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Predator-induced defences under tropicalisation: A biogeographic approach

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Abstract

Aim: The biogeography of predator-induced defences is an understudied area of predator–prey dynamics. Range overlap with predators that induce the response and local demographics (e.g., prey abundances) are likely to be important factors for determining the biogeographic distribution of induced defences within species. However, with climate warming, range-expanding warm-water predators are increasingly preying upon temperate species. This is a consequence of a wider phenomenon known as tropicalisation. We aim to determine: (i) if individuals of a temperate barnacle with induced defences ('bent morphs') are primarily present where they co-occur with range-expanding warm-water predators (muricid snails) and, (ii) if bent morphs are size-structured within populations.

Location: North-eastern Pacific rocky intertidal zone (~26–40° N).

Taxon: *Tetraclita rubescens* (Nilsson-Cantell, 1931), Balanomorpha.

Methods: We use photoquadrats from sites across the range of *T. rubescens* to determine the biogeographic distribution of populations with bent morphs and to assess size-structure. We use a combination of field surveys, literature, and museum occurrences to assess range overlap between cool and warm-water predators of *T. rubescens* and their association with populations with bent morphs and abundance patterns of *T. rubescens*.

Results: Bent morphs are commonly found within the equatorward portion of the species' range (where abundances are highest), in populations overlapping with range-expanding warm-water predators. Bent morphs primarily occur within the smaller size classes.

Main conclusions: To be partly resilient to the effects of tropicalisation, temperate prey must acclimatise/adapt to altered predator–prey dynamics. Predator-induced defences are one way to do this. We show that bent morphs within a temperate prey species (*T. rubescens*) are largely restricted to populations that overlap with large-bodied and range-expanding warm-water predators. This is evidence for the partial resilience of *T. rubescens* to tropicalisation and provides the rationale for further exploration of the eco-evolutionary consequences of tropicalisation in this study system and others.

KEYWORDS

Barnacles, *Mexacanthina*, Muricidae, predator-induced defence, predator–prey dynamics, range shifts, rocky intertidal zone, *Stramonita*, *Tetraclita rubescens*, tropicalisation

1 | INTRODUCTION

Many species have morphological defences that are only displayed when exposed to certain predators (Harvell, 1990). Such predator-induced defences are dependent upon several factors—including the genetic capacity of prey species to produce a phenotypic response (Tams et al., 2020), the magnitude of predation pressure, the types of predators and their cues, and associated costs and benefits to producing the defensive strategy (Harvell, 1990; Trussell & Smith, 2000; Weiss & Tollrian, 2018); all of which can be highly variable across space and time. Over the past few decades, researchers have developed theory (Tollrian & Harvell, 1999), studied the mechanisms (Harvell, 1986; Lively, 1986; Murua et al., 2014), and even uncovered the molecular basis of predator-induced defences in some species (Evans et al., 2022; Kishida et al., 2007).

Despite these advances, there are several knowledge gaps in our understanding of the spatio-temporal dynamics of predator-induced defences. Notably, it is unknown how inducible defences are distributed across the geographic ranges of prey species or if they are biogeographically structured to only occur where certain predators are present. This has been hard to test because most studies do not cover the full range extent of prey species (but see Lively, 1999). Further, we do not know if climate-induced range shifts of predators have affected the modern and potential future geographic distribution of inducible defences within prey species. These knowledge gaps are important to study because it will help researchers determine the potential for prey species to acclimatise or adapt to some of the ecological impacts of climate change. A biogeographic approach should be the first step toward exploring these ideas.

In coastal marine systems, recent work has shown that predator consumption rates peak around biogeographic transitions from warm temperate to subtropical regions (Whalen et al., 2020). This is thought to be due to a combination of turnover in predator species composition and their functional traits, which can include body size, prey selectivity, dispersal capabilities, and rates and/or modes of feeding. Ultimately, species turnover at biogeographic transition regions will be caused by shifts in oceanographic and physical conditions such as sea-surface temperature, upwelling, and habitat availability (Fenberg et al., 2015; Fenberg & Rivadeneira, 2019). This, in turn, may be associated with a spatial shift in the relative effect that predators have on individual prey species and communities (Whalen et al., 2020). Whether these biogeographic patterns are also associated with the distribution of predator-induced defences is unknown. However, the global increase in sea-surface temperature and incidence of marine heatwaves is causing a re-structuring of coastal marine communities (Hesketh & Harley, 2022; Sanford et al., 2019). Indeed, populations of warm-water predators that have historically been restricted to subtropical and tropical regions are now becoming established within temperate communities. This phenomenon is known as tropicalisation, which has primarily been observed within shallow water marine ecosystems (Vergés et al., 2019; Zarzyczny et al., 2022).

Tropicalisation could therefore contribute to an overall poleward increase in predation pressure and consumption rates of temperate prey. This, in turn, may result in selection for predator-induced defences within equatorward populations of temperate prey species where they are more likely to overlap with range-expanding warm-water predators. Alternatively, temperate prey may be naïve to range-expanding warm-water predators (Anton et al., 2020) and not exhibit inducible defences because of a presumed lack of a shared history. In fact, they may be more likely to exhibit induced defences in areas where they share an extensive history with cool-water temperate predators. Of course, species ranges are also dynamic over longer time scales (e.g., over glacial/inter-glacial cycles; Addicott, 1966; Marko et al., 2010), so the determination of shared histories of predator and prey should not be based solely on contemporary range overlap.

The geographic pattern of the abundance of a prey species should also be related to the predation pressure it experiences on local and regional scales (Gobin et al., 2022; Holling, 1959). Where a prey species is abundant, predation should increase as more food will be available for predators (i.e., as a functional response); this, in turn, may cause an increase in predator abundance (Stenseth et al., 1997; Wieters et al., 2008). Conversely, where a prey species is less abundant, resident predators may prey on different species if they are generalists (Murdoch, 1969). Therefore, the spatial dynamics of predator and prey abundance may affect the prevalence and distribution of predator-induced defences, causing them to be more common at locations where prey abundance is high; but again, this has not yet been studied.

Furthermore, selective or intense predation pressure can have impacts on the life history of prey, which may be reflected by the size distribution of defended versus un-defended individuals in a population. For example, juveniles and small adults can be more vulnerable to predation compared to individuals from larger size classes, which sometimes gain a size refuge from predation (Paine, 1976, 1981). Alternatively, juveniles may be rarely preyed upon, but predator cues may induce the defensive strategy in this stage, so they are defended by the time they reach a suitable size for predation (Jarrett, 2009; Weiss & Tollrian, 2018). Defended individuals may also grow slower than un-defended individuals

(Jarrett, 2009; Lively, 1986), causing them to be more common within smaller size classes. While much is known about the life history and size patterns of induced defences among some model species in localised and laboratory settings (e.g., *Daphnia*; Tollrian, 1995; Riessen, 1999), we are not aware of any studies that have examined the size-structures of populations across the geographic range of a prey species with a predator-induced defence. This is important to study because it allows for a comparison of the spatial demographics of populations with and without predator-induced defences and provides a baseline for future comparative studies as tropicalisation progresses.

In marine invertebrates, predator-induced defences usually take the form of morphological change, including production of defensive spines and thickening of shells (Harvell, 1990). Some rocky intertidal barnacles, for example, exhibit a 'bent' morphology in locations that receive high predation pressure when exposed to certain muricid gastropod predators (Jarrett, 2008, 2009; Lively, 1986; Murua et al., 2014). In bent morphs, the rim of the opercular opening grows perpendicularly relative to the base, compared with the typical conic morphs. Bent-morph barnacles have slower growth and lower reproductive output compared with the conic morphs, suggesting a life history trade-off (Jarrett, 2009, 2018; Lively, 1986). Importantly, however, not all barnacle species or populations that are preyed upon by muricid gastropods have individuals with bent morphs. This suggests that only some muricid species can induce a bent response; only some barnacle species/populations experience sufficient predation pressure to induce a response; and/or that only some barnacle species or populations have the genetic capacity to produce bent morphs.

Rocky intertidal marine invertebrates from the north-eastern Pacific coast are a good study system for exploring the biogeography of predator-induced defences. In this region, species have essentially one-dimensional north–south trending ranges, the distributions of predator and prey species are well-documented, and the physical and environmental characteristics are well known (Fenberg et al., 2015). There are three barnacle species in this region known to have bent morphs: *Chthamalus anisopoma* (Lively, 1986; Raimondi et al., 2000), *C. fissus* (Jarrett, 2008), and *Tetraclita stalactifera* (P. Raimondi, personal observation). Field and experimental studies on the *Chthamalus* species have given valuable insight to the mechanisms involved in producing the inducible response and have led to the development of eco-evolutionary theory (Lively, 1999; Lively et al., 2000). In these species, the bent morphs are induced in very young individuals when they encounter certain muricids. The probability of developing into a bent morph is positively related to the encounter rate with predators, though not all exposed individuals produce the bent morph. Approximately, 20%–40% of individuals in such populations develop the bent morphology (Lively, 1986; Raimondi et al., 2000). Currently, however, there are no studies that have characterised the range-wide occurrence and population structure of bent and conic morphs in any barnacle species. Nor do we know if range-expanding warm-water predators are important for structuring the modern biogeographic distribution of predator-induced defences.

Here, we quantify the geographic distribution of populations with and without bent morphs across the range of a common temperate barnacle (*Tetraclita rubescens*) along the north-eastern Pacific coast. There are no previously published observations of this species having a bent morph, despite its large range and common occurrence. Based on prior research on other barnacle species (see above), we assume that the bent morph in *T. rubescens* is a predator-induced defence, although we do not test this connection experimentally. In this study, we test the hypothesis that bent morph individuals are largely restricted to equatorward populations where they overlap with range-expanding warm-water predators. If supported, this would suggest that some temperate prey species are at least partly capable of acclimatising or adapting to the indirect effects of tropicalisation. Secondly, we hypothesize that where they occur, bent morph individuals are primarily found in the smaller size classes. To do this, we categorise populations as those with and without the bent morphology across the range of *T. rubescens*. We then measure the size-structure of *T. rubescens* populations and categorise individuals by morphotype (i.e., bent or conic; Figure 1). We also assess the range-wide abundance of *T. rubescens* and map the overlap in range of predators that are known to feed on *T. rubescens* to look for spatial concordance between the range-wide pattern of abundance of *T. rubescens*, the types of predators present, their functional traits (e.g., body size, feeding strategies), and their association with the geographic distribution of populations with bent morphs.

2 | MATERIALS AND METHODS

2.1 | Study species

Tetraclita rubescens has a geographic range that extends from northern California (Cape Mendocino, ~40.3°N) to Baja California Sur (Magdalena Bay, ~24.5°N); mostly within cool and warm temperate biogeographic provinces (Mendocinian, Montereyan, Southern Californian, Ensenadian, ~40–27°N), but also within the subtropical Magdalenian province (27–24.5°N; Blanchette et al., 2008). Individuals primarily live within the mid-rocky intertidal zone as solitary individuals or in dense aggregations. Once they reach maturity around 2 years, *T. rubescens* brood and release tens of thousands of larvae in a single breeding season (Hines, 1978). Larvae have a pelagic duration of 3–4 weeks (Dawson et al., 2010). *Tetraclita rubescens* has undergone a well-documented poleward range expansion, which has been linked to climate warming (Connolly & Roughgarden, 1998; Dawson et al., 2010; Sanford et al., 2019). Populations are increasing in abundance in the expanded portion of its range, especially during El Niño years and other warm-water events, which are associated with high recruitment (Sanford et al., 2019). Individuals can reach large sizes (>40 mm shell diameter) compared to other co-occurring barnacle species and have thick shell wall plates (four) with external ribbing. Their opercular plates are usually recessed well below a narrow diamond/kite-shaped opening (Sanford & Swezey, 2008).

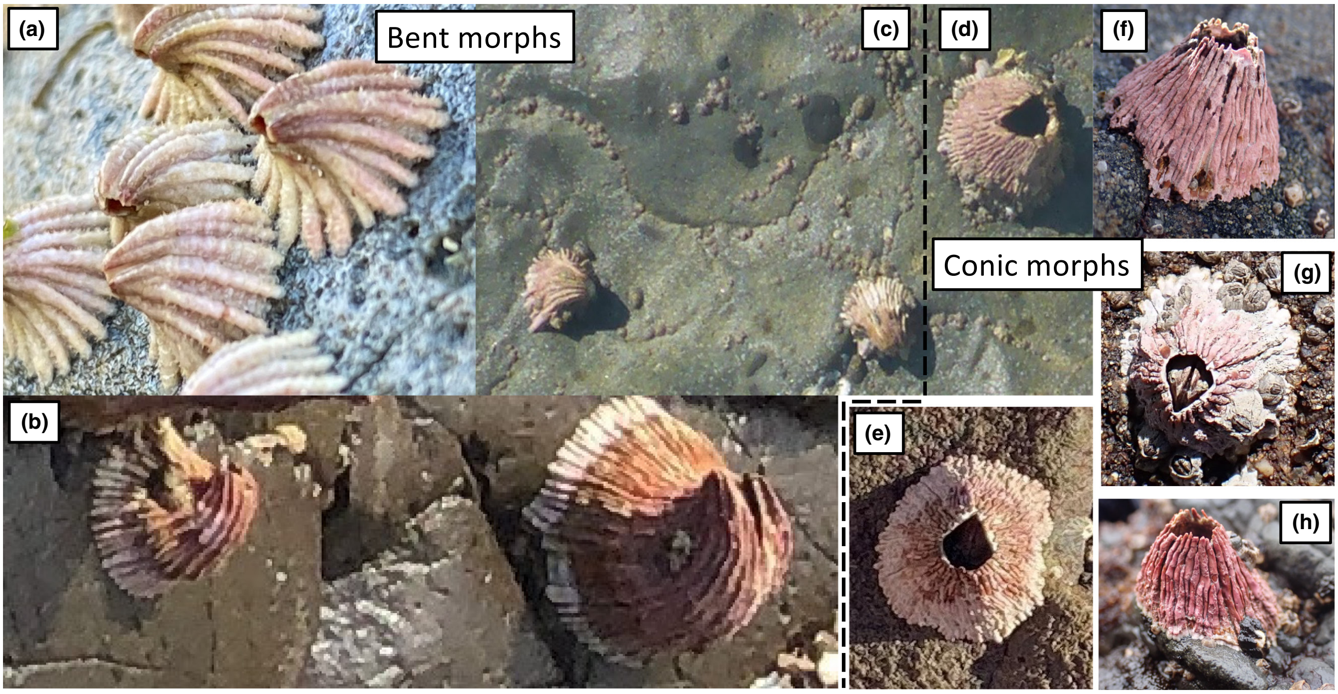

FIGURE 1 Examples of bent and conic morphs of *Tetraclita rubescens*. In the bent morphs (a–c), the rim of the opercular opening is orientated perpendicular to its base, whereas in the conic morphs (d–h) it is parallel to the base. Both morphs co-occur in the same microhabitat (c, d).

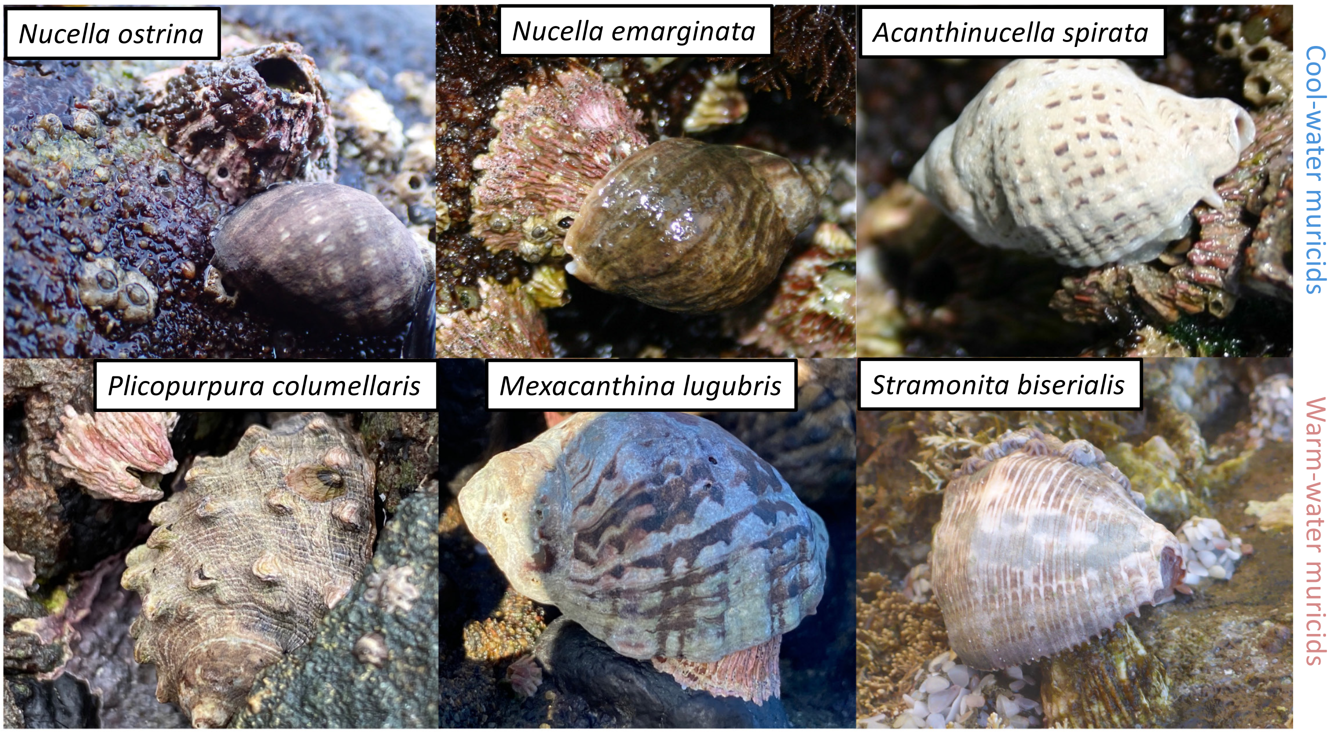

FIGURE 2 Photographs of the cool and warm-water muricids known to prey upon *Tetraclita rubescens* (minus *Nucella canaliculata*, a rare predator of *T. rubescens*). Each photograph was taken during an active predation event on *T. rubescens*. The cool-water muricids are medium-sized (maximum shell lengths ~30–40 mm) whereas the warm-water muricids are large bodied (maximum shell lengths ~60–100 mm).

The large range extent of *T. rubescens* means that it overlaps with multiple species of muricid predators (Figure 2) that broadly fall under two categories based on their biogeographic affinities: cool and warm-water species. For the cool-water species, *T. rubescens* is readily preyed upon by *Nucella emarginata* (Sanford & Swezey, 2008; West, 1986), and only rarely by *N. ostrina*, *N. canaliculata*, and *Acanthinucella spirata*. All are medium-sized species with maximum shell lengths of ~30–40 mm. In the equatorward portion of its range, *T. rubescens* overlaps with at least three species of large warm-water muricids (>60 mm in maximum shell length), all of which are currently undergoing poleward range expansions: *Mexacanthina lugubris*, *Stramonita biserialis*, and *Plicopurpura columellaris*. We provide more information about the ecology and feeding strategies of the muricid predators, as well as information on recent poleward range expansions of the warm-water species in the supplementary information.

2.2 | Geographic distribution and size-structure of the bent morphology

We characterised *T. rubescens* individuals as conic or bent as previously described for *Chthamalus* species (Jarrett, 2008; Lively, 1986). Typical conic morphs are cone shaped with the rim of the opercular opening parallel to its base. For bent morphs, the rim of the opercular opening is angled perpendicularly relative to its base (Figure 1). To test the hypothesis that the bent morphology is largely restricted to equatorward populations, we assessed the geographic distribution of populations with bent morphs at 30 sites, spanning nearly the entirety of its geographic range from 26.2 to 39.3° N. At each site, we examined photo-quadrats taken within *T. rubescens* habitat (Table S1), noting whether bent morphs were present. If present, we categorised sites by whether bent morphs are common or rare. All photo-quadrats were taken between 2017 and 2022. 16 sites are from long-term monitoring plots (50 × 75 cm) established by MARINe (multi-agency rocky intertidal network; marine.ucsc.edu). These sites are concentrated within the central range of *T. rubescens* in southern California and on the Channel Islands from ~32 to 34° N. For some MARINe sites ($n = 6$), we examined multiple years of permanent photo-quadrats (between 2017 and 2020) to determine if there has been a change in the frequency/presence of bent morphs over time. Photo-quadrats (50 × 50 cm) from the remaining 14 sites were taken during a single low-tide between 2017 and 2021 and largely cover the poleward (35.5–39.3° N, $n = 4$) and equatorward geographic distribution of *T. rubescens* (26.7–31.9° N, $n = 10$). In total, we examined 901 photo-quadrats. We supplemented this database by visually examining each geo-referenced and confirmed photograph of *T. rubescens* uploaded to iNaturalist (inaturalist.org). In total, 1172 photographs (taken from July 2005 to March 2020), spanning most of its geographic range (26.25–39.35° N), were checked for the presence of the bent morph. All in situ and photo identifications of bent morphs were from a single person (PBF) to reduce observer bias.

To test the hypothesis that the bent morphology is size-structured within *T. rubescens* populations (where it is present), we assessed the size-frequency distribution of populations using photo-quadrats at 12 sites evenly spanning its geographic range (Table S2). After setting the scale, we measured the basal diameter (mm) of individuals using ImageJ and categorised individuals as bent or conic. In total, we measured the basal diameters of 12,634 individuals. Where the bent morph is present, we tested for differences in size between bent and conic morphs per site using Wilcoxon rank-sum tests (due to violations of normality). We only measured individuals in which their full basal diameters were visible and orientated in a plane even with the substrate on which the quadrat was photographed. In localised areas, *T. rubescens* sometimes live within dense aggregations and individual basal diameters are difficult to discern; we did not measure these individuals. *Tetraclita rubescens* abundances can be highly variable at local and regional scales. Therefore, the number of photo-quadrats analysed per site was chosen to estimate the size-frequency distribution of local populations, not their abundances.

2.3 | Range-wide abundance of *T. rubescens* and range overlap with muricid predators

We used field data provided by MARINe to examine the range-wide abundance pattern of *T. rubescens*. Percentage cover of *T. rubescens* per site was calculated using a point-intercept sampling method, as described in Blanchette et al. (2008). The dataset covers 99 sampled sites that span nearly the entirety of the geographic range of *T. rubescens* (26.70–40.34° N). We determined the modern extent of range overlap of each muricid predator of *T. rubescens* across its range to determine which predators are found at locations with bent morphs. We relied on literature sources to assess range extents for the cool-water species (*N. emarginata*, *N. ostrina*, *N. canaliculata*, *A. spirata*). For the warm-water species (*M. lugubris*, *S. biserialis* and *P. columellaris*), we used a combination of recently published work (Wallingford & Sorte, 2022), field surveys from 2017 to 2022, and confirmed recent records from iNaturalist. For the field surveys, we conducted 1-h timed searches at 15 locations on the Pacific side of the Baja peninsula from 23.0 to 29.9° N in 2017, 2018, and 2021/22. At each location, we recorded the presence or absence of the warm-water muricids and made notes of their local abundance. The historic poleward range limit of each warm-water muricid was estimated using a combination of pre-1980's museum records and literature sources based on museum records (e.g., Fenberg & Rivadeneira, 2019; Keen, 1971). We then compared the historic and modern poleward limits to estimate the extent of range expansion. Finally, we mapped the ranges of each muricid species onto the range-wide abundance pattern of *T. rubescens*, noting which populations have bent morphs.

3 | RESULTS

3.1 | The geographic distribution of the bent morphology and size-structure

We refer to three equal portions of the range of *T. rubescens* throughout the results and discussion: its poleward (35.0–40.3° N), central (29.8–35.0° N), and equatorward range (24.5–29.8° N). Bent morph individuals are only common within populations from the equatorward portion of its geographic range (Figure 3; Table S1), from 26.23 to 29.43° N. All populations in the central and poleward portion of its range, from 30.43 to 39.27° N consist only of conic individuals, except for one bent individual noted from Ensenada in 2021 (31.89° N) and one at Punta Baja (29.95° N) in 2022. All photographs examined from iNaturalist, which are heavily biased towards the central and poleward range of *T. rubescens*, consist only of conic individuals. Thus, the bent morphology is primarily a feature of equatorward *T. rubescens* populations (Figure 3), supporting our first hypothesis. This suggests that bent morph individuals are either completely absent or very rare within the central and poleward portions of its geographic range.

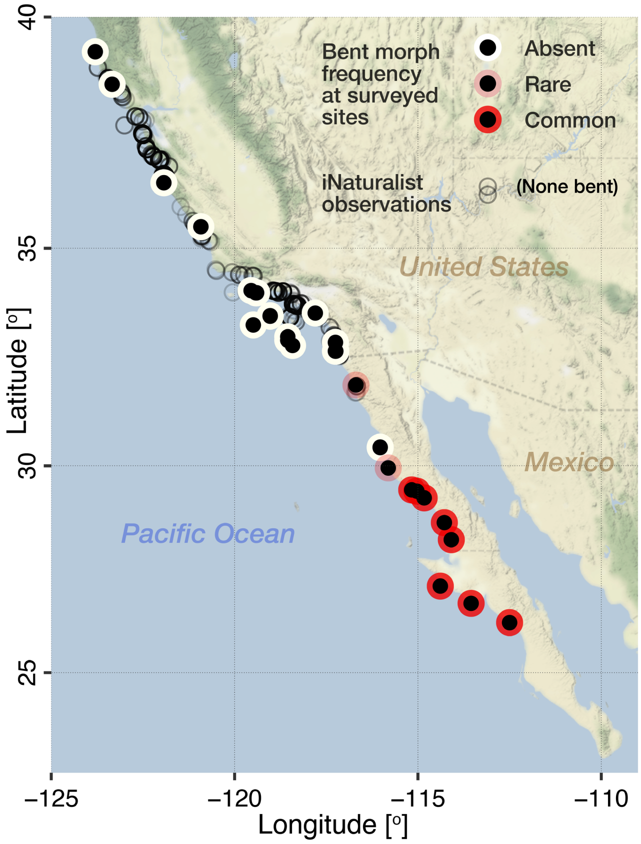

FIGURE 3 Distribution of populations with and without bent morph individuals across the geographic range of *Tetraclita rubescens*. Circles with borders (red, white, pink) show locations (26.2–39.3° N) where we surveyed the frequency of bent morphs in quadrats of *T. rubescens* habitat ($n = 30$; Table S1). Bent morphs are common at the surveyed sites within the equatorward portion of the species' range ($n = 8$; red bordered circles; 26.23–29.43° N). However, a single bent morph individual was found in two populations surveyed, Punta Baja (29.95° N) and Ensenada (31.89° N) in 2021/2022 within its central range in northern Baja California (pink bordered circles). The overplotted grey open circles ($n = 1172$) show locations of confirmed identifications of *T. rubescens* photographs (no bent morphs found) taken between 2005 and 2020 for iNaturalist (inaturalist.org/observations?taxon_id=121682).

Of the 12 locations where we measured the size-frequency of *T. rubescens* (from 27.12 to 39.27° N), bent morphs are common at the five southernmost locations (27.12–29.39° N) and present (rare) in one population (Ensenada). Where they are common, bent morph individuals make up an average of 29% of populations (SE = 0.04) and are significantly smaller than conic individuals ($p < 0.0001$; Figure 4b), supporting our second hypothesis. Bent morphs are particularly common in the juvenile and small size classes (~5–15 mm in diameter) and conic morphs are more common in the medium to large size classes (>15 mm). Bent morphs larger than 15 mm are uncommon (except at Adams), as are small conic morphs (<10 mm), but they are occasionally present. There appears to be high recruitment in the equatorward range, judging from the bimodal distributions with modes in the juvenile size classes (Figure 4b). Size-frequency distributions of the remaining six locations in the central and poleward range (Figure 4a; ~32–39° N) are spatially variable, within and across regions. For example, at San Clemente Island (32.92° N), the site is dominated by small- to medium-sized individuals (~5–20 mm), whereas at a similar latitude (32.67° N) on the mainland at Cabrillo National Monument, there is a much wider range of size classes, with individuals reaching upwards of 45 mm in basal diameter. The northernmost sampled sites (from ~35 to 39° N) have few small individuals (<10 mm), suggesting sporadic annual recruitment (see also Sanford et al., 2019).

3.2 | Range-wide abundance of *T. rubescens* and range overlap with muricid predators

Local abundances of *T. rubescens* can be highly variable, but at a broad scale, there are three regions with peaks in abundances (Figure 5b). In the poleward portion of its range, population abundances peak on the Big Sur coast (~36.5° N), south of Monterey Bay. North of here, population abundances are low (except on the Farallon islands; 37.69° N) until its northern range limit near Cape Mendocino (~40.3° N). In the central range, population abundances peak in southern California and the Channel Islands (~33–34° N), but there is high site-to-site variability, and survey effort is high in this region. Abundances reach their highest in the equatorward portion of its range in Baja California Sur, between Punta Eugenia/Isla Natividad and Punta San Roque (27.17–27.88° N). Although there is lower sampling effort, this region clearly sustains high local abundances. This is reflected, in part, by the high recruitment in the region (Figure 4b). Previous studies using similar datasets are also indicative of these abundance patterns (Blanchette et al., 2008; Dawson et al., 2010; Sagarin & Gaines, 2002). Bent morphs therefore are only common within the equatorward range of *T. rubescens* where population abundances reach their highest.

Nucella emarginata is a common predator of *T. rubescens* in the central portion of its range (from southern to central California), but there are no populations where bent morphs are common where they overlap in range (only a total of two bent morphs were found where they overlap in northern Baja; Figure 5). The

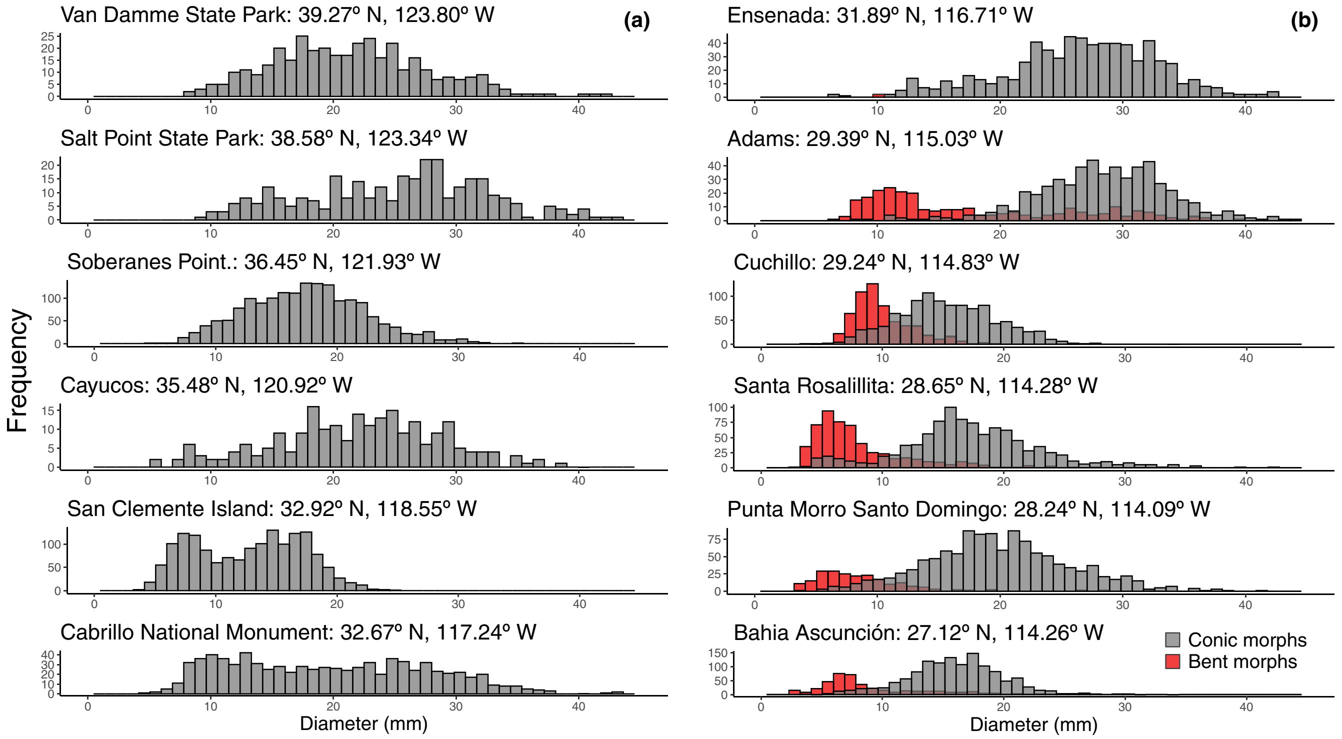

FIGURE 4 Size-frequency distributions of 12 *Tetraclita rubescens* populations across its geographic range (27.12–39.27° N), with individuals categorised as bent or conic. Plots are arranged in descending latitude. (a) populations where bent morphs are absent, within the central and poleward portions of the range of *T. rubescens*. (b) populations where bent morphs are present. Note, only one bent individual was found in the Ensenada population (10.5 mm basal diameter). Where they are present, the bent morph individuals are primarily found within the small size classes (~5–15 mm), whereas the conic morphs dominate the medium to large size classes (>15 mm). Note the large number of small individuals at all locations where the bent morphs are common, suggesting high recruitment within the equatorward portion of its range where local abundances are highest (Figure 5).

other cool-water muricids (*N. canaliculata*, *N. ostrina*, *A. spirata*) are uncommon predators of *T. rubescens* and their ranges also do not overlap with any populations where bent morphs are common (Figure 5). Within the equatorward range of *T. rubescens*, individuals are preyed upon by at least three species of warm-water muricids (*M. lugubris*, *P. columellaris*, and *S. biserialis*). Each species is currently undergoing a poleward range expansion, are large bodied (>60 mm in shell length) and have morphological (labral spines; *M. lugubris*), behavioural, or physiological traits (secretions/toxins; *P. columellaris* and *S. biserialis*) to accelerate the consumption of a wide variety of prey species (Table S3; Section 4). All three species have been observed to feed on *T. rubescens* where bent morphs commonly occur (Figures 2 and 5; Phillip B. Fenberg, personal observation). Details of the poleward range expansions of each warm-water muricid are given in the supplementary information but can be visualised in Figure 5.

4 | DISCUSSION

Predator–prey interactions are major drivers of the evolution of animal morphology (Vermeij, 1994). Balanomorph barnacle morphology, for example, is partly a product of their long evolutionary history with predatory gastropods, dating back to the Cretaceous (Palmer, 1982). Shell morphological features of *T. rubescens* that are thought to be evolutionary adaptations to muricid predation are: thickened and reduced number of shell wall plates (four), external ribbing, and recessed opercular plates (Palmer, 1982; Sanford & Swezey, 2008). In addition, their relatively large size (maximum size: 40–45 mm basal shell diameter) should give some individuals a size refuge from predation. Across its range, however, some populations will experience higher predation pressure either because of demographic factors (e.g., predator/prey abundance) and/or because of biogeographic turnover in predator species composition and their functional traits. If the standard conic morphology is not sufficient to defend against regionally or locally high predation pressure and/or because predation by a particular species is difficult to defend against, then selection (via predation pressure) may favour plasticity in the development of induced defences (bent morphs). If the factors that cause these changes in predation risk are geographically structured, then we hypothesized that the geographic distribution of populations with bent morphs (which we assume to be a predator-induced defence) should mirror this structure. We also suggest that the range-expanding warm-water predators cause this spatial structure or enhance a pre-existing structure. The biogeographic patterns we find in *T. rubescens* are consistent with these ideas.

We find that populations with bent morphs are only commonly found within the equatorward range of *T. rubescens* (26.23–29.43° N) and primarily among the smaller size classes (Figures 3 and 4). Here, populations overlap with range-expanding warm-water muricid predators (*M. lugubris*, *S. biserialis*, *P. columellaris*). Within the central and poleward portion of its range, individuals with the bent morphology are largely absent (apart from two bent individuals observed in the central range), suggesting that predation by cool-water muricids (*N. emarginata*, *N. ostrina*, *N. canaliculata*, *A. spirata*) will not induce the bent morphology. We give several potential explanations as to why the bent morphology is associated biogeographically with the warm-water predators but not the cool-water predators.

The conic morphology is likely enough protection from predation risk posed by the cool-water muricids. Indeed, Sanford and Swezey (2008) show that *T. rubescens* individuals are rarely preyed upon in the most poleward portions of its range. This is thought to be due to robust shell features compared to co-occurring barnacle species (e.g., *Semibalanus cariosus*), which pose less of a challenge for predation. In the central portion of its range, however, *T. rubescens* are commonly preyed upon by *N. emarginata*. Here, they share an extensive region of range overlap with a long history of interaction (Sanford & Swezey, 2008), but bent morphs are largely absent where they co-occur (Figure 5). This could be due to several non-mutually exclusive reasons: (i) predation pressure is lower where *T. rubescens* and *N. emarginata* overlap, compared to its equatorward range where they do not overlap, (ii) the mode of predation by *N. emarginata* is different from the warm-water muricids and therefore the bent morphology might not be a suitable defence, and/or (iii), central and poleward populations do not have the genetic capacity to produce bent morphs. Although we do not directly measure predation pressure, nor do we know if there are genetic differences between populations with and without bent morphs, we may begin to tease apart important differences in what causes the bent morphology by comparing the functional traits and modes of predation between the cool and warm-water muricids.

Body size is one of the key differences between these groups (Table S3). The warm-water muricids attain maximum sizes ranging from 60 to 100 mm in shell length. Whereas the cool-water muricids do not achieve sizes larger than ~40 mm in shell length, and even individuals this large are uncommon. Therefore, body size asymmetries between predators and *T. rubescens* increases toward its equatorward range. Such asymmetries often determine the outcome of predator–prey interactions, with larger predators dominating (Peters, 1986; Urban, 2007; Wilson, 1975). In addition, larger predators will consume more and may be more efficient at hunting larger prey, compared to smaller predators. Thus, the relatively large size of *T. rubescens* may be sufficient protection against the medium-sized cool-water predators but less so against the larger warm-water

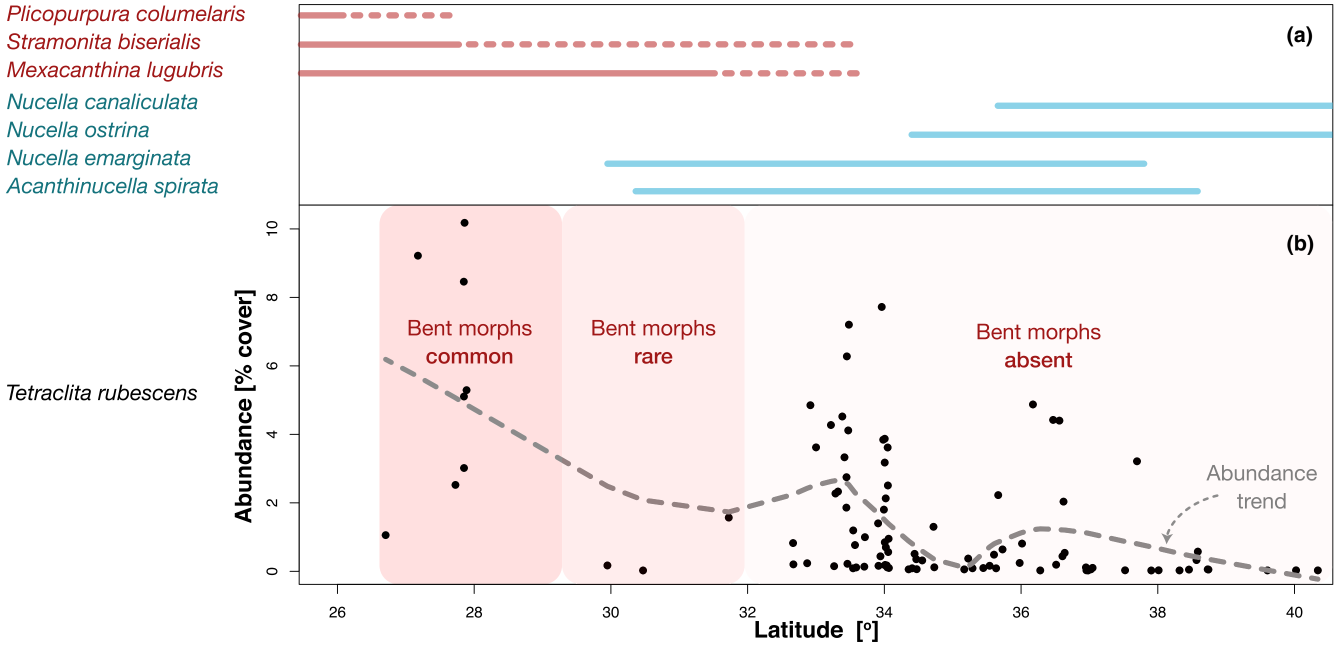

FIGURE 5 The range-wide abundance pattern of *Tetraclita rubescens*, and range overlap with its muricid predators. Abundance is expressed as percentage cover, measured from 99 locations spanning its geographic range (26.70–40.34° N), collected from the Multi-agency Rocky Intertidal Network, MARINe (marine.ucsc.edu). (a) the geographic range extents of all muricid species known to feed on *T. rubescens* with the warm-water species in red and the cool-water species in blue. Only the warm-water species overlap with *T. rubescens* at locations where the bent morphs are common. All three warm-water species are currently undergoing a poleward range expansion and therefore, contributing to tropicalisation of the broader region. Estimated extents of their modern range expansions are shown as red dotted lines. (b) Three portions of the *T. rubescens* range have peaks in local abundance shown by the grey local regression curve (LOESS; span = 0.5). The equatorward portion of its range, where bent morphs are common, sustains populations with the highest abundances (although sampling is more geographically sparse compared with central and poleward portions of its range).

predators. Furthermore, while the use of toxins to enhance predation appears to be common among the predator species (Table S3), the larger warm-water muricids will be able to use a proportionally larger amount of toxin to subdue prey. Given the above, we believe that predator body size is an important functional trait that contributes to the geographic distribution of the bent morph.

Differences in the attack location and mode of predation may also shed light on which species cause the bent morph. Preventing attack via the opercular opening is likely the reason for the bent morph as it makes it harder for predators to access the opercular plates (Jarrett, 2008). Most of the species that commonly attack *T. rubescens* appear to do so via the opercular opening, by either drilling through the opercular plates or between them (Table S3). Therefore, we must look for differences in how the cool versus warm-water muricids attack the opercular opening. The use of labral spines to aid predation of barnacles is a well-known adaptation among some muricids, including the warm-water *Mexacanthina lugubris* and the cool-water *A. spirata* (Marko & Vermeij, 1999). *Acanthinucella spirata* is an uncommon predator of *T. rubescens*. On the other hand, *M. lugubris* is commonly observed to prey on *T. rubescens* (Phillip B. Fenberg and Karolina M. Zarzyczny, personal observations; Figure 2) and is abundant to common at locations with bent morphs (Table S4). Although only reported in the barnacle *Chthamalus fissus* (Jarrett, 2008), *M. lugubris* rams its labral spine into the opercular opening to force or break apart opercular plates to gain access to soft tissues. This mode of predation removes the need for drilling and the use of toxins, making it an efficient predator of barnacles. In fact, both *M. lugubris* and its sister species in the Gulf of California (*M. angelica*) are known to cause bent morphs in *C. fissus* and *C. anisopoma*, respectively (Jarrett, 2009; Lively, 1986). Interestingly, the relative length of the labral spine may be shorter among individuals of *M. lugubris* in locations where they preferentially feed on *C. fissus* compared to the larger *T. rubescens* (Figure S2); as observed among their congeners within the northern Gulf of California (Paine, 1966; Yensen, 1979).

Given that there is extensive range overlap between *T. rubescens* and *M. lugubris* (Figure 5), a shared history along the Pacific coast of the Baja California peninsula (Fenberg et al., 2014), and high abundance where bent morphs occur (Table S4), it is likely that *M. lugubris* can induce the bent morph in *T. rubescens*. However, abundant *M. lugubris* populations also overlap with *T. rubescens* in its central range where the bent morph is rare in northern Baja California and absent in southern California (Figure 5). Assuming *M. lugubris* can induce the bent morph, juveniles are still likely to be exposed to the predator cue in central range where they overlap (~30–33°N), yet bent morphs largely do not occur here. This could be due to insufficient predation pressure to induce bent morphs, or central populations do not have the genetic capacity to produce bent morphs. The former possibility could be due to prey switching behaviour by *M. lugubris* centred around northern Baja. In this region, *T. rubescens* abundances are relatively low (~30–32°N; Figure 5) whereas an alternate prey species, *C. fissus*, are abundant and have many bent/narrow opening individuals caused by *M. lugubris* predation (Fenberg et al., 2014; Jarrett, 2008). Therefore, *M. lugubris* likely predate upon *C. fissus* more than *T. rubescens* in this region because of differences in their relative abundance. This is supported by recent offshore cyprid larval sampling nearby in southern California, which revealed that *C. fissus* dominated all samples while *T. rubescens* are uncommon (Yamhure et al., 2021). In addition, we have observed multiple predation events by *M. lugubris* on the mussel *Mytilus californianus* where they form extensive beds in northern Baja (Punta Baja; ~30°N; Figure S1), where bent morphs of *T. rubescens* are rare. Extensive *M. californianus* beds become less common south of Punta Baja, which is approximately the region where *T. rubescens* become abundant and bent morphs appear (Figure 5). Thus, the biogeographic distribution of the bent morph in *T. rubescens* appears to be partly a function of prey switching behaviour by *M. lugubris* caused by shifts in prey species abundance centred around Punta Baja. Indeed, our field observations indicate that *M. lugubris* consume a wide variety of prey species in northern Baja (Figure S1), supporting a generalist diet. This region also coincides with changes in sea-surface temperature and strong upwelling (Zaytsev et al., 2003), which are associated with a biogeographic boundary and changes in community structure (Blanchette et al., 2008; Fenberg et al., 2015). Thus, there may ultimately be an indirect effect of regional oceanography that helps explain the current distribution of the bent morphology in *T. rubescens*.

The other warm-water muricids may also be capable of causing the bent morph, but more research on their feeding ecology is required. *Plicopurpura columellaris* is the largest of the range-expanding warm-water muricids and feeds by using secretions to immobilise its prey (Naegel & Cooksey, 2002). However, *P. columellaris* does not reach as far north as the most northerly population with bent morphs (Figure 5). *Stramonita biserialis* is a generalist like *M. lugubris* (Herbert, 2004) and both co-occur and prey on *T. rubescens* at each location where bent morphs are common, suggesting that one or both species induce the bent morph.

Regardless of which warm-water predator (or combination) induces the bent morph, all three are currently undergoing poleward range expansions and thus, are contributing to tropicalisation of the broader region. Two of the warm-water species (*S. biserialis* and *P. columellaris*) have high dispersal potential (pelagic larval duration >2 months; Table S3), suggesting that continued expansion could be rapid. *Tetraclita rubescens* has also undergone an expansion over the last few decades (Dawson et al., 2010; Sanford et al., 2019), and in southern California it is becoming more common, while one of its main space competitors, *M. californianus*, suffers declines (Miner et al., 2021). These modern range shifts have parallels with expansion-contraction dynamics over the Quaternary period (Addicott, 1966; Marko et al., 2010). Pleistocene deposits in southern California and northern Baja also contain warm-water muricids and *T. rubescens* (Emerson, 1956; Kern, 1977; Lipps et al., 1968; Muhs, 2022; Valentine, 1980). For *S. biserialis* and *M. lugubris*, their modern poleward limits in southern California are near their fossil range limits during the last interglacial period (~125,000 Kya; Muhs, 2022). Modern sea-surface temperatures are now on par with this period (Hoffman et al., 2017), strongly suggesting that the warm-water muricids are tracking their thermal limits. We should therefore expect reports of bent morphs north of their current distribution (Figure 3) as the warm-water predators become more common and expand further with climate warming.

In addition to being biogeographically structured, we also find that bent morphs are size-structured within equatorward populations (Figure 4). There are several potential explanations of this pattern. Firstly, we know that the bent morph forms in the juvenile stage because the shell plates around the opercular opening (i.e., the bent part of the shell) are mostly grown at this time (Crisp & Bourget, 1985). Therefore, the shell plates surrounding the opercular opening are the oldest growth and the newest growth is at the base. As individuals get older, the opercular opening becomes larger through erosion/abrasion (Darwin, 1854; W. Newman, personal communication), which likely reduces their bent appearance. Thus, some larger individuals may have started their lives as bent, but now appear as conic. While there are some medium-sized bent individuals, they are rare. Alternatively, bent morphs may grow slower than conic morphs (Jarrett, 2009; Lively, 1986), causing the faster growing conic morphs to reach a size refuge from predation more quickly than bent morphs and become dominant in the medium to large size classes. Such differences in growth rate may also cause the maximum size of bent morphs to be smaller than that of the conic morphs. Furthermore, consistently high recruitment within equatorward populations (Figure 4) will increase the number of juveniles exposed to predators that induce bent morphs, which would also contribute to their dominance in the smaller size classes. There is also the possibility of higher mortality among medium-sized bent morphs, which could be caused by high predation pressure in these size classes. Finally, predation pressure could have increased very recently among equatorward populations due to range expansions and increases in abundance of the warm-water muricids. If so, the larger/older conic morphs may have started their lives during a period of comparatively lower predation pressure than the smaller/younger bent morphs. Since individuals can live upwards of 15 years (Dawson et al., 2010), this change in predation pressure could have occurred within the lifespan of some of the conic morphs.

5 | CONCLUSIONS

If temperate prey species are to be partly resilient to the impacts of tropicalisation, they must cope with not only enhanced thermal stress, but also altered predator–prey interactions. One way to do this is through predator-induced defences. We find that the bent morph of *T. rubescens* is only commonly found within the equatorward portion of its range where it overlaps with range-expanding warm-water predators, and primarily within the smaller size classes. There are, however, several outstanding questions and avenues for future research.

Currently, we cannot say whether individuals from central and poleward populations of *T. rubescens* are either not capable of developing into bent morphs or if they do not have sufficient cues to induce bent morphs. Future studies should conduct long-term monitoring, field sampling, experiments, and genomic studies of populations with and without bent morphs to fully understand how and why the bent morph is only common within the equatorward portion of its range. Such studies are also needed to determine which predators can induce the bent morph, and to assess its life history and eco-evolutionary consequences. Our study provides the rationale for exploring these changes in this study system and other areas currently affected by tropicalisation (Vergés et al., 2019). With multi-year datasets, we can test for differences in recruitment, growth, and mortality. These data will provide key information to determine why the bent morphs are mostly found within the smaller size classes. Sampling of individuals will allow us to test for differences in reproductive output, soft tissue anatomy, and shell structure. We also need to test if spatial differences in predation pressure and modes of predation by cool versus warm-water muricids explain the geographic distribution of the bent morph. Future studies should also consider if oceanographic conditions and patterns of gene flow in *T. rubescens* underlie the biogeography of the bent morph, now and into the future.

Experimental studies are needed to isolate which predators induce the bent response, including treatments with *T. rubescens* individuals from different portions of its geographic range to determine if all populations are capable of the bent morph. These experimental and field studies should be complemented with genomic screening to determine if bent morph individuals are genetically different from conic morphs. If they are different, it would provide evidence that the bent morph is an evolutionary adaptation to predation by warm-water muricids. With the above information, multispecies biogeographic and eco-evolutionary models (Haller & Messer, 2023) can be used to help understand and predict the broader consequences of altered predator–prey dynamics due to ongoing tropicalisation.

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CONFLICT OF INTEREST STATEMENT

We declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data used in this research are archived in the supplementary information tables and at Dryad: https://doi.org/10.5061/dryad.djh9w0w5q.

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BIOSKETCH

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Author contributions: Phillip B. Fenberg conceived of the idea for the paper, analysed the photo-quadrat data, and wrote all drafts. All authors carried out essential fieldwork (especially helpful during the pandemic when international travel was limited), commented on drafts, and helped steer the direction of the paper.

SUPPORTING INFORMATION

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

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