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Abstract.—The hypothesis that the egg production capacity of northeast Pacific seabirds is reduced in years with higher spring sea-surface temperatures was tested with data collected on Glaucous-winged Gulls breeding on Triangle Island, British Columbia, Canada, from 2002 to 2011. The mean clutch size varied from 2.3 to 2.9 eggs nest^{-1}, but contrary to prediction, there was little relationship between clutch size and ocean temperature. In contrast, the mean egg size increased with temperature (opposite to the predicted decrease), but that effect was modest in size and limited to clutches of one and three eggs. The within-clutch variation in egg size differed little from year to year, and was unrelated to temperature. The results suggest that higher sea-surface temperatures do not compromise egg production in Glaucous-winged Gulls, a situation unlike that for some other species of marine birds on Triangle Island *Received 6 December 2011, accepted 18 February 2012.*

Key words.—clutch size, egg size, Glaucous-winged Gull, sea-surface temperature, third-chick disadvantage.

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How many eggs to lay and how large the eggs should be, are two fundamental life-history decisions for egg-laying vertebrates (Parker and Begon 1987). For birds, egg production is a nutritionally demanding process (Williams 2005) that can be limited by the quantity and quality of food available to the female as she forms her clutch (Stevenson and Bryant 2000). Some of the best evidence that food can limit avian egg production has come from experimental work with Lesser Black-backed Gulls (*Larus fuscus*), in which food supplementation resulted in increases in both egg size and clutch size (Hiom *et al.* 1991; Bolton *et al.* 1993; Verboven *et al.* 2010). Experimental work with gulls has also shown that females induced to lay four eggs experienced marked reductions in their productivity (Monaghan *et al.* 1998) and post-breeding survival rates (Nager *et al.* 2001) compared to females that laid the normal clutch of three eggs.

For marine gulls, large-scale oceanographic conditions can limit egg production through their effects on the prey base. Several examples will illustrate this point. First, cold-water conditions caused a delay in the arrival of capelin (*Mallotus villosus*) into nearshore waters off the east coast of Newfoundland, creating unfavorable feeding conditions that drove reductions in egg size and clutch size in Black-legged Kittiwakes (*Rissa tridactyla*) (Regehr and Montevecchi 1997). Second, euphausiid prey were more available to Red-billed Gulls (*Larus novaehollandiae*) during the positive phase of the Southern Oscillation Index, and increased prey availability enabled the gulls to lay larger eggs and clutches (Mills *et al.* 2008). Third, higher sea-surface temperatures in the early spring were linked to reduced clutch size in Black-tailed Gulls (*L. crassirostris*), because life-cycle events in the euphausiid prey taken by the gulls occurred too early in warm years (Tomita *et al.* 2009). And finally, Blight (2011) proposed that long-term reductions in the forage fish base in the Salish Sea, a body of water shared by British Columbia and Washington State, had caused long-term declines in both egg size and clutch size in Glaucous-winged Gulls (*L. glaucescens*).

Food availability can also influence egg-laying decisions through indirect mechanisms. For example, most *Larus* gulls lay clutches of three eggs, with the first two almost always larger than the third (Parsons 1975; Mills 1979). The third-hatched offspring therefore experiences a handicap relative to its two older and larger siblings, in what is commonly called the "third-chick disadvantage" (hereafter TCD). Increasing the within-clutch variation in egg size, by reducing the size of the third egg relative to the first two, enables female gulls to facilitate brood reduction in food-poor years (Kilpi *et al.* 1996). Recently, Saino *et al.* (2010) showed that female gulls might be particularly predisposed to do this if the third embryo is male.

Here, I use data collected over ten years (2002-2011) to test the hypothesis that sea-surface temperature (hereafter, SST) influences egg production in Glaucous-winged Gulls breeding on Triangle Island, British Columbia, Canada. SSTs have been well above long-term averages in the northeast Pacific through much of the last three decades, usually to the detriment of marine predators because the effects of temperature cascade within the food web (Mackas *et al.* 2007). In other seabirds breeding on Triangle Island, including Cassin's Auklet (*Ptychoramphus aleuticus*), an oceanic zooplanktivore, and the Tufted Puffin (*Fratercula cirrhata*), a generalist feeder that includes both fish and zooplankton in diets, previous work has linked warm SSTs to low productivity (Hipfner 2008; Gjerdrum *et al.* 2003). Further, warm SSTs were linked to low breeding propensity in the Black Oystercatcher (*Haemotopus bachmani*), a marine shorebird that lays eggs at about the same time as Glaucous-winged Gulls (starting in mid-May) and feeds on intertidal invertebrates (Hipfner and Elner *submitted*)—prey types that form the major component of the early season diet of Glaucous-winged Gulls on Triangle Island (Vermeer 1982). Therefore, I predicted that (1) both the yearly mean egg size and the yearly mean clutch size would decline with increasing spring SSTs, reflecting direct food limitation of egg production in warm-water years; but that (2) the size of the yearly mean TCD would increase with increasing spring SSTs, as females set the stage for brood reduction in warm-water years.

Methods

Field work on Triangle Island (UTM Zone 09, 0494480E 5634395N, WGS84) was conducted in 2002 to 2011. The timing of egg-laying in Glaucous-winged Gulls was loosely tracked by monitoring a handful of nests that field crews passed each day on their regular work routine. In mid-June, just prior to the start of hatching, all eggs in ~50 clutches were measured on a single day in a dense colony atop Puffin Rock, a small islet connected to Triangle Island at low tide. At this stage of their breeding season, most pairs will be incubating complete clutches (Blight 2011). Empty but well-formed nests were recorded, but excluded from the tally for clutch size. The length and maximum breadth of eggs were measured to within 0.1 mm using dial calipers, and as a measure of egg size, I calculated an egg volume index (hereafter, EVI) using the formula:

$$\text{EVI (cm}^3\text{)} = \text{length} \times \text{maximum breadth}^2 \div 1000.$$

Eggs in clutches of two and three were ranked in terms of their relative size: large, medium and small in 3-egg clutches; large and small in 2-egg clutches. Following Sydeman and Emslie (1992), and assuming that the smallest egg was always the last to be laid, I defined TCD in three-egg clutches as:

$$((\text{EVI of largest egg} + \text{EVI of medium egg}) \div 2) - \text{EVI of smallest egg}.$$

In the statistical analyses, three response variables were linearly regressed against the mean April SST measured at the Kains Island lightstation, located ~90 km to the southeast of Triangle Island: (1) the annual mean clutch size, (2) the annual mean egg size (EVI), separately considering individual eggs in clutches of one, two and three eggs, as well as total clutch EVI in 2- and 3-egg clutches; and (3) the yearly mean TCD. April SST has proven useful in studies on other seabirds on Triangle Island, and SSTs are correlated from month to month in the same spring (Hipfner 2008). Regressions were considered to be statistically significant if the 95% confidence intervals on the parameter estimates (i.e. the slopes of the lines) did not bound zero.

Results

Clutch size in Glaucous-winged Gulls on Triangle Island ranged from one to four eggs, the latter in just two cases, and the median and modal values were three in all ten years (Fig. 1). The mean clutch size ranged from 2.3 to 2.9 eggs nest^{-1} (in 2011 and 2006 respectively), while mean SSTs in the month of April ranged from 7.9 to 9.6°C (in 2008 and 2003 respectively). However, contrary to prediction, the mean clutch size was not significantly related to SST ($r^2_9 = 0.14$, $\beta = 0.11$ eggs °C^{-1} ± 0.18 (95% CI)).

Overall, EVI ranged from 120.8 to 235.0 cm^3. Across all years, the largest eggs averaged 181.9 cm^3 ± 0.67 (SE) in 3-egg clutches and 177.5 cm^3 ± 1.31 (SE) in 2-egg clutches, while eggs in single-egg clutches averaged 177.1 cm^3 ± 3.91 (SE). EVI was significantly related to the mean April SST for the lone eggs in single-egg clutches, and for the two

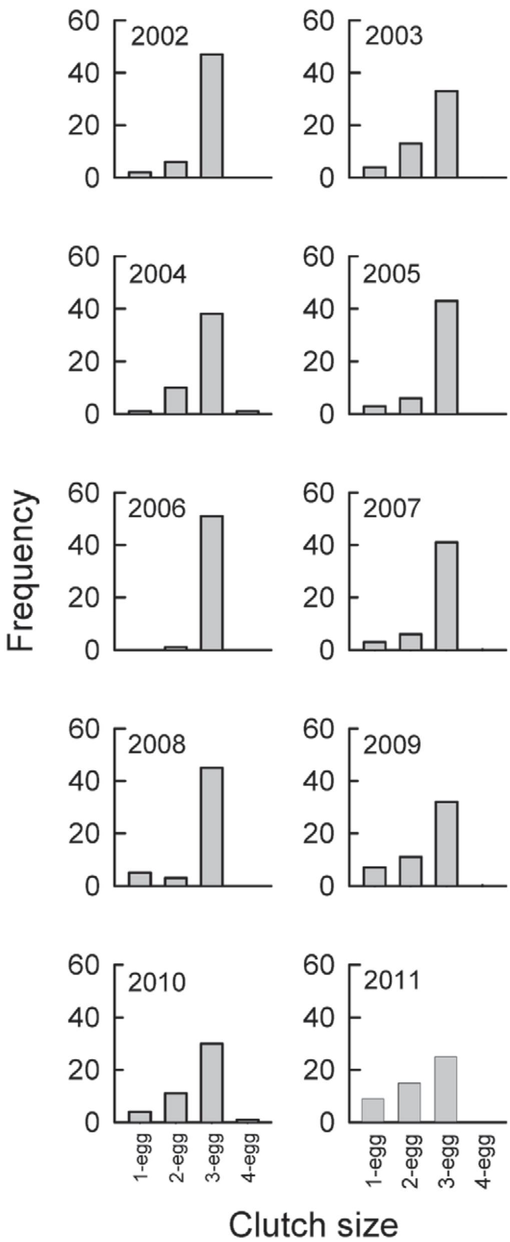

Figure 1. Frequency distributions for clutch size in Glaucous-winged Gulls breeding on Triangle Island in 2002-2011.

larger eggs, as well as the total clutch volume, in 3-egg clutches (Table 1). But contrary to prediction, all of these relationships were positive, i.e. gulls laid larger eggs, not smaller eggs, in years with warmer spring SSTs (Table 1, Fig. 2). In 3-egg clutches, SST accounted for variation of ~6 cm^3 of volume index for the largest eggs, and ~15 cm^3 of total clutch volume index, based on 1.7°C variation in SST and the slopes of the respective lines—in both cases, ~3% of average values. For the smallest eggs in 3-egg clutches, the positive relationship with SST was not statistically significant, and none of the EVI of larger eggs, smaller eggs or total clutch volume in two-egg clutches was related to SST (Table 1).

The annual mean TCD varied little from year to year, ranging only from 9.2 cm^3 ± 1.22 (SE) in 2010 to 12.9 cm^3 ± 1.21 (SE) in 2003. Contrary to prediction, the annual mean TCD did not increase significantly with increasing spring SST ($r^2_9 = 0.07$, ß = 0.56 ± 1.41 (95% CI)).

DISCUSSION

For Glaucous-winged Gulls breeding on Triangle Island, the mean clutch size ranged from 2.3 to 2.9 eggs $nest^{-1}$ in the ten years of this study. This closely matched the extent of variation reported in the same species over a 50-year period at several breeding colonies in the Salish Sea (Blight 2011), and closely matched the between-year difference in clutch size at a single colony in Alaska (Murphy *et al.* 1984). But contrary to prediction, there was no systematic effect of SST on the mean clutch size. That result is surprising given that SST was variable through the period relative to long-term trends (Mackas *et al.* 2007), that SST had strong effects on egg production in the Black Oystercatcher (Hipfner and Elner *submitted*), which consumes many of the same prey types as the gull (Vermeer 1982), and that SST influences clutch size in other species of gulls (Regehr and Montevecchi 2007; Tomita *et al.* 2009).

Nonetheless, there are a number of plausible explanations for the negative result. These include: (1) SST did not determine food availability coarsely enough to affect how many eggs are produced by female Glaucous-winged Gulls, which benefit from courtship feeding by their mates (Salzer and Larkin 1990) and have the option to scavenge for food. (2) Egg losses to predators varied among years, but this went undetected on the single nest checks just prior to hatch-

Table 1. Slopes of lines (cm^3 °C^{-1}) relating the annual mean egg volume index (EVI) in Glaucous-winged Gulls breeding on Triangle Island to the April mean sea-surface temperature in n = 10 years (2002-2011). Slopes that do not bound zero are in bold.

Clutch size	Egg or clutch measure	ß (95% confidence interval)	r^2
3-egg	Largest	**3.26 (2.65)**	0.43
	Intermediate	**3.03 (2.63)**	0.39
	Smallest	2.59 (2.90)	0.28
	Total clutch VI	**8.88 (7.90)**	0.37
2-egg	Larger	0.21 (5.41)	0.00
	Smaller	-0.22 (4.61)	0.00
	Total clutch VI	0.03 (9.54)	0.00
1-egg	Single[1]	**6.97 (2.98)**	0.76

[1]Sample size is nine, because no single-egg clutches were laid in 2006.

ing. However, few empty nests were found in any year—a maximum of four, in 2010—which suggests that the loss of eggs to predators was not an important factor. (3) Food availability acts strongly on breeding propensity, such that fewer females that would otherwise have been constrained to lay small clutches of one and two eggs did so in warm-water, putatively food-poor years. This has been reported in the Red-billed Gull (Mills *et al.* 2008), and could explain the positive direction of the weak relationship between clutch size and SST. Lastly, (4) predation danger varied among years. Increased danger has been linked to reductions in clutch size in passerine birds, because fear elicits behavioral and physiological responses that draw resources away from reproduction (Travers *et al.* 2010). In this study, the mean clutch size tended to be smaller from 2009 to 2011 (2.3-2.6 eggs nest^{-1}) than in the seven earlier years (2.6-2.9 eggs nest^{-1}) when Peregrine Falcons (*Falco peregrinus*) prevented Bald Eagles (*Haliaeetus leucocephalus*) from harassing seabirds atop Puffin Rock (Hipfner *et al.* 2011). Blight (2011) previously suggested that the range-wide recovery of Bald Eagles might have been a factor in the decades-long declines in egg production by Glaucous-winged Gulls in the Salish Sea.

While SST had no discernible effect on clutch size, it did influence egg size. But contrary to prediction, gulls laid larger eggs, not smaller eggs, in years when the ocean was warmer. That effect was limited to the eggs in clutches of one and three, however, and it was modest in size, with warmer water explaining a ~3% increase in egg size. For comparison, Blight (2011) reported a decline in mean egg volume of ~5% over a 108-year period for Glaucous-winged Gulls in the Salish Sea. Given that larger eggs, with their larger reserves of yolk, decrease the likelihood that young gulls will starve to death soon after hatching (Parsons 1970; Bolton 1991), it may be beneficial to produce larger eggs in warm-water years. Parallels may exist in the fact that egg size increased with laying date in Western Gulls (*L. occidentalis*) (Sydeman and Emslie 1992), and that Lesser Snow Geese (*Anser caerulescens caerulescens*) laid larger eggs when spring temperatures were lower (Williams and Cooch 1995).

In proximate terms, one simple explanation for the production of larger eggs in warm-water years is that females foraging in a warmer environment expend less energy on self-maintenance, leaving them with more productive energy to invest in eggs. Positive correlations between ambient temperature and egg size have been reported in passerine birds (Magrath 1992), although not always (Christians 2002). Larger eggs could also be a consequence of food limitation if a trade-off exists between egg size and clutch size, but there was no indication that clutches were smaller in the warm-water years, when eggs were larger. Dietary differences from one year to the next could also be a factor: in experiments, female gulls fed protein-enhanced diets exhibited greater egg-production capacity than females fed lipid-enhanced diets, and females fed chicken eggs fared better than those fed fish (Bolton *et al.*

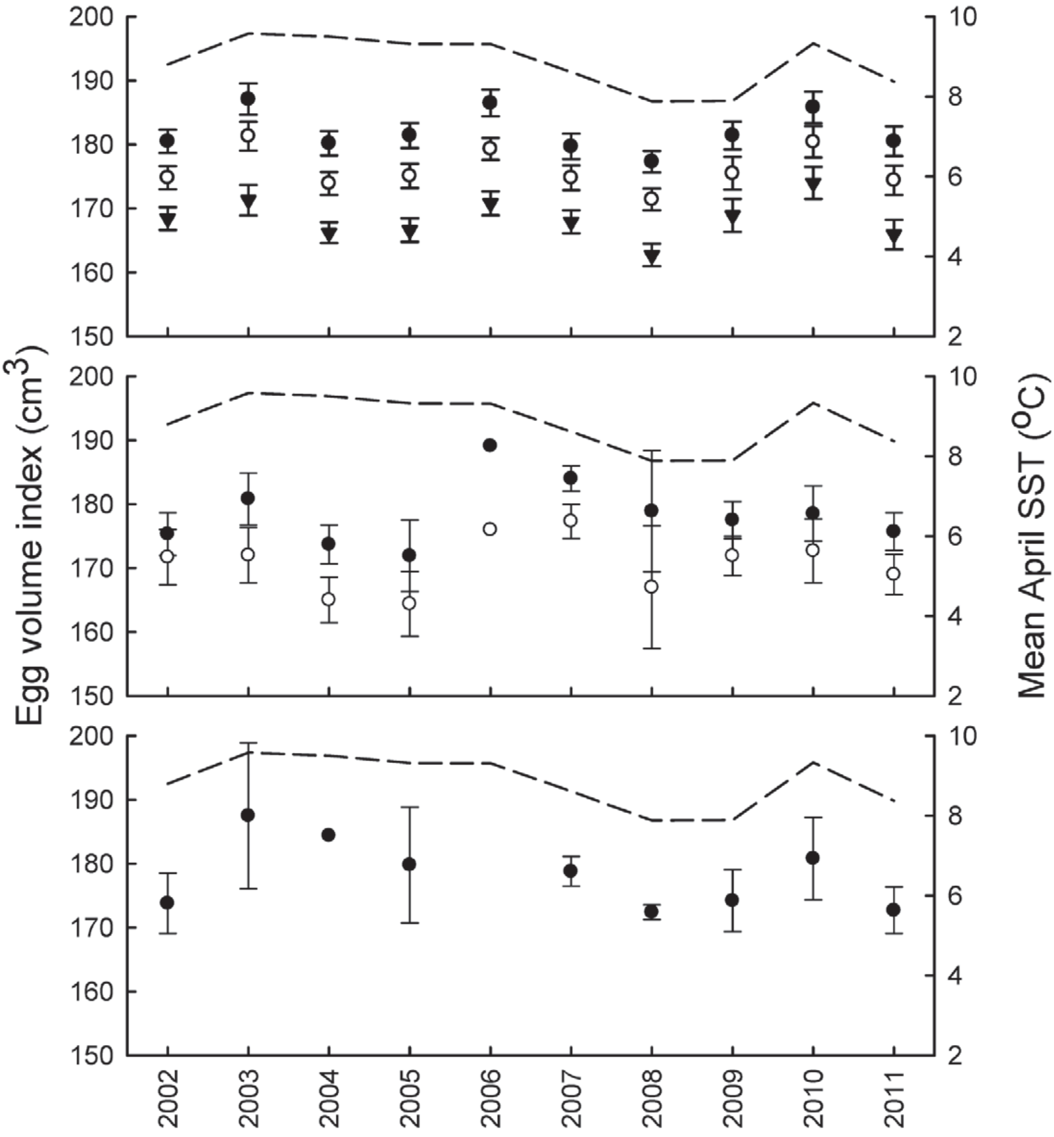

Figure 2. Egg size (mean ± SE) of Glaucous-winged Gulls breeding on Triangle Island in clutches of 3 (top), 2 (middle) and 1 (bottom) eggs (left y-axis). Dashed line is the mean April sea-surface temperature (right y-axis).

1992). A naturally-occurring difference in diet quality between two years likewise affected clutch size in Glaucous-winged Gulls, but Murphy *et al.* (1984) did not report on whether egg size was affected. In any case, none of these explanations easily accounts for the fact that SST influenced egg size in clutches of one and three eggs, but not two eggs.

The laying of third eggs that are variably smaller than the first two eggs in the same clutch is a consistent feature of *Larus* biology, and has been attributed in ultimate terms to the facilitation of brood reduction when beneficial (Kilpi *et al.* 1996), and more recently, to sex-biased investment decisions (Saino *et al.* 2010); proximately, the laying of small third eggs has been attributed to hormonally-mediated female reproductive recrudescence (Ramírez *et al.* 2011). Pierotti and Bellrose (1986) found no appreciable difference in egg size in Western Gull clutches (i.e. TCD ~0) where feeding conditions prior to laying were very good, while Reid (1987) showed that food supplementation eliminated the TCD in Glaucous-winged Gulls. Thus food can play a strong mediating role (Sydeman and Emslie 1992). I found that TCD varied little among years and with no effect of spring SST in Glaucous-winged Gulls. The simplest explanation for this is that feeding conditions during the period when female gulls were producing eggs did not vary appreciably among years. In fact, experiments show that adjusting the degree of hatching asynchrony, which I did not measure, may be a more effective method by which female gulls can maximize their production of offspring under variable feeding conditions (Royle and Hamer 1998).

The results of this study suggest that Glaucous-winged Gulls breeding on Triangle Island, which feed in an extremely variable marine environment (Mackas *et al.* 2007), do not experience constraints on egg production in warm-water years. A generalist feeding strategy, which includes the option to scavenge, plus courtship feeding by their mates (Salzer and Larkin 1990), may buffer female gulls against the poor feeding conditions that other marine birds experience in warm-water years on Triangle Island. Comparing these results from a relatively pristine, offshore site with the long-term declines in egg size in the Salish Sea (Blight 2011) suggests that food webs in the Salish Sea, an enclosed marine system located close to major urbancenters, may be compromised. Yet the smaller clutches laid by Glaucous-winged Gulls in the later years of this study on Triangle Island were perhaps best explained as a consequence of increased exposure to Bald Eagles. It is worth noting that clutch size was markedly reduced in the Salish Sea in two recent years (2008 and 2009) compared to the mid-1980s (Blight 2011), given that the intervening years were a period in which Bald Eagle numbers increased rapidly in British Columbia (Elliott *et al.* 2011).

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