



Sea-surface temperature affects breeding density of an avian rocky intertidal predator, the black oystercatcher *Haematopus bachmani*

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ABSTRACT

Data collected in ten years (2003–2012) on Triangle Island, British Columbia, Canada were used to test the hypothesis that the annual breeding effort of black oystercatchers (*Haematopus bachmani*) declines with increasing spring sea-surface temperature. In all ten years, between nine and 15 oystercatcher pairs laid eggs in May and June, and as predicted, the number of active nests was negatively correlated with the mean sea-surface temperature in April. However, contrary to prediction, neither mean clutch size nor mean egg size declined with temperature. Clutches composed of just a single egg, probably indicative of recruitment by inexperienced females, appeared only in the five years with sea-surface temperatures below 9 °C. A reduction in the breeding propensity of individual females, rather than increased rates of mortality or emigration, better explained why fewer oystercatcher pairs bred in warm-water years. We infer that the breeding propensity of oystercatchers is indirectly affected by sea-surface temperature, mediated by effects of temperature on the behavior and physiology of the birds' invertebrate prey. Our results suggest a novel mechanism by which ocean warming might affect predator–prey interactions in intertidal ecosystems.

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1. Introduction

The integrity of coastal ecosystems is being compromised by a wide variety of environmental stressors (Harley et al., 2006). These stressors include sea-level rise (Chu-Agor et al., 2011), increases in the frequency and severity of extreme storm events (Wethey et al., 2011), warming (Richardson, 2008) and acidification of the ocean (Gaylord et al., 2011), the discharging of oil (Lance et al., 2001) and industrial development (Buller and Chapman, 2010). In order to predict and mitigate the future impacts of these and other stressors on coastal ecosystems, there is need to better understand how these systems function under current levels of environmental variation.

The oystercatchers (Family Haematopodidae), a group of ten extant species of large shoreline birds (Thomas et al., 2004), have proven reliable indicators of the state of coastal ecosystems (Carlson-Bremer et al., 2010). As top predators, oystercatchers often play important roles in structuring the intertidal communities in which they feed (Coleman et al., 1999; Frank, 1982; Marsh, 1986). However, with the exception of the Eurasian oystercatcher (*H. ostralegus*), which has been comprehensively studied (Goss-Custard, 1996; Van de Pol et al., 2010), there is little information on the role of environmental factors in driving variation in the demography of this avian family. Further, the biology of oystercatchers has been studied mainly in altered or degraded habitats, and focused on the effects of anthropogenic factors: habitat loss (Duriez et al.,

2012), the oiling of nesting and feeding beaches (Andres, 1999), shellfish fisheries (Verhulst et al., 2004), eutrophication (Garcia et al., 2010), the introductions of non-native predators (Dowding and Murphy, 2001) and prey (Caldow et al., 2007), and human disturbance (Leseberg et al., 2000). Importantly, while there is a rich literature on the effects of large-scale oceanographic variation on the demography of oceanic birds such as northern fulmars (*Fulmaris glacialis*) (Thompson and Ollason, 2001) and black-legged kittiwakes (*Rissa tridactyla*) (Aebischer et al., 1990), understanding is poor for shoreline birds such as oystercatchers.

The demography of oystercatchers is likely to be strongly influenced by marine environmental conditions, because parameters such as sea-surface temperature affect the behavior, physiology and demography of many types of invertebrates eaten by these birds (Dahlhoff and Menge, 1996; Grenon and Walker, 1981; Menge et al., 2008). Further, stable isotope analysis indicated that the trophic ecology of one species, the African black oystercatcher (*Haematopus moquini*), accurately gauged both the large-scale influence of oligotrophic vs. eutrophic water masses and the small-scale influence of the community composition of prey species (Kohler et al., 2011).

Here, we used data collected over ten years (2003–2012) to test the hypothesis that interannual variation in sea-surface temperature influences the breeding effort of black oystercatchers (*Haematopus bachmani*) at a remote site on Triangle Island, British Columbia, Canada. Sea-surface temperatures in the northeast Pacific Ocean have been variable but frequently well above long-term averages through much of the last three decades, often to the detriment of marine predators (Mackas et al., 2007). For example, several species of oceanic birds

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breeding on Triangle Island, including secondary and tertiary consumers, have experienced reduced productivity in warm-water years due to effects of elevated temperatures on the food webs that support them (Gjerdrum et al., 2003; Hipfner, 2008). In addition, long-term studies in the Dutch Wadden Sea have shown that intertidal invertebrates have lower body mass following winters with higher sea temperatures (Zwarts, 1991), potentially creating nutritional stress for avian predators (Beukema, 1992). Therefore, we predicted that breeding density, clutch size, and egg size of black oystercatchers would decline with increasing spring sea-surface temperatures.

2. Materials and methods

2.1. Study species

The black oystercatcher is a rocky shore specialist, widely distributed along the Pacific coast of North America (Andres and Falxa, 1995), feeding mainly on *Mytilus* mussels and limpets of several genera (Frank, 1982; Hartwick, 1976; Lindbergh et al., 1987). The birds lay a clutch of one to three eggs (rarely four) in a shallow depression in beach gravel. Physical characteristics of a territory influence a pair's productivity, so the territories are defended aggressively and reused from one year to the next (Hartwick, 1974; Hazlitt and Butler, 2001). Black oystercatchers can be resident or migratory; we suspect that the group on Triangle Island is resident, like others in British Columbia (Johnson et al., 2010), because individuals that we banded as adults and pre-fledglings in August of 2003 to 2008 were present when we arrived on the island in March of the following year (Hipfner et al., 2012). For more northerly, migratory populations, spring migration begins in early April (Johnson et al., 2010).

2.2. Field methods

Field work on Triangle Island (50°52'N, 129°05'W) was conducted during the egg-laying period of black oystercatchers, mid-May through late June (Hipfner et al., 2012), in each year from 2003 to 2012. The uninhabited island is located 40 km seaward of Cape Scott at the north-western tip of Vancouver Island, and remains in a relatively pristine state, supporting neither commercial activities nor introduced predators or prey.

Accessible shoreline areas on Triangle Island totaling approximately 4.0 km in length were systematically searched at ~1–3 d intervals by crews of 2–3 people (Fig. 1). The rest of the island was inaccessible due to the ruggedness of the shoreline and the presence of Steller's sea-lion (*Eumetobius jubatus*) rookeries. When an egg was first found in an oystercatcher nest, the egg was marked with a felt tipped pen, and a marker such as a colored fishing float was placed at the top of the beach above the nest so that the nest could be found quickly, but otherwise avoided so as to minimize disturbance. After ~5 d, crews returned to obtain a GPS reading at the nest, record the final clutch size, and measure all of the eggs (length and maximum breadth, to within 0.1 mm with dial calipers). There was only one instance, in 2011, when an egg disappeared between the time the nest was first found and when it was later rechecked.

2.3. Statistical analyses

We estimated the volume of each egg using the formula: Volume = $0.51 \times \text{length} \times \text{breadth}^2$ (Nol et al., 1984). The total volume of each clutch was calculated by summing volumes of its individual eggs. In the statistical analyses, three response variables: (1) number of active nests found in each of the ten years, (2) annual mean clutch size, and (3) annual mean total clutch volume, were regressed against the mean April sea-surface temperature measured at the Kains Island lightstation, ~90 km southeast of Triangle Island. We considered both linear and quadratic forms for all regressions, and used $\alpha = 0.05$ to

define statistical significance. We used mean temperature in April as the independent variable because locally, the transition from winter to spring oceanographic conditions occurs as early as the start of that month (Borstad et al., 2011).

3. Results

Between nine and 15 black oystercatcher pairs laid eggs annually in the 4.0 km of shoreline searched by field crews on Triangle Island in 2003–2012 (Fig. 1). This equates to breeding densities of 2.2 to 3.7 pairs km^{-1} of shoreline. Mean April sea-surface temperatures ranged from 7.8 to 9.6 °C, and as predicted, the number of active nests declined with increasing temperature (for the quadratic relationship, $r^2 = 0.94$, $F_{2,7} = 61.37$, $P < 0.0001$). There were 14 or 15 nests in all five years with temperatures < 9 °C, but only nine to 11 nests in the five warmer years (Fig. 2). There was also an underlying temporal trend, with generally fewer nests in the earlier years, but more in the later years. However, the study spanned transitions from warm to cold states (in 2006–2007 and 2010–2011), and from cold to warm states (in 2009–2010), and across all three transitions the number of nests closely tracked spring water temperatures.

Clutch size varied from one to three eggs, with modal values of two and more commonly three (Fig. 3). The annual mean clutch size ranged from 2.1 to 2.8 eggs nest^{-1} , but contrary to prediction, did not decline with April sea-surface temperature; rather the linear relationship was non-significantly positive ($r^2 = 0.29$, $F_{1,8} = 3.20$, $P = 0.11$) (Fig. 2). This reflects, at least in part, that clutches composed of just a single egg were laid only in the five years in which the mean April sea-surface temperature was < 9 °C (Fig. 3).

Total clutch volumes ranged from 106.6 to 140.8 cm^3 in three-egg clutches, and from 78.3 to 94.2 cm^3 in two-egg clutches. The yearly mean total clutch volume of three-egg clutches varied from 124.3 to 130.1 cm^3 , and was not related linearly to sea-surface temperature ($r^2 = 0.02$, $F_{1,8} = 0.16$, $P = 0.70$). For two-egg clutches, the yearly mean total clutch volume varied from 84.3 to 89.3 cm^3 , and it too was unrelated to temperature ($r^2 = 0.01$, $F_{1,8} = 0.04$, $P = 0.85$).

4. Discussion

As predicted, the number of black oystercatcher pairs that laid eggs on Triangle Island in May and June in each of ten years declined with increasing mean April sea-surface temperature. One or more of four processes operating within the population could account for that pattern: a lack of recruitment by inexperienced females and/or skipped breeding by experienced females in warm years – both indicative of reduced breeding propensity; and increased mortality and/or emigration of adult birds in warm years.

Features of black oystercatcher biology, observations on a small number of birds banded on Triangle Island, and comparison with close relatives indicate that a reduction in breeding propensity offers the more parsimonious explanation. In other Charadriiform birds, inexperienced females lay later than experienced females, and they lay smaller clutches (Coulson and White, 1958; Nisbet et al., 1984). In this study, single-egg clutches appeared only in the five years in which ocean temperature was < 9 °C; seven of the total of nine single-egg clutches were laid later in the year than any two- or three-egg clutches; and at four of the five sites where single-egg clutches were laid in 2011 (three) and 2012 (one), one member of the pair had been banded as a juvenile and not bred previously (Hipfner et al., 2012; J.M.H. unpubl. data). Thus, females appeared more likely to recruit in cold, putatively food-rich years – a phenomenon also seen in red-billed gulls (*Larus novaehollandiae*) (Mills et al., 2008). As for skipped breeding by experienced females, we note that one individual banded as an adult breed at the same site from 2003 to 2009, occupied that site but did not breed in the warm year of 2010,

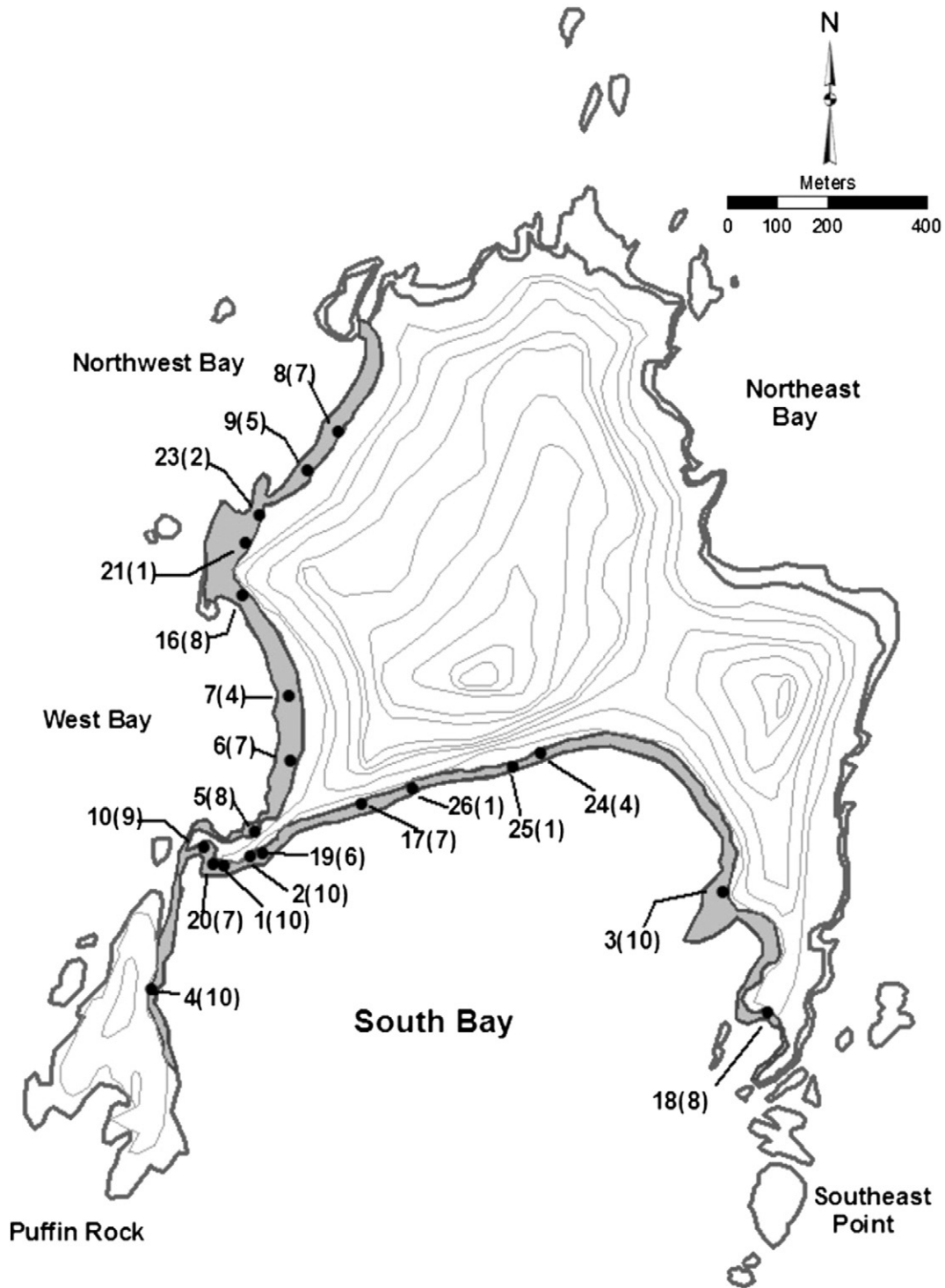


Fig. 1. Map of Triangle Island showing locations of black oystercatcher nests found in shoreline areas searched by field crews in 2003–2012 (these areas are shaded in gray). Contour intervals are 20 m. Nests were numbered in the order they were found over the ten years; numbers in brackets are the number of years of the study in which the nest was active. Nests 11–15 and 22 were located outside the area searched in all years, and are not indicated on the map.

then bred again in the cold years of 2011 and 2012 (Hipfner et al., 2012; J.M.H. unpubl. data).

Conversely, there is little to suggest that mortality or emigration rates were higher in warm-water years. First, there were large flocks of 25 or more non-breeding oystercatchers on Triangle Island in all years. Second, oystercatchers appear to reside year-round on Triangle Island, are strongly territorial (Hartwick, 1974) and exhibit strong fidelity to breeding sites (Hazlitt and Butler, 2001). Finally, resighting rates for six adults banded on Triangle Island in 2007 suggested a survival rate in excess of

~90% per annum (Hipfner et al., 2012), while the survival rate of Eurasian oystercatchers was not strongly impacted by winter food shortages (Camphuysen et al., 1996).

What mechanism(s) could link high ocean temperatures to reduced breeding propensity in black oystercatchers? The effects of temperature are likely to operate through the food web, rather than directly on the birds themselves. Under this scenario, warm spring sea temperatures create poor feeding conditions, causing the birds to start their breeding season in poor body condition. Poor body condition has been linked to

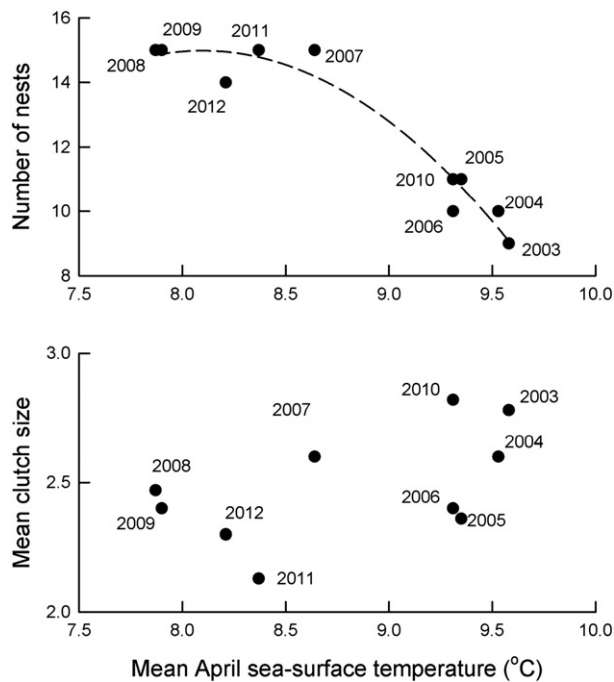


Fig. 2. The number of active black oystercatcher nests on Triangle Island in a year declined with increasing mean April sea-surface temperature measured at Kains Island, in 2003–2012 (top). The mean clutch size for black oystercatchers at Triangle Island was not significantly related to the mean sea-surface temperature measured at Kains Island in 2003–2012 (bottom).

recruitment failure (Atkinson et al., 2005) and low breeding success (Durell et al., 2001) in Eurasian oystercatchers, as in other shorebirds (Hegyi and Sasvari, 1998). That breeding density closely tracked temperature earlier in the same spring suggests that temperature affected behavioral and/or physiological attributes of prey that determined their availability and/or nutritional value to oystercatchers. If effects on the demography of prey were involved, e.g., reduced recruitment into mussel populations in warm years (Beukema et al., 2010), then a lagged relationship between temperature and breeding density would have been expected (Beukema, 1992).

Along British Columbia's outer coast, black oystercatchers feed mainly on the thick-shelled California mussel (*Mytilus californianus*) by stabbing their bills between gaping valves and severing the adductor muscle (Hartwick, 1976). They feed secondarily on limpets by delivering a sharp jab that dislodges the prey from the substrate (Hartwick, 1976). Consequently, feeding conditions for oystercatchers could vary with factors such as the amount of time that mussels spend gaping, the speed with which mussels contract their adductor muscle to close the valves, and by the tenacity with which limpets grip the substrate. Experiments indicate that these traits can be temperature dependent in these taxa. For example, in warm water, limpets (*Patella vulgata*) contracted their foot muscles more powerfully, thus maintaining a stronger grip on the substrate (Grenon and Walker, 1981); and Mediterranean mussels (*M. galloprovincialis*) spent more time with their valves closed (Anestis et al., 2007). In terms of nutritional quality, blue mussels (*Mytilus edulis*) lost more mass over the course of warm winters than cold winters in the Wadden Sea, indicative of a greater energetic deficit (Zwarts, 1991).

Our prediction that clutch size and egg size of black oystercatchers would decline with ocean temperature was not fulfilled. Nonetheless, an analysis of geographic variation across the species range does suggest a role for food in limiting clutch size. In general, clutch size varied little among years and sites, with means consistently between 2.3 and 2.8 eggs nest⁻¹ (Andres, 1999; Drent et al., 1964; Gill et al., 2004; Hazlitt and Butler, 2001; Morse et al., 2006; Vermeer et al., 1992a; Webster, 1941; but see Kenyon, 1949). On Triangle Island, the mean

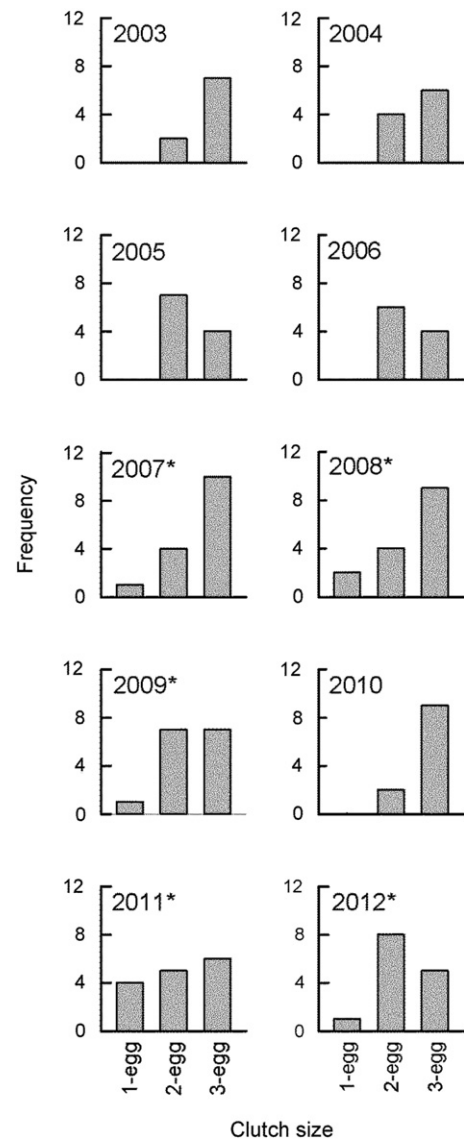


Fig. 3. Frequency distributions for clutch size in black oystercatchers at Triangle Island, 2003–2012. Note that single-egg clutches were laid only in the five years in which the mean April sea-surface temperature was <9 °C (those indicated with a star).

clutch size fell outside this range (2.1 eggs nest⁻¹) only in 2011, when many single-egg clutches were laid. In contrast, the mean clutch size in nine years on Cleland Island, British Columbia, where breeding density exceeded that at any other site by at least an order of magnitude (~40 pairs km⁻¹; Hipfner et al., 2012), ranged only from 1.9 to 2.2 eggs nest⁻¹, with a mode of two in all years (Groves, 1984; Hartwick, 1974; L'Hyver and Miller, 1991; Vermeer et al., 1992b). The link between unusually high breeding density and unusually small clutch size is suggestive of a density-dependent ceiling on egg production.

To summarize, we found that the density at which black oystercatchers bred on Triangle Island declined as spring sea-surface temperatures increased, and that no single-egg clutches, indicative of recruitment, were laid in warm-water years. Those results imply that egg-production capacity in oystercatchers can be affected by oceanographic conditions, probably operating via the effects of temperature on the behavior and physiology of prey. We suggest that further research on this simple predator–prey system might reveal new mechanisms by which climate change can affect trophic relations in intertidal communities (Menge et al., 2011; Moore et al., 2011).

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