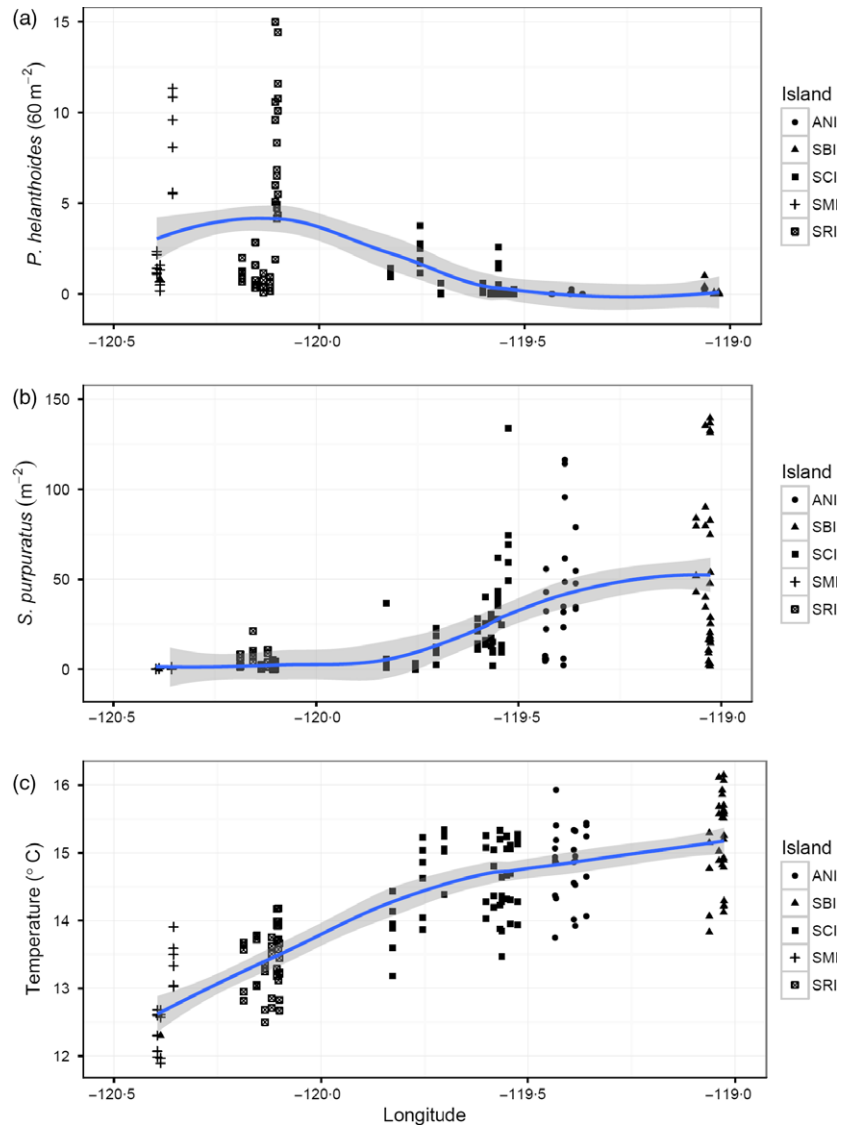


Fig. 1. Variation in *Pycnopodia helianthoides* (a), *Strongylocentrotus purpuratus* (b) and temperature (c) from west to east across the Channel Islands. ANI, Anacapa Island; SBI, Santa Barbara Island; SCI, Santa Cruz Island; SMI, San Miguel Island; SRI, Santa Rosa Island. Line is a loess smoother with 95% confidence interval. [Colour figure can be viewed at wileyonlinelibrary.com]

later plateaued by depleting all prey (depending on the combinations of temperature, urchin and starfish size). Therefore, predation rate was calculated on data from the first 48 h.

To test the interactive effects of size and temperature on the *per capita* predation rates, we used an experimental design with three factors: Temperature (T), a fixed factor with 2 levels (low and high); Starfish size (Ss), a fixed factor with 2 levels (small and large) and Urchin size (Us), a fixed factor with 2 levels (small and large). Three replicates were used per experimental cell. The effect of urchin and starfish size and temperature on the predation rates was tested with a three-way ANOVA testing for the three main effects and all possible interactions. All tests met the assumption of homogeneity of variance (Cochran's C-test). Subsequent pairwise comparisons were performed using Student-Newman-Keuls (SNK) tests.

Results

RELATIONSHIPS BETWEEN WATER TEMPERATURE, *P. HELIANTHOIDES* AND *S. PURPURATUS*

Pycnopodia helianthoides and *S. purpuratus* exhibited a clear inverse pattern in abundance across the Channel

Islands that broadly corresponds to the large-scale temperature gradient (Fig. 1). *Pycnopodia helianthoides* was abundant at the western islands (SMI and SRI) where mean annual temperatures were <14 °C, and *S. purpuratus* were abundant at the eastern islands (ANI and SBI) where mean annual temperatures were >14 °C (Table S1). At Santa Cruz Island, which lies in the center and straddles the temperature gradient, densities of *P. helianthoides* declined from west to east, whereas *S. purpuratus* densities increase. There was no clear variation in maximum size of *P. helianthoides* among sites across the Channel Islands (Fig. S2) and no clear variation in depth or wave exposure among sites across the Channel Islands (Fig. S3).

Distance based linear modelling revealed that *P. helianthoides* abundance was significantly related to mean annual temperature, but not depth or fetch (Table 1a). The best model included temperature and fetch ($R^2 = 0.30$), but fetch only explained a small amount of additional variation (c. 2%). The relationship between *P. helianthoides* abundance and temperature was nonlinear with densities high, yet variable, at temperatures less

Table 1. Distance-based linear modelling of *Pycnopodia helianthoides* (a) and *Strongylocentrotus purpuratus* (b) densities in relation to depth, fetch and temperature

(a) Marginal tests							
Variable	SS(trace)	Pseudo-F	<i>P</i>	Prop.			
Depth	0.86972	1.4771	0.241	0.0089			
Fetch	0.37957	0.64139	0.431	0.0039			
Temperature	27.727	65.081	0.001	0.2829			
Best model							
Variable	AICc	SS(trace)	Pseudo-F	<i>P</i>	Prop.	Cumul.	res.df
Temperature	-140.43	27.727	65.081	0.001	0.2829	0.28286	165
+ Fetch	-143.41	2.0971	5.0429	0.022	0.0214	0.30426	164
(b) Marginal tests							
Variable	SS(trace)	Pseudo-F	<i>P</i>	Prop.			
Depth	15.664	7.3173	0.011	0.0425			
Fetch	10.153	4.6698	0.037	0.0275			
Temperature	128.51	88.211	0.001	0.3484			
<i>P. helianthoides</i>	154.15	118.45	0.001	0.4179			
Best model							
Variable	AICc	SS(trace)	Pseudo-F	<i>P</i>	Prop.	Cumul.	res.df
<i>P. helianthoides</i>	46.057	154.15	118.45	0.001	0.4179	0.41788	165
+ Temperature	21.88	31.235	27.916	0.001	0.0847	0.50255	164
+ Depth	21.067	3.1723	2.8675	0.092	0.0086	0.51115	163

than 14 °C (Fig. 2a). Densities typically declined at temperatures greater than 14 °C and *P. helianthoides* was increasingly absent. *P. helianthoides* was present at 94% (63/67) of sites where temperatures were <14 °C, whereas it was absent from 63% (63/100) of sites where mean temperatures exceeded 14 °C. The presence of *P. helianthoides* was strongly governed by temperature (Fig. S4, Logit = 4.92 - (0.12 × temperature); *Z*-value = -6.567, *P* < 0.001), with the probability of occurrence dropping below 0.5 at a mean annual temperature of 14.65 °C.

The density of *S. purpuratus* was most strongly related to *P. helianthoides* (Table 1b; $R^2 = 0.42$), followed by temperature ($R^2 = 0.35$). The best model included *P. helianthoides*, temperature and depth ($R^2 = 0.51$), but depth only explained c. 1% of additional variation. There was a positive relationship between *S. purpuratus* and temperature (Fig. 2b), and a strong inverse relationship between *S. purpuratus* and *P. helianthoides* (Fig. 3; Log-Log regression model: *t*-value = -11.02, *P* < 0.001, $R^2 = 0.42$). *S. purpuratus* densities were high where *P. helianthoides* were rare or absent, and *S. purpuratus* density was low where *P. helianthoides* were common. The abundance of *S. purpuratus* was 4.8 times ($CL_{95\%} = 3.2, 7.1$) higher when *P. helianthoides* were absent (Binary regression model: *t*-value = -7.75, *P* < 0.001, $R^2 = 0.27$). Where *P. helianthoides* were present, the mean density of *S. purpuratus* was 5.3 (95% CI = 4.1, 6.8), and where

P. helianthoides were absent, mean *S. purpuratus* density was 25.3 (95% CI = 18.5, 34.2).

Structural equation modelling provided greatest support for the 'Partial-mediation' model that included both direct and indirect effects (Table 2, Fig. 4). This indicates that while *P. helianthoides* explains part of the effect of temperature on urchin abundance, some other processes are influencing the direct relationship between temperature and urchin abundance. There was, however, greater support for the 'Complete mediation' (indirect effects only) model than for the 'No mediation' (direct effects only) model (Table 2) indicating that the indirect mechanism is more important.

The inverse relationship between *P. helianthoides* and *S. purpuratus* was also evident in the long-term data from these monitoring sites (Fig. 5). At sites from the cold region of the Channel Islands, where mean annual temperatures were <14 °C, peaks in urchin density coincided with low *P. helianthoides*. These peaks were followed by an increase in the density of *P. helianthoides*, subsequent declines in *S. purpuratus* and an increase in kelp. These sites typically had low *S. purpuratus* densities and more persistent kelp compared to the warm region sites where annual mean temperatures exceeded 14 °C. At these sites *P. helianthoides* was rare, sea urchins were abundant and kelps uncommon, except during periodic declines in sea urchins.

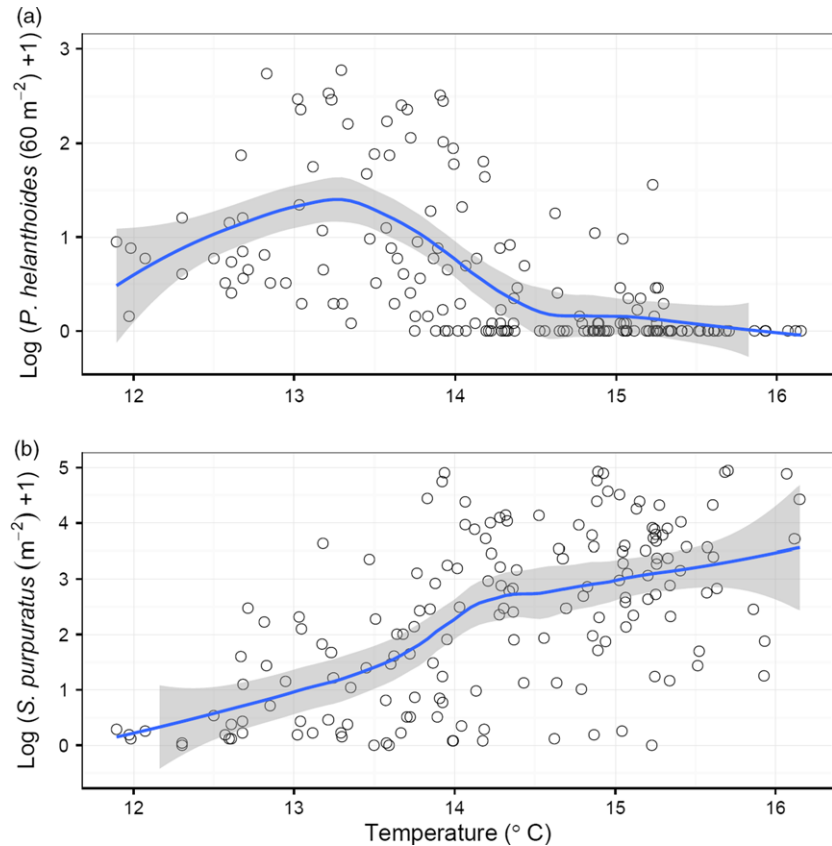


Fig. 2. *Pycnopodia helianthoides* (a) and *Strongylocentrotus purpuratus* (b) densities (m^{-2}) as a function of temperature at the northern Channel Islands, California. Each point is a site-year mean for data collected at the 31 kelp forest monitoring sites from 2006 to 2011. Temperature measurements are the mean temperature over the 365 days prior to sampling. Line is a loess smoother with 95% confidence interval. [Colour figure can be viewed at wileyonlinelibrary.com]

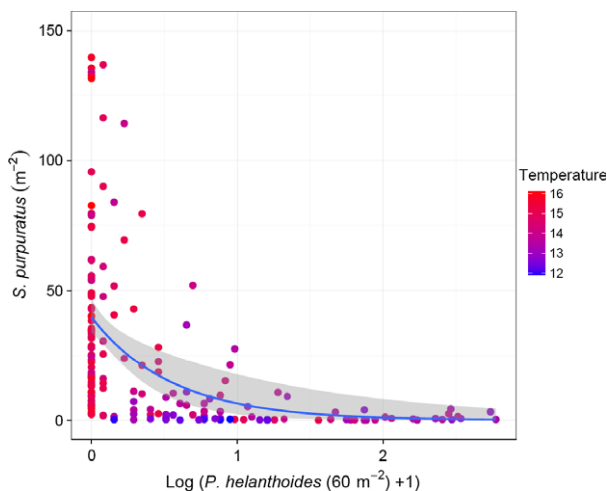


Fig. 3. Relationship between *Pycnopodia helianthoides* and *Strongylocentrotus purpuratus* density at kelp forest monitoring sites at the northern Channel Islands, California. Each point is a site-year mean for data collected at the 31 kelp forest monitoring sites from 2006 to 2011. Symbols are colour-coded according to mean temperature over the 365 days prior to sampling (Table S1). Blue line is a Log-Log function with 95% confidence interval. [Colour figure can be viewed at wileyonlinelibrary.com]

EFFECTS OF TEMPERATURE ON PREDATOR–PREY INTERACTION STRENGTH

Predation rate was significantly lower at 16.6 °C than at 12.7 °C (Table S1, Fig. 6). At low temperature, large

P. helianthoides consumed small and large *S. purpuratus* with similar rates, whereas small *P. helianthoides* only consumed small urchins (Table S1, Fig. 6). At high temperature, predation rates were very low regardless of size for both *P. helianthoides* and *S. purpuratus* (Table S1, Fig. 6). In control trials with no predators, all urchins remained in good condition and no mortalities were recorded.

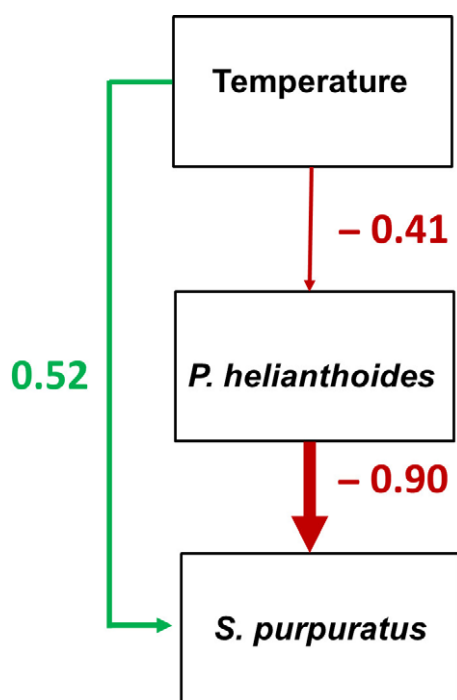
Discussion

Sea surface temperature changes may provoke ecosystem shifts by affecting the interaction strengths among species (Sanford 1999; Paine & Trimble 2004). In this context, it is important to evaluate which key species respond to temperature changes and how interactions with other components of their ecosystem are affected (Paine & Trimble 2004; Russell *et al.* 2011). The aim of this study was to understand whether temperature changes affected the local abundance and predation rate of a key predator species in kelp forest communities.

Our study indicates that temperature has a strong influence in controlling the presence of *P. helianthoides*. *P. helianthoides* reached the highest densities at sites when the mean annual temperature was below 14 °C. In contrast, when mean annual temperature was >14 °C *P. helianthoides* was generally absent or at low abundances. This pattern suggests that the temperature occurring in the eastern part of the Channel Islands, the southern limit

Table 2. Chi-squared likelihood ratio tests and comparison between three models investigating the degree to which the relationship between *Strongylocentrotus purpuratus* and temperature is mediated by *Pycnopodia helianthoides*

Model	<i>N</i>	χ^2	df	<i>P</i>	AIC	χ^2 diff	Pr(> χ^2)
Partial mediation (direct and indirect)	167	0.00	0	<0.0001	1299.3	–	–
Complete mediation (indirect only)	167	26.25	1	<0.0001	1323.6	26.251	<0.0001
No mediation (direct only)	167	100.61	2	<0.0001	1396.6	74.363	<0.0001

**Fig. 4.** Path diagram from a structural equation model showing how sea urchin *Strongylocentrotus purpuratus* density is both directly and indirectly related to temperature (Partial-mediation model). The indirect effects are mediated through predation by the starfish *Pycnopodia helianthoides*. Arrow thickness is weighted according to the un-standardized coefficients and all paths are significant ($P < 0.05$). See Table 2 for comparison among other models. [Colour figure can be viewed at wileyonlinelibrary.com]

in the geographical distribution of *P. helianthoides*, represents a critical environmental limit for the activity of this species.

Conversely, the sea urchin *S. purpuratus* reached high densities at sites when the mean annual temperature exceeded 14 °C. The results of this study indicated that this pattern was both a result of direct effects of temperature (or other processes correlated with temperature) and an indirect effect mediated by *P. helianthoides*. Given that *S. purpuratus* has a broad biogeographic range, extending from southern Alaska to the central Baja California, it is unlikely that temperatures occurring at the Channel Islands are a limiting factor for this species (Hammond & Hofmann 2010). While other factors may elevate *S. purpuratus* densities in the warmer eastern parts of the

Channel Islands, such as enhanced recruitment as shown for other invertebrate species (Blanchette, Broitman & Gaines 2006), our analyses provided greater support for the hypothesis that *P. helianthoides* is the primary determinant of *S. purpuratus* density. This study therefore suggests that the low densities of *S. purpuratus* at the cooler sites are primarily due to the abundance of *P. helianthoides*, and therefore the positive relationship between *S. purpuratus* and temperature is largely an indirect result of the strong inverse relationship between *S. purpuratus* and *P. helianthoides*.

This scenario was confirmed by both the time series of *P. helianthoides* and *S. purpuratus* densities along the Channel Islands and the results obtained during the laboratory experiments. Time-series data showed a typical mechanism where increases in sea urchin density were quickly followed by an increase in starfish density at sites where mean annual temperature was >14 °C. In turn, the increase in the *P. helianthoides* population size coincided with a drop in *S. purpuratus* density. Aggregations of starfish in response to increased food availability have been observed world-wide, causing the decimation of their food sources (Sloan & Aldridge 1981; Gaymer, Himmelman & Johnson 2001; Bonaviri *et al.* 2009; Tuya & Duarte 2011; Agüera *et al.* 2012). A possible explanation for the rapid response in *P. helianthoides* density was that starfishes reside in deep, cold water, and move up to shallow water when food availability (sea urchins) increases (Gaymer, Himmelman & Johnson 2002).

Our laboratory experiments showed that *S. purpuratus* did not reach a size escape from *P. helianthoides* and that under warm conditions the feeding rates of *P. helianthoides* were reduced. In predator–prey systems, feeding rates are expected to increase with temperature until an optimum, after which the feeding rate declines (Vucic-Pestic *et al.* 2011; Sentis, Hemptinne & Brodeur 2014; Öhlund *et al.* 2015). Our results contrast those observed for *P. ochraceus* whose predation rate increased by 47% in the same temperature range as our study (Gooding, Harley & Tang 2009). Both *P. helianthoides* and *P. ochraceus* live in the rocky coast of Northeastern Pacific at the same latitudinal zone. However, *P. ochraceus* is an intertidal species that routinely experiences dramatic oscillations in temperature and avoids overheating by filling its coelom with cold water during the high tide (Pincebourde, Sanford & Helmuth 2009). In contrast, *P. helianthoides* is a subtidal species and therefore is presumably less tolerant to temperature changes.

Fig. 5. Time series of *Pycnopodia helianthoides*, *Strongylocentrotus purpuratus* and kelp density at long-term kelp forest monitoring sites at the northern Channel Islands, California. Sites are grouped based on mean annual temperatures: <14 and >14 °C. This coincides with a division of sites between the western and eastern Channel Islands. Mean annual temperature based on daily temperature data from 2005 to 2011. [Colour figure can be viewed at wileyonlinelibrary.com]

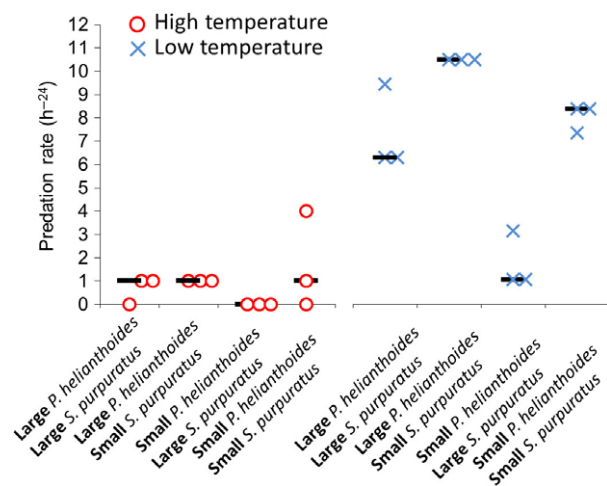
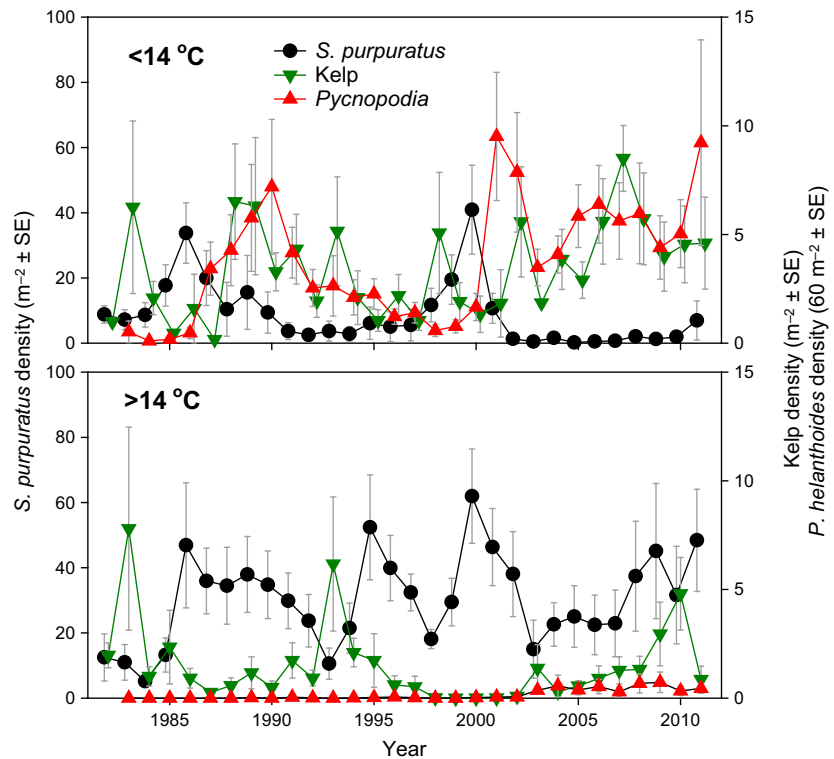


Fig. 6. Per capita predation rate on small and large *Strongylocentrotus purpuratus* by small and large *Pycnopodia helianthoides* at low (cross) and high temperatures (circle). Open circles show measurements for each experimental observation. Black lines show the group medians. [Colour figure can be viewed at wileyonlinelibrary.com]

Long-term data from the Channel Islands indicate the importance of *P. helianthoides* in controlling *S. purpuratus* and indirectly kelp. In the cold region *P. helianthoides* are effective at controlling *S. purpuratus* abundance and kelp dominates, except during periodic outbreaks of urchins such as in the mid-1980s and late 1990s that occurred following sea star mortalities (Eckert, Engle & Kushner 2000). However, in warmer waters where *P. helianthoides* are rare, *S. purpuratus* are abundant and kelp is typically

rare. In this region period declines in sea urchins and concurrent increases in kelp are associated with other mechanisms such as urchin disease (Lafferty 2004). Other predators, such as lobster and sheephead that are potentially capable of controlling sea urchins are typically rare in unprotected areas due to fishing (Lafferty 2004; Hamilton *et al.* 2010; Caselle *et al.* 2015). Therefore our results demonstrate that *P. helianthoides* is an important predator in Californian kelp forests but its effects are likely to be restricted to areas where mean annual temperatures are <14 °C. However, even within such areas the abundance and predation rate of *P. helianthoides* is likely to be reduced during warm periods such as those associated with El Niño conditions.

Unprecedented die-offs of sea stars including *P. helianthoides* have occurred throughout the northeast Pacific region in recent years (Stokstad 2014). While these mortalities are primarily caused by a viral pathogen (Hewson *et al.* 2014), emerging evidence (Eisenlord *et al.* 2016; Kohl, McClure & Miner 2016) suggests that the prevalence and effect of the disease has been exacerbated by elevated ocean temperatures (Hartmann 2015). The ecological consequences of die-offs of *P. helianthoides* have already been seen in some areas with increases in sea urchins (Schultz, Cloutier & Côté 2016). Similarly, previous seastar mortality events at the Channel Islands have occurred during warm periods, such as following the 1982–1983 and 1996–1997 El Niños (Eckert, Engle & Kushner 2000), and were followed by outbreaks of sea urchins and deforestation of kelps (Fig. 5). These results suggest that with ocean warming, and potentially increased frequency and intensity of El

Niño events, the role of *P. heliantoides* in controlling sea urchin populations will be further reduced over large areas with cascading effects on kelp forest communities.

Catastrophic shifts from productive kelp forest to impoverished urchin barrens are conspicuous phenomena on temperate rocky reefs (Ling *et al.* 2015). Global climate change may favour this process directly by physical damage on kelp provoked by storms and extreme weather (Ebeling, Laur & Rowley 1985; Steneck *et al.* 2002; Graham, Vasquez & Buschmann 2007; Byrnes *et al.* 2011) or indirectly by driving either range extension of efficient thermophilic grazers (i.e.: urchins, Ling *et al.* 2015 and tropical fishes, Vergés *et al.* 2014; Bennett *et al.* 2015) or range contraction of cool-water, habitat-forming macroalgae (Smale & Wernberg 2013). Furthermore, warmer temperatures may decrease the resilience of kelp beds by affecting bottom-up process such as recruitment and growth of kelp (Wernberg *et al.* 2010) and increase feeding rates of sea urchins (Carr & Bruno 2013). Our findings suggest that warming conditions may also reduce the top-down control of kelp forests by directly reducing predation rates and potentially causing a large-scale range contraction of an important predator.

Temperature is a fundamental driver in the biology of any organism, and subtle variations may exert huge effects on communities. However, we are still not able to predict those effects across different ecosystems, as evidenced for instance by possible idiosyncratic response on predator–prey interactions (our study, Gooding, Harley & Tang 2009; Vucic-Pestic *et al.* 2011). It is also possible that thermophilic predator species may substitute species excluded by either overfishing or warming condition. A recent study suggests that a novel synergistic interaction including a thermophilic species re-established the trophic control of keystone grazers in temperate systems (Galasso *et al.* 2015). Careful field observations and experimental approaches are important in determining the individual effect of temperature increase on key species and the whole community.

Authors' contributions

C.B. and N.T.S. conceived the ideas and designed methodology, collected and analysed the data, and wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility

The biological data used in this paper are archived in the Ecological Archives data paper (Kushner *et al.* 2013), data available from <https://doi.org/10.6084/m9.figshare.c.3306321.v1> (Kushner *et al.* 2016). Environmental data are provided in Table S1. The data of the experimental part are provided in Table S3.

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Supporting Information

Details of electronic Supporting Information are provided below.

Fig. S1. Location map showing mean annual sea surface temperature from 2005 to 2011 (MODIS: http://spg.ucsd.edu/Satellite_Data/California_Current/) and site locations at the northern Channel Islands, California.

Fig. S2. Variation in maximum size of *Pycnopodia helianthoides* among sites across the Channel Islands. Line is a loess smoother with 95% confidence interval.

Fig. S3. Variation in depth and fetch from west to east across the Channel Islands. Line is a loess smoother with 95% confidence interval.

Fig. S4. Probability of *Pycnopodia helianthoides* being present as a function of temperature based on logistic regression (line \pm 95% confidence interval).

Table S1. Site information.

Table S2. Results of three-way ANOVA testing for effects of temperature, starfish size and sea urchin size on the predation rates of *Pycnopodia helianthoides* on *Strongylocentrotus purpuratus*.

Table S3. Data of the experiments on the effects of temperature on predator–prey interaction strength.