

NOTE

Indirect effects of the availability of capelin and fishery discards: gull predation on breeding storm-petrels

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ABSTRACT: The Northwest Atlantic has undergone large-scale perturbations which have had profound effects on pelagic food webs. Over the past century, the increasing availability of human refuse and fishery discards have promoted the growth of *Larus* gull populations. During the 1990s, cold surface-water events have delayed the inshore movements of spawning capelin *Mallotus villosus* and fisheries closures have eliminated massive tonnages of discards. These circumstances have interacted to intensify food stress on gulls. We investigated gull predation in a large colony of Leach's storm-petrels *Oceanodroma leucorhoa* as an indirect consequence of the availability of prey and fishery discards. Predation did not differ between storm-petrels nesting in forest and open habitats even though gull nests were more often in close proximity to storm-petrel burrows in open habitat. In 1996 and 1997, gull predation on storm-petrels varied seasonally, with a significant decrease following the inshore movement of spawning capelin, a primary food that gulls consume and feed to their chicks. Capelin availability occurred considerably later in 1997, when gull predation on storm-petrels was greater and prolonged. The intensity of gull predation on storm-petrels appears to depend on the availability of spawning capelin inshore.

KEY WORDS: Indirect effects · Fishery discards · Capelin · Predation · Gulls · Storm-petrels

During the past century, and particularly during recent decades, the Northwest Atlantic has undergone large-scale natural and anthropogenic perturbations. Long-term trends in the Northwest Atlantic involve a general warming of surface-waters (Colbourne et al. 1994, Drinkwater 1996) and major increments in the technological sophistication and intensity of fishing activities (Warner 1977, Hutchings & Myers 1995). Rapid-onset, short-term changes, during the early 1990s, include anomalous cold surface-water events

(Drinkwater 1996, Montevecchi & Myers 1996) and the closure of the Eastern Canadian ground-fishery. The interactive effects of these perturbations were initially detected in dietary shifts (Montevecchi & Myers 1995, 1997) and reproductive success (Regehr & Montevecchi 1997) of seabirds. These oceanographic and anthropogenic perturbations have had profound influences on pelagic food webs on the Newfoundland Shelf. For example, changes in the movement patterns of migratory pelagic fish and squid were attributed to cold surface-waters in the Northwest Atlantic (Montevecchi & Myers 1995, 1996, 1997). Second-order or indirect effects of these interactions have been seen in breeding failures of surface-feeding seabirds (Regehr & Montevecchi 1997). Owing to ecosystem complexity (Patten 1991, Lavigne 1996), other indirect effects at other trophic levels may take longer to detect.

Gull populations, particularly those of herring gulls *Larus argentatus*, have increased markedly in the Northwest Atlantic since the beginning of the 20th century (Kadlec & Drury 1968, Drury 1973, Howes & Montevecchi 1993, Chapdelaine & Rail 1997). As is the case with gulls and skuas in other oceanographic regions (Furness et al. 1992, Oro et al. 1996, Phillips et al. 1997), the range expansion and population growth of gulls in the Northwest Atlantic has been supported by an increasing availability of human refuse and fishery discards (Kadlec & Drury 1968, Drury 1973). However, since the initiation of the Eastern Canadian ground-fishery moratorium in 1992, huge tonnages of fishery discards from vessels and processing plants have no longer been available. Thus, the anthropogenically elevated gull populations have been forced to seek alternative food sources, and predatory pressures on other seabirds increased considerably during the 1990s (Regehr & Montevecchi 1997, see also Russell & Montevecchi 1996). These developments, in conjunction with anomalous cold water events in the

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early 1990s (Drinkwater 1996), which delayed the inshore movements of spawning capelin *Mallotus villosus* by 4 wk or more (Carscadden & Nakashima 1997), produced intense food stress on gulls (see Howes & Montevecchi 1993, Russell & Montevecchi 1996, Regehr & Montevecchi 1997).

Gulls are major predators on Leach's storm-petrels *Oceanodroma leucorhoa* at breeding colonies, where predation risk is an important aspect of habitat suitability (Lima & Dill 1990, Stenhouse 1998). Leach's storm-petrel is the smallest and most abundant seabird breeding in the Northwest Atlantic (Montevecchi et al. 1992) and the species' major ecological traits (i.e. coloniality on remote islands, nocturnality, burrow-nesting, pelagic-feeding) appear to have been largely shaped by predator avoidance (Sklepkovych & Montevecchi 1989, Huntington et al. 1996).

We investigated gull predation on Leach's storm-petrels nesting in forests and open meadows in a large colony on Great Island, Newfoundland, Canada, in relation to the timing of the availability of the gulls' primary prey, spawning capelin. We hypothesized that gull predation on storm-petrels would be highest in close proximity to nesting gulls and most intense prior to the arrival and availability of capelin inshore.

Methods. This study was conducted on Great Island (47° 11' N, 52° 49' W) in the Witless Bay Ecological Seabird Reserve, Newfoundland, Canada, from June to September 1996 and from May to August 1997. The island is approximately 1200 m long (N-S) and ranges from 150 to 700 m wide (E-W) and has a precipitous rocky shoreline, topped by steep grassy slopes, leveling out to gently sloping grass-*Rubus* meadows and a central area of dense conifers, predominantly dwarfed balsam fir *Abies balsamea* and black spruce *Picea mariana*. Nine seabird species breed on the island, including estimated populations of 340 000 pairs of Leach's storm-petrels; 123 000 pairs of Atlantic puffins *Fratercula arctica*; 23 000 pairs of black-legged kittiwakes *Rissa tridactyla*; 3000 pairs of common murre *Uria aalge*; 2770 pairs of herring gulls; and up to 80 pairs of great black-backed gulls *Larus marinus* (Cairns et al. 1989, Rodway et al. 1996).

'Forest' habitat was defined as an area of grass, shrub or fern vegetation and/or bare peat under a dense canopy of coniferous trees, and 'open' habitat was defined as an area of grass and shrub vegetation open to the sea and sky. In 1997, storm-petrel burrows were counted in 50 random 2 × 2 m plots established in each habitat, and assessed for occupancy (i.e. egg laid) during 3 visits over the season (Stenhouse 1998). The distance from the central point of each plot to the nearest gull nest was measured along the ground to the nearest 0.1 m. Nests more than 25 m from the plot, or where no nests were found, were recorded as

>25 m. Gull predation on storm-petrels was examined from June to September 1996, and from May to August 1997. A 2 m wide, 435 m transect, established in early June 1996, passed through each habitat type and a herring gull colony. All evidence of storm-petrels killed (clusters of loose feathers on the ground) and regurgitated by gulls (boluses of oily feathers and/or bones) along the transect were recorded and removed weekly. On Great Island, gulls appear to catch storm-petrels on the ground at night and kill-sites were assumed to indicate capture locations. However, regurgitations are not indicative of the capture location and were used as an overall index of gull predation on the island. Most regurgitations were found within the gull colony, yet no storm-petrels were found to have been killed in this area. The number of storm-petrels killed was standardized by applying the mean burrow occupancy for each habitat (Stenhouse 1998), enabling comparison of the number of storm-petrels killed per occupied burrow in relation to habitat, year, and the availability of capelin. The inshore movement and availability of capelin to gulls and other seabirds in Witless Bay was indicated, as in previous studies (Rodway & Montevecchi 1996), by the appearance of capelin in the diets of common murre and Atlantic puffin chicks on Great Island (C. Walsh & S. Wilhelm pers. comm.). These dates coincided with observations of capelin spawning inshore at Bauline South, a small community approximately 2 km west of Great Island.

The proportion of plots <25 m from a gull nest in each habitat were compared using the G-test of independence, employing the Williams' correction for a 2 × 2 table (Sokal & Rohlf 1995). Statistical comparison of storm-petrels killed per occupied burrow were made using a General Linear Model (Data Desk 5.0, Data Description Inc., Ithaca, NY). We applied arcsin square-root transformations to proportional data prior to analysis (Sokal & Rohlf 1995). Error distributions were examined for homogeneity, normality and independence of residuals (Simpson & Schneider unpubl.) and found to be acceptable.

Results and discussion. Proximity of gull nests to burrow plots ranged from 2.1 to >25 m in forest and from 0.9 to >25 m in open habitat. The proportion of burrow plots <25 m from a gull nest was significantly higher in open (96%) than in forest (36%) habitat ($G_{adj} = 45.3$, $df = 1$, $p < 0.001$). In 1996, a total of 49 kills and 186 regurgitations, and in 1997, a total of 175 kills and 452 regurgitations were recorded along the transect. However, the number of storm-petrels killed per occupied burrow did not differ significantly between forest and open habitat in 1996 and 1997 ($F_{1,53} = 1.94$, $p = 0.17$). Interestingly, the number of storm-petrels killed per occupied burrow varied seasonally in both years, with a significantly greater number of storm-

petrels killed per occupied burrow prior to the availability of capelin (Fig. 1; $F_{1,51} = 25.9$, $p < 0.001$). Overall, significantly more storm-petrels were killed per occupied burrow in 1997 than in 1996 ($F_{1,51} = 13.2$, $p < 0.001$). Capelin appeared in the diet of common murre and Atlantic puffin chicks in the third week of June 1996, and 2 wk later in the first week of July 1997. The number of storm-petrels killed per occupied burrow (Fig. 1) and the total number of regurgitated storm-petrels (Fig. 2) show similar patterns in both years. This correspondence suggests that the number of storm-petrels killed per occupied burrow is a reasonable measure of overall predation by gulls on Great Island.

Gull nests were consistently closer to storm-petrel burrows in open than in forest habitat. Pierotti & Annett (1991) found herring gulls that specialized in preying on storm-petrels nested significantly more often than expected in open meadows. In view of the proximity of gull nests and the specialist nature of these individuals, predation risk for Leach's storm-petrels might be expected to be greater in open habitat than in forest. However, the standardized predation rates (storm-petrels killed per occupied burrow) that we found did not differ significantly between open and forest habitats.

In both 1996 and 1997, predation was generally highest in May and June, and lowest in July (Fig. 1).

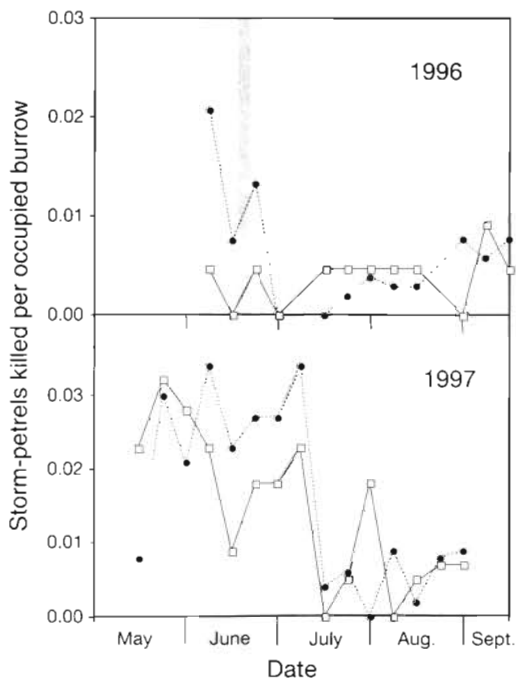


Fig. 1 Number of Leach's storm-petrels killed per occupied burrow in open (□) and forest (●) habitats in 1996 and 1997 on Great Island, Newfoundland, Canada. The shaded bar represents the timing of the inshore movement of capelin

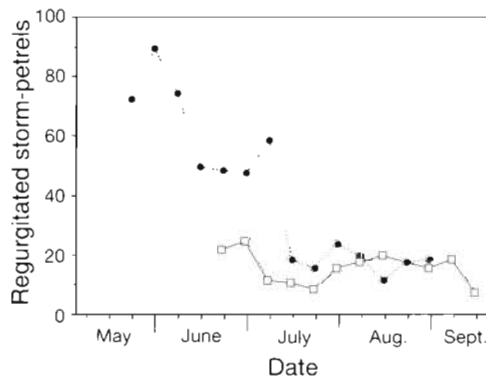


Fig. 2. Number of regurgitated Leach's storm-petrels found along transect in 1996 (□) and 1997 (●) on Great Island, Newfoundland

Storm-petrels killed per occupied burrow (Fig. 1) and overall predation (Fig. 2) decreased precipitously on Great Island, at a time when storm-petrels remained widely available and gull energy requirements were high. The sudden decrease in gull predation on storm-petrels, in late June 1996 and early July 1997, coincided with the inshore movement of spawning capelin (Fig. 1). In 1997, when the inshore movement of capelin was 2 to 3 wk later, gull predation on storm-petrels was higher and prolonged. In the late 1970s, herring gulls on Great Island exhibited dietary shifts from storm-petrels, blue mussels *Mytilus edulis* and refuse to capelin and short-finned squid *Illex illecebrosus* immediately after gull chicks hatched in early- to mid-June (Pierotti 1983, Pierotti & Annett 1987). The dietary shift by gulls, observed indirectly in this study through storm-petrel depredation, occurred up to 3 wk later than in the 1970s and is consistent with the later inshore arrival of capelin (Carscadden & Nakashima 1997). As capelin have spawned later in the 1990s (Montevecchi & Myers 1992, Carscadden & Nakashima 1997), the period of high predation by gulls on storm-petrels appears to have been prolonged. Moreover, as capelin have exhibited an increasing tendency to spawn offshore during the 1990s (Shackell et al. 1994), gulls may be preying more extensively on storm-petrels throughout the breeding season, as has been demonstrated for gull predation on kittiwakes in Newfoundland (Regehr & Montevecchi 1997). A similar situation has also been observed in Shetland, where great skuas *Catharacta skua* switched to predation on seabirds after a dramatic decline in the availability of sandeels *Ammodytes marinus* (Hamer et al. 1991).

Storm-petrel mortality due to gull predation at colonies is considered to involve largely nonbreeding storm-petrels (Morse & Buccheister 1977, Huntington et al. 1996). However, nonbreeding storm-petrels tend to prospect at colonies late in the season (Waters 1964,

Scott 1970, Furness & Baillie 1981), e.g. July and August in Newfoundland. If nonbreeding storm-petrels mainly visit the colony on Great Island late in the season, as supported by casual observations of increased prospecting activity in late July (pers. obs., C. Walsh pers. comm.), then the prolonged predation that we document may be directed at breeding storm-petrels and have little effect on nonbreeders.

In conclusion, the intensity of predation pressure imposed on Leach's storm-petrels by gulls appears to be associated with the temporal availability of capelin. Predation pressure by gulls (1) has likely increased with increasing gull populations, (2) is intensified by the elimination of discards due to fishery closures, and (3) is extended by the delayed inshore arrival of capelin. Clearly, the availability of forage fishes (Springer & Speckman 1997) and fishery discards (Tasker et al. unpubl.) can have both immediate effects on the reproductive success of seabirds and more subtle, cumulative indirect effects on interspecific interactions that may be much more far-reaching (e.g. Regehr & Montevecchi 1997). It is essential to delineate the indirect effects of prey availability and of fishing activity on seabird community interactions to better understand the complexities and implications of the large-scale ecosystem perturbations which have taken place in the Northwest Atlantic and elsewhere.

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