Predation on marine-phase Atlantic salmon (*Salmo salar*) by gannets (*Morus bassanus*) in the Northwest Atlantic

W.A. Montevecchi, D.K. Cairns, and R.A. Myers

Abstract: Predation on Atlantic salmon (*Salmo salar*) has been recorded in rivers and estuaries, but there is little documentation of predation at sea. Prey landed by gannets (*Morus bassanus*) over 24 years in a large colony off northeast Newfoundland included small proportions of post-smolt Atlantic salmon. Before 1990, when shifts in oceanographic conditions and pelagic food webs occurred in the Labrador Sea, post-smolts, on average, made up 0.29% of estimated intake by gannets during August 1977–1989. In contrast, during the 1990s, this estimate increased to 2.53%, peaking at 6.37% in 1993. Model estimates with wide error margins projected that gannets consumed a mean of 1.6 t and 19.2 t of post-smolts during August 1977–1989 and 1990–2000, respectively, making up 0.22% and 2.70% of estimated North American post-smolt biomass during these periods. The migratory routes of post-smolt Atlantic salmon pass through the foraging ranges of gannet colonies, but limited sampling at colonies other than Funk has not revealed salmon in gannet diets. Sampling seabird diets is an economic, biological means of investigating the ecology and natural mortality of Atlantic salmon. Spatial and temporal expansion of this sampling would enhance its oceanographic context and reduce uncertainty associated with estimates of predation by seabirds.

Résumé : La prédation exercée sur le saumon de l'Atlantique (*Samo salar*) a été étudiée dans les rivières et les estuaires, mais elle reste mal connue en mer. Les proies capturées par les fous de Bassan (*Morus bassanus*) d'une grande colonie au large de la côte nord-est de Terre-Neuve au cours d'une période de 24 ans incluent une faible proportion de saumons de l'Atlantique de stade post-saumoneau. Avant 1990, lorsque les changements des conditions océaniques et des réseaux alimentaires pélagiques se sont produits, les post-saumoneaux représentaient en moyenne 0,29% de la valeur estimée du régime alimentaire des fous durant la période d'août 1977–1989. En revanche, durant les années 1990, l'estimation a augmenté à 2,53 % pour atteindre un sommet de 6,37 % en 1993. Les estimations d'un modèle avec de grandes marges d'erreur indiquent que les fous ont consommé en moyenne 1,6 t de saumons au stade post-saumoneau durant la période d'août 1977–1989 et 19,2 t en 1990–2000, quantités qui représentent respectivement 0,22 % et 2,70 % de la biomasse estimée des saumons de ce stade en Amérique du Nord à ces périodes. Les routes migratoires des saumons de l'Atlantique au stade post-saumoneau traversent les territoires d'alimentation des colonies de fous, mais un échantillonnage restreint des colonies autres que celle de Funk n'indique pas la présence de saumons dans le régime alimentaire des fous. L'échantillonnage des régimes alimentaires des oiseaux marins est une méthode biologique économique d'étudier l'écologie et la mortalité naturelle des saumons de l'Atlantique. En étendant cet échantillonnage dans l'espace et le temps, on élargirait le contexte océanique de l'étude et on réduirait l'incertitude associée aux estimations de prédation par les oiseaux marins.

[Traduit par la Rédaction]

Introduction

Numbers of adult Atlantic salmon (*Salmo salar*) of North American origin have been declining since the early 1980s, a trend that intensified in the 1990s (ICES 1999). In November 2000, the U.S. Fish and Wildlife Service listed Atlantic salmon in the Gulf of Maine as endangered, and in May 2001 the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) listed Atlantic salmon associated with rivers in the inner Bay of Fundy as endangered (WWF 2001). Fisheries, predation, disease, parasites, degradation of riverine habitat, forest pesticide spraying, and marine environmental conditions have all been suggested as causative agents of the decline, but there is no clear evidence to link the decrease to any or any combination of these factors (Dempson et al. 1998). During the Atlantic salmon's de-

W.A. Montevecchi.[1] Biopsychology Programme, Memorial University of Newfoundland, St. John's, NF A1B 3X9, Canada.
D.K. Cairns. Science Branch, Department of Fisheries and Oceans, Box 1236, Charlottetown, PEI C1A 7M8, Canada.
R.A. Myers. Biology Department, Dalhousie University, Halifax, NS B3J 4J1, Canada.

[1]Corresponding author (e-mail: mont@mun.ca).

cline, the densities of fry and parr in many major salmon rivers have remained high (ICES 1999). These circumstances and an evaluation of hypotheses that might explain the decline of Atlantic salmon (Cairns 2001) suggest that much or most of the decrease is due to increased mortality during the fish's marine phase. Similar arguments have been advanced regarding the recent decline of steelhead (*Oncorhynchus mykiss*) in British Columbia (Welch et al. 2000).

Almost all studies of predation on Atlantic salmon have been conducted in rivers and in estuaries (Scheel and Hough 1997; Beland et al. 2001). Avian, fish, and mammalian predators often aggregate near estuaries, and predation rates can be high in such restricted environments (e.g., Scheel and Hough 1997). Yet, elucidation of mortality factors affecting marine-phase salmon, especially during the first year, is hampered by limited understanding of salmon movements, behavior, and ecology at sea (Reddin and Friedland 1993). Information on migratory patterns in the Northwest Atlantic has been derived primarily from previous captures of tagged fish in commercial nets, yet because there were no directed fisheries for post-smolts, very little is known about their movement patterns following departure from natal rivers (Ritter 1989; Reddin and Short 1991). Aspects of post-smolt biology have also been inferred from characteristics of scales and otoliths obtained from returning adults (Friedland et al. 1999).

Seabirds have provided additional information on post-smolts that is not readily obtained by conventional survey techniques (Cairns 1992). Northern gannets (*Morus bassanus*), the largest seabird species breeding in Canada, plunge-dive into surface waters to capture pelagic prey (Garthe et al. 2000), including post-smolt Atlantic salmon that frequently swim in surface waters. Levels of prey consumption by gannets nesting on Funk Island off the northeast Newfoundland coast is positively correlated with fishery catches and research indices of abundance over multiple spatial and temporal scales (Montevecchi and Myers 1995). During the late 1970s and 1980s, the gannets' prey landings were dominated by warm-water pelagic migrants (mackerel, *Scomber scombrus*; short-finned squid, *Illex illecebrosus*; Atlantic saury, *Scomberesox saurus*). These prey were essentially replaced in the gannets' diets during the 1990s by cold-water pelagic species (capelin, *Mallotus villosus*; herring, *Clupea harengus*). Interdecadal dietary changes and concomitant fisheries and physical data suggested that cold surface water events (Drinkwater 1996) inhibited movements of warmwater pelagic prey into the region and amplified effects of apparent overfishing of squid in the late 1970s (Montevecchi and Myers 1995, 1996). Incidence of salmon in the gannets' food loads on Funk Island has been rare and sporadic but increased notably from the 1980s to the 1990s (Montevecchi and Myers 1997).

Atlantic salmon smolts leave natal rivers in the spring. Some post-smolts from rivers in Maine, the Maritime Provinces, Quebec, and Newfoundland move to the Newfoundland Shelf within several weeks of river exit, and others remain in local waters at least until autumn (Dutil and Coutu 1988; Ritter 1989). Some post-smolts migrate east of Newfoundland, while others, primarily those from the Gulf of St. Lawrence, move through the Strait of Belle Isle (Montevecchi et al. 1988*b*). Much of the habitat moved

through or occupied by the post-smolts is within the foraging radius (approximately 180 km, Kirkham et al. 1985) of the three gannet colonies in the Gulf of St. Lawrence and of the three in eastern Newfoundland.

This paper examines avian predation on post-smolt Atlantic salmon at sea, using dietary data collected from northern gannets in the colony on Funk Island from 1977 through 2000. Gannet diet is used to (*i*) infer salmon movements and distributions in the context of recent oceanographic changes, (*ii*) assess potential predation by gannets on Atlantic salmon populations, and (*iii*) recommend research activities to improve understanding of the behavior, abundance, and mortality of Atlantic salmon at sea.

Methods

Prey items were sampled from gannets at their breeding colony on Funk Island off Newfoundland's northeast coast in North Atlantic Fisheries Organization (NAFO) Area 3K (Fig. 1) from 1977 through 2000, excluding 1981 when sea conditions prevented access to the island. A total of 7521 regurgitations were sampled with an annual range from 50 to 914. These regurgitations contained 40 120 prey items. Food samples were obtained by approaching gannets at roosts and in the colony, which induces birds to regurgitate (Montevecchi and Myers 1997). Regurgitations usually include multiple items, and regurgitations of the smallest prey (capelin) contained the highest number of individual prey. About 5% of the regurgitations contain more than one species. Samples were collected almost entirely during August with a small portion taken in July and September. Prey were identifiable to species, and lengths of relatively intact specimens were measured and relatively fresh ones were weighed with Pesola spring scales.

The gannets' consumption of salmon was estimated using a bioenergetics model (e.g., Cairns et al. 1991). Adult energy requirements were estimated as 4865 kJ·day^{-1}, based on doubly labeled water measurements of energy use by gannets on Funk Island (Birt-Friesen et al. 1989). Our energetic model sums energy needs of adult and chick metabolism and egg formation and divides them by assimilation efficiency to obtain food requirements (see Table 1 for input parameters). Food requirements are in turn converted to consumption estimates using dietary data and the energy densities of prey. All calculations were based on estimated prey mass, rather than numbers. Colony populations for 1977–2000 were taken from aerial photographic censuses (Nettleship and Chapdelaine 1988; Chardine 2000; G. Chapdelaine, Canadian Wildlife Service, Ste. Foy, QC G1V 4H5, unpublished data) and from linear interpolation and extrapolation for uncensused years (Fig. 2). Pre-breeder numbers were estimated with the aid of a life table submodel based on literature values of age of first breeding, hatching and fledging success, and adult survivorship (Cairns et al. 1991). Numbers of pre-breeders as a proportion of breeders were calculated from the life table after post-fledging survival was varied until the population exhibited the increase estimated for that year.

Our energetics model operates in deterministic mode, with fixed input values, and in stochastic mode, in which inputs are randomly varied according to a normal distribution whose mean is the original input value. Input distributions

604

Can. J. Fish. Aquat. Sci. Vol. 59, 2002

Fig. 1. Locations of the six northern gannet (*Morus bassanus*) colonies in North America: Funk Island, Baccalieu Island (BAC), Cape St. Marys (CSM), Magdalen Bird Rocks (MAG), Anticosti Island (ANT), and Bonaventure Island (BON). Circles are 60 and 180 km in radius and represent the median and maximum foraging ranges of northern gannets. Populations (pairs) are from a 1999 census (Chardine 2000; G. Chapdelaine, Canadian Wildlife Service, Ste. Foy, QC G1V 4H5, unpublished data). Arrows indicate post-smolt migration routes as proposed by Reddin (1988) and Montevecchi et al. (1988*b*).
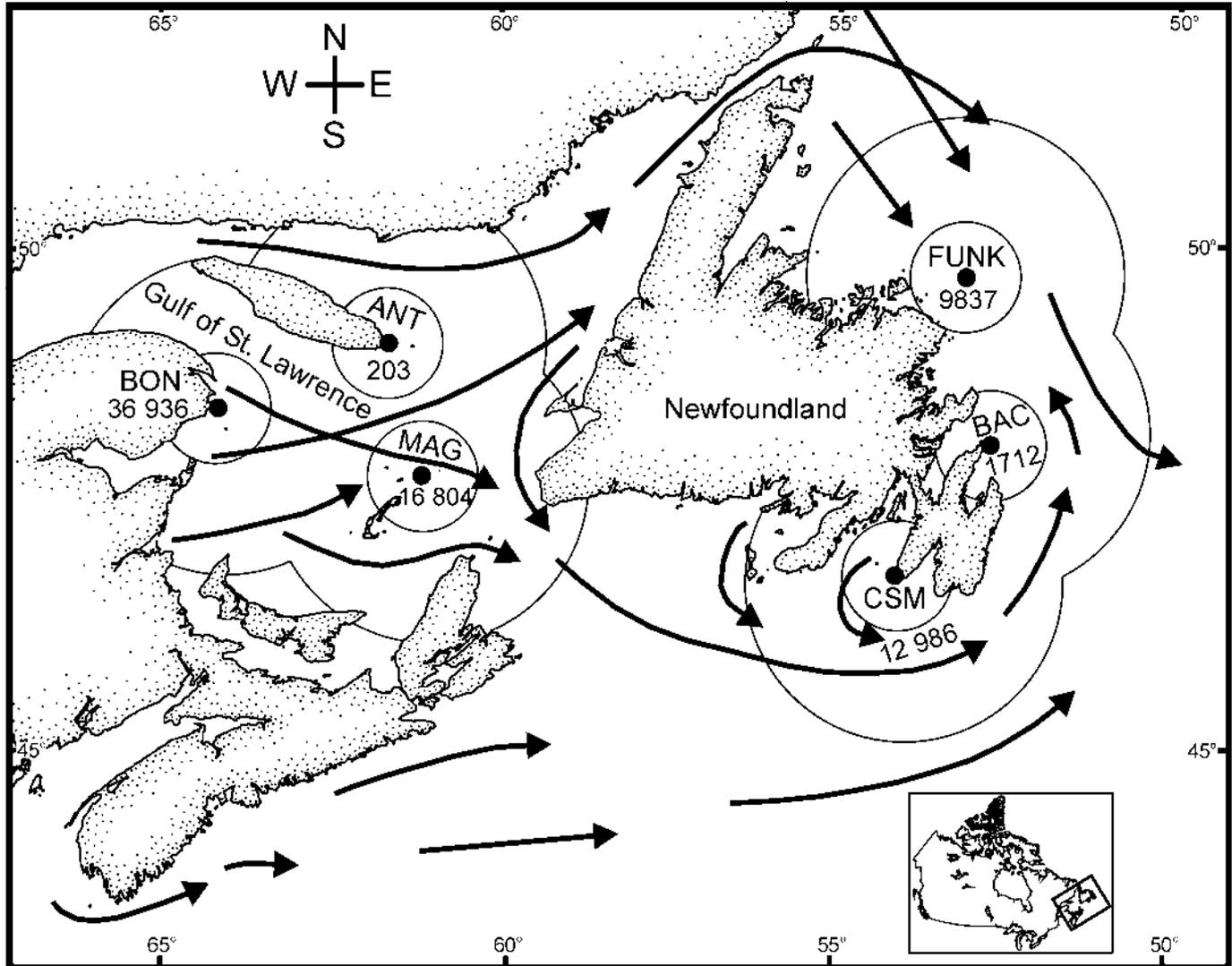
are truncated at 0 (and 1 in the case of proportions). In stochastic runs the standard deviation (SD) of the randomized input value was set at one half of the mean for percentage of salmon in the gannets' diet and for pre-breeders as a proportion of breeders, and one fourth of the mean for all other inputs. Stochastic results are presented as means, medians, SD, and as 5th, 50th (median), and 95th percentiles of 10 000 Monte Carlo outcomes.

The consumption of Atlantic salmon by gannets in the Funk Island colony was estimated for August of each year. Consumption estimates were compared with biomass of post-smolt salmon, as estimated by Cairns and Reddin (2000) for the same period. Briefly, these authors fitted logistic curves to observed weights of marine-phase salmon to derive weight curves, and estimated numbers alive from Lorenzen's (1996) equation for ocean fish, which estimates mortality as an allometric function of body weight. Esti-

mates of post-smolt biomass involve substantial uncertainty because total North American smolt production is poorly known and because there are no empirical measures of mortality during the post-smolt year (Cairns and Reddin 2000).

We compared the gannets' estimated consumption of salmon from 1990 to 2000 with the period 1977–1989. We did this to reflect differences consistent with a shift in the gannets' diet from warm- to cold-water pelagic prey (Montevecchi and Myers 1995) that indicated a larger regime shift in pelagic food webs on the Newfoundland Shelf (Montevecchi and Myers 1996), coincident with decadally anomalous cold-water events (Drinkwater 1996).

The percentage of salmon in the gannets' diet was compared with mean August sea surface temperature (SST) east of St. John's, Newfoundland, at Station 27, whose signals indicate condition fluctuations over the Labrador Shelf (Myers et al. 1990). August temperatures for 1978, 1981, and 1982,

Table 1. Input values for energy model of gannet (*Morus bassanus*) requirements breeding on Funk Island in the Northwest Atlantic.

	Value	CV[a]	Source
Breeding population (pairs, 1999)	9837	0.25	Chardine 2000
Age at first breeding (years)	5		Nelson 1978
Adult annual survivorship	0.94		Nelson 1978
Clutch size	1	0.25	Nelson 1978
Hatching success (eggs hatched·eggs laid^{-1})	0.88	0.25	Montevecchi et al. 1988*a*
Incubation period (days)	44	0	Poulin 1968
Fledging success (chicks fledged·eggs hatched^{-1})	0.8	0.25	Montevecchi et al. 1988*a*
Chick period (days)	91	0	Poulin 1968
Pre-breeding population as proportion of the breeding population	0.321	0.50	Life table model (see text)
Adult metabolism (kJ·day^{-1})	4865	0.25	Birt-Friesen et al. 1989
Energy content of an egg (kJ)	442	0.25	Ricklefs and Montevecchi 1979
Chick metabolism (kJ·day^{-1})	136–2228	0.25	Montevecchi et al. 1984
Assimilation efficiency	0.836	0.25	Bennett and Hart 1993

Note: See text for explanations of model design and functions.

[a]Coefficient of variation (standard deviation·mean^{-1}) of the randomized parameter values used in SHAGIT (program available from CairnsD@dfo-mpo.gc.ca).

Fig. 2. Breeding populations of northern gannets (*Morus bassanus*) in North America. Data are from Nettleship and Chapdelaine (1988), Chardine (2000), and G. Chapdelaine, Canadian Wildlife Service, Ste. Foy, QC G1V 4H5, unpublished data. Colonies (from top to bottom) are open, Funk Island; dots, Baccalieu Island; diagonal lines, Cape St. Mary's; vertical lines, Magdalen Islands; solid, Bonaventure Island. The population of the Anticosti colony is too small to be visible at this scale.
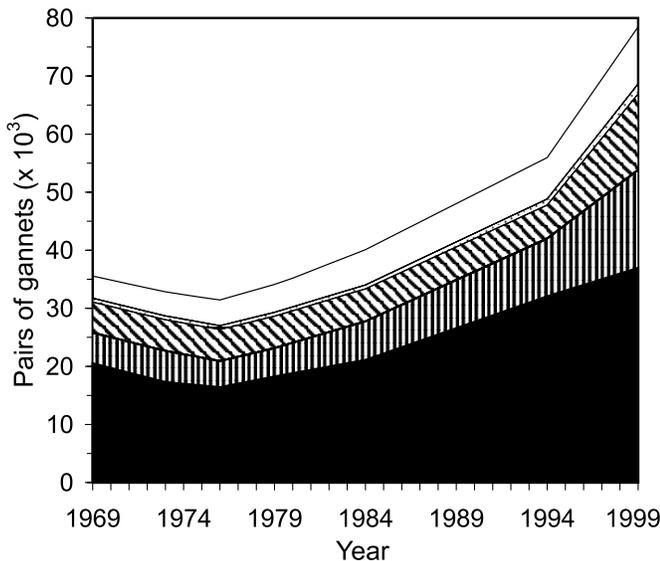
for which data were missing, were estimated from July and September data by a regression equation.

Results

Salmon constituted from 0 to 6.37% of the food that gannets were recorded to have landed on Funk Island during 1977–2000 (Table 2). Before 1990, salmon was a rare item that contributed less than 1% to diet in all but one year. The percentage of salmon in food loads rose sharply during the 1990s, peaking at 6.37% in 1993, and thereafter declined to 0% in 1999 and 2000 (Fig. 3). During 1977–1989 and 1990–

2000, the mean relative contributions of salmon to the gannets' diet were 0.29% and 2.78%, respectively (Table 2).

The mean (±SD) fork length of 21 fresh Atlantic salmon regurgitated by gannets on Funk Island on a mean date of 9 August was 23.4 ± 1.9 cm (range 18.5–26.1 cm, Fig. 4). Based on the length–mass relationship calculated for post-smolt Atlantic salmon taken in September–October in the Labrador Sea (mass = 0.181 × length$^{2.213}$, masses in g and lengths in cm; Cairns and Reddin 2000), these fish had a mean mass of 196 g. Figure 4 also shows the length distributions of other fish species preyed on by gannets at Funk Island. Owing to decadal dietary shifts from predominantly large pelagic fishes during the 1970s and 1980s to predominantly small ones during the 1990s, the length of prey decreased while the number of prey per food load increased (Fig. 5).

In 1991, SST in the region around Funk Island dropped precipitously, but temperatures returned to previous levels by mid-decade (Fig. 3). The temperature decrease during 1991 occurred one year after the initial increase in salmon in the gannets' diets, and the percent salmon consumed was not significantly correlated with SST ($r = 0.343$, $n = 23$, $P = 0.110$).

Estimates from model simulations of the tonnes of salmon consumed during years of high (1993), medium (1996), and low (1998) predation by gannets were skewed to the right (Fig. 6). As a consequence, means of these distributions were greater than medians (Table 2). Consumption estimates from deterministic model runs were intermediate between stochastic mean and median values. The estimated consumption of Atlantic salmon by gannets on Funk Island during August varied from 0 to 43.4 t (median values; Table 2). Means of median consumption levels were 1.6 t for 1977–1989 and 18.1 t for 1990–2000. The gannet population of Funk Island more than doubled between 1977 and 1999 (Fig. 2) and contributed to the higher estimated consumption of salmon during later years.

Estimated salmon consumption by gannets on Funk Island during August was less than 1% of total estimated biomass of post-smolt Atlantic salmon of North American origin in all but one year between 1977 and 1989 (Table 2). During the 1990s, when salmon predation by gannets increased, the

Table 2. Estimated consumption by gannets (*Morus bassanus*) at Funk Island, Newfoundland, of post-smolt Atlantic salmon (*Salmo salar*) and of total prey, and estimated consumption (t) of post-smolt biomass, during August, as a percentage of post-smolt biomass, based on deterministic and stochastic model runs.

| Year	No. gannet samples	No. prey	% salmon in gannet diet	Post-smolt biomass August (t)	Annual consumption, all prey[b] (t)	Salmon consumption in August[a]						% post-smolt biomass[b,c]
						Deterministic	Stochastic					
							Mean[b]	Median[b]	SD[b]	5th percentile[b]	95th percentile[b]	
1977	146	332	0.00	810	2922	0.0	0.0	0.0	0.0	0.0	0.0	0.00
1978	914	1 080	0.00	496	3082	0.0	0.0	0.0	0.0	0.0	0.0	0.00
1979	393	586	0.36	1020	3242	1.8	2.0	1.7	1.4	0.3	4.5	0.16
1980	219	608	0.00	1783	3401	0.0	0.0	0.0	0.0	0.0	0.0	0.00
1982	193	360	1.06	450	3742	6.1	6.6	5.6	5.8	0.9	14.9	1.25
1983	494	1 242	0.32	1264	3982	1.9	2.1	1.8	1.6	0.3	4.8	0.15
1984	227	882	0.00	1240	4078	0.0	0.0	0.0	0.0	0.0	0.0	0.00
1985	184	770	0.00	1123	4177	0.0	0.0	0.0	0.0	0.0	0.0	0.00
1986	493	1 294	0.91	1103	4246	5.9	6.5	5.5	4.7	0.9	14.7	0.50
1987	354	2 506	0.45	986	4367	3.0	3.3	2.8	2.4	0.5	7.5	0.28
1988	572	1 836	0.33	706	4405	2.2	2.5	2.1	3.2	0.3	5.6	0.29
1989	410	1 388	0.00	763	4480	0.0	0.0	0.0	0.0	0.0	0.0	0.00
1990	342	4 550	2.94	630	4555	20.3	21.9	18.9	15.8	2.9	50.1	3.00
1991	405	3 468	2.23	954	4617	15.6	17.1	14.8	12.2	2.2	39.3	1.55
1992	288	1 710	3.87	914	4723	27.5	30.1	26.0	22.2	4.3	68.6	2.84
1993	255	1 508	6.37	555	4780	45.9	50.1	43.5	36.0	6.9	114.9	7.84
1994	50	779	1.62	523	4800	11.9	13.0	11.1	9.6	1.8	29.7	2.12
1995	278	3 951	5.72	715	5132	45.1	49.3	42.8	35.0	7.1	112.1	5.99
1996	334	3 834	3.68	647	5553	31.4	34.6	29.9	24.4	4.9	78.1	4.62
1997	244	1 376	1.07	706	5980	9.7	10.8	9.4	7.6	1.5	24.3	1.33
1998	445	4 398	0.33	706	6277	3.2	3.5	3.0	2.5	0.5	7.9	0.43
1999	97	551	0.00	706	6652	0.0	0.0	0.0	0.0	0.0	0.0	0.00
2000	184	1 111	0.00	706	7100	0.0	0.0	0.0	0.0	0.0	0.0	0.00
x̄1977–1989			0.29	979	3844	1.7	1.9	1.6	1.6	0.3	4.3	0.22
x̄1990–2000			2.53	706	5470	19.2	20.9	18.1	15.0	2.9	47.7	2.70
x̄1977–2000			1.42	855	4479	10.5	11.4	9.9	8.3	1.6	26.1	1.41
Totals	7521	40 120										

Note: SD, standard deviation.

[a]Based on a mortality of 20% at river exit. Post-smolt biomasses for 1997–2000 are the mean of values for 1990–1996.

[b]Based on 10 000 Monte Carlo simulations of gannet consumption.

[c]Based on median estimated consumption of salmon.

Fig. 3. Mean sea surface temperature (diamonds) at Station 27 (east of St. John's, Newfoundland) and the percent contribution of Atlantic salmon (*Salmo salar*) (open bars) to diets of gannet (*Morus bassanus*) chicks at Funk Island during August 1977–2000. Dietary data are unavailable for 1981.
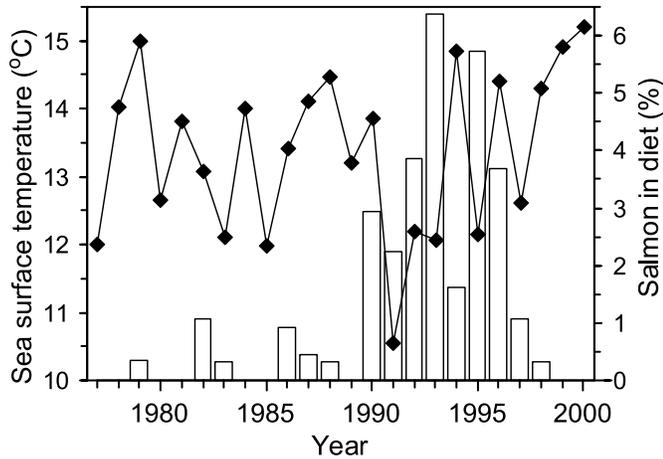
Fig. 4. Length–frequency distributions of (*a*) capelin (*Mallotus villosus*), (*b*) Atlantic salmon (*Salmo salar*), (*c*) Atlantic herring (*Clupea harengus*), (*d*) Atlantic saury (*Scomberesox saurus*), and (*e*) mackerel (*Scomber scombrus*) preyed on by gannets (*Morus bassanus*) from the breeding colony on Funk Island during August.
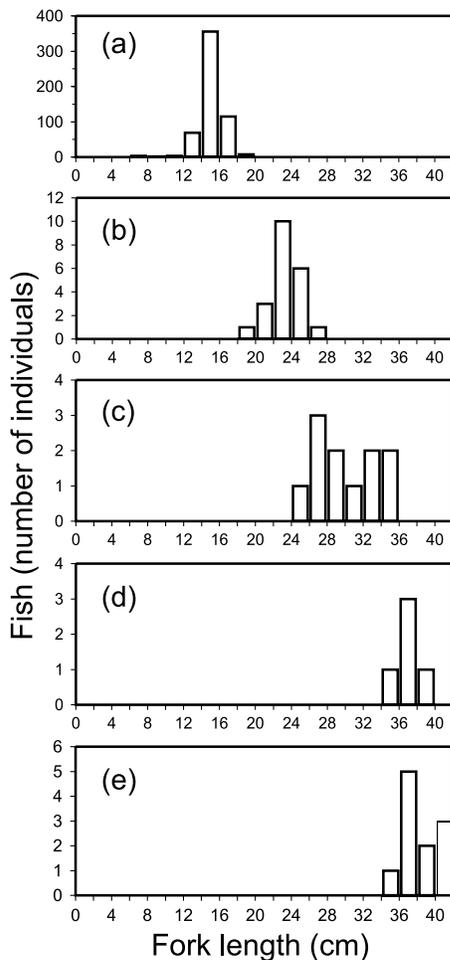
Fig. 5. (*a*) Average number of prey per food load and (*b*) average length of prey landed by gannets (*Morus bassanus*) on Funk Island, 1977–2000.
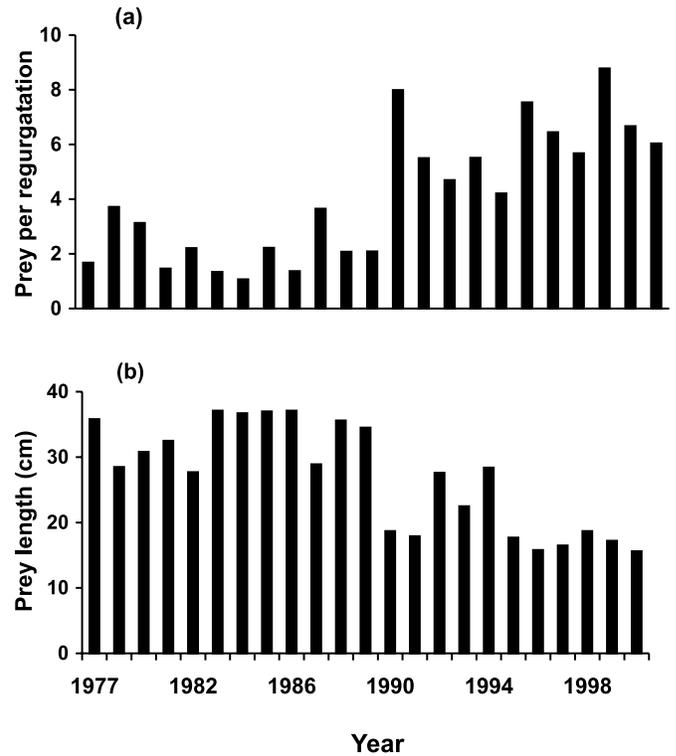

birds' estimated consumption relative to post-smolt biomass increased, peaking at 7.84% in August 1993. Overall, gannets consumed an estimated 0.22% of post-smolt biomass in August 1977–1989 and 2.70% in August 1990–2000.

Foraging gannets range up to 180 km or more from their colonies to obtain food, although feeding effort is most intense within 60 km of the colony (Kirkham et al. 1985). The probable migratory routes of post-smolt Atlantic salmon overlap with the foraging ranges of all North American gannet colonies (Fig. 1). Dietary samples from two colonies in the Gulf of St. Lawrence (Bonaventure Island and Great Bird Rock, Magdalen Islands) include a variety of pelagic fishes and squid, but no Atlantic salmon (Table 3), although sampling efforts at these sites has not been nearly as intensive and extensive as those at Funk Island. Dietary data are unavailable for other North American colonies.

Lengths of nonsalmon prey were compiled from samples from Funk Island to assess the range of prey lengths that are vulnerable to predation by gannets. Capelin, the smallest prey, had mean and minimum lengths of 15.2 cm and 7.6 cm, respectively (Fig. 3). Mackerel, the largest prey, had mean and maximum lengths of 38.6 cm and 41.7 cm, respectively. Post-smolt Atlantic salmon enter the sea at lengths that range from 13 to 18 cm and attain an estimated length of ~42 cm by early November (Hutchings and Jones 1998; Cairns and Reddin 2000). Thus, post-smolt salmon are of a size that could be preyed on by gannets throughout the entire period between river departure until gannets depart from eastern Canadian waters (mid- to late October).

When the mean salmon contribution to diet at Funk Island

608

Can. J. Fish. Aquat. Sci. Vol. 59, 2002

Fig. 6. Frequency distributions of estimated consumption of Atlantic salmon (*Salmo salar*) by gannets (*Morus bassanus*) on Funk Island during August during years of (*a*) high (1993), (*b*) medium (1996), and (*c*) low (1998) predation from 10 000 stochastic runs for each year.
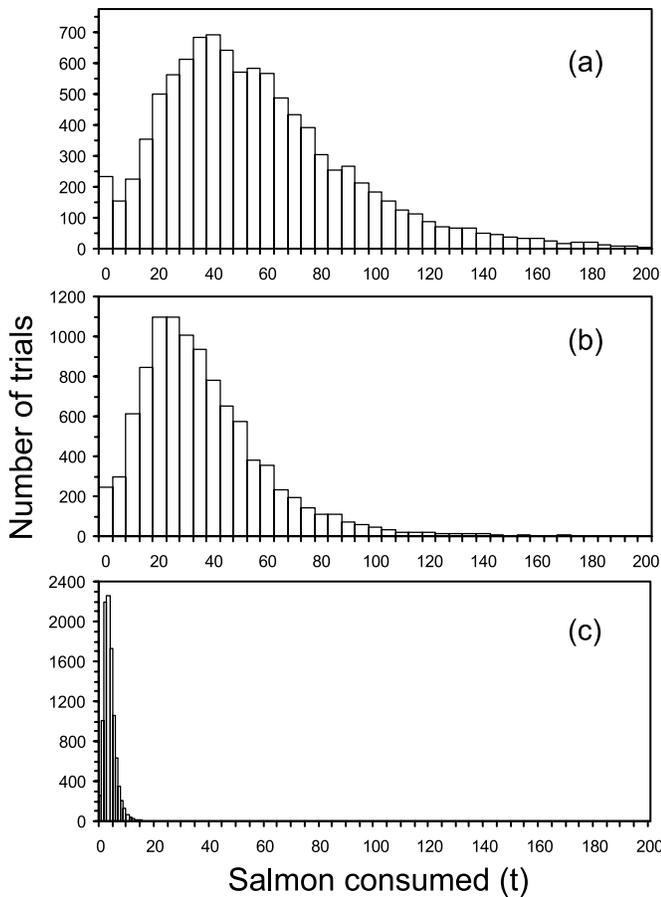
for August 1990–2000 (2.53%) was assumed to apply to all Newfoundland colonies, estimated consumption during August totaled 5.0% of post-smolt biomass. Enumerated diet samples from the Gulf of St. Lawrence total 321 (Table 3), indicating that salmon would not likely be detected if they were less than 1/321 (0.31%) of diet. When salmon were assumed to contribute 2.53% of Newfoundland diet and 0.31% of Gulf diet throughout the breeding season, estimated consumption of post-smolt biomass by gannets increased markedly.

Discussion

Gannets as indicators of the marine ecology of Atlantic salmon

Dietary records of gannets on Funk Island in NAFO Area 3K provide the only long-term time series of post-smolt salmon in the Northwest Atlantic. Post-smolts have been taken in small numbers on research cruises in the Labrador Sea during September–October in 1987, 1988, 1991, and 1998, and the area is viewed as a major staging area for post-smolt salmon (Reddin and Short 1991). The occurrence of salmon in gannet regurgitations at Funk Island demon-

Table 3. Diet of northern gannets (*Morus bassanus*) in the Gulf of St. Lawrence taken from the literature.

Prey	N	Date	Location	Prey size range	Source
Herring *Clupea harengus*, mackerel *Scomber scombrus*, *Loligo* squid	NR	June–Sept. 1966–1967	Bonaventure I		Poulin 1968
Herring, mackerel, *Loligo* squid, redfish *Sebastes* spp.	NR	1968	Bonaventure I	18–30 cm	Lafleur 1969
Mackerel, herring, smelt *Osmerus mordax*, sand lance *Ammodytes* spp., cunner *Tautogolabrus adspersus*	80	15–17 Aug. 1995	Bonaventure I		Rail et al. 1996
Capelin *Mallotus villosus*, sand lance, mackerel, smelt, *Crangon* shrimp, American eel *Anguilla rostrata*, lumpfish *Cyclopterus lumpus*, *Illex* squid, cod *Gadus morhua*, yellowtail *Limanda ferruginea*, other flatfish	189	3 June – 10 Aug. 1977–1978	Bird Rock, Magdalens	7–41 cm	Burton 1980
Mackerel, Atlantic saury *Scomberesox saurus*, herring, sand lance, *Loligo* squid	52	17–29 Sept. 1987–1988	Bird Rock, Magdalens	20–520 g	Cairns et al. 1991; D.K. Cairns, unpublished data

Note: NR, sample sizes not reported.

strates that post-smolts also occupy the southern Labrador Sea in August.

Post-smolts were found in gannet regurgitations at Funk Island in six of 12 years from 1977 to 1989 and in nine of 11 years from 1990 to 2000. The increase of salmon in the birds' diets was associated with a radical shift from warm-water (mackerel, saury, squid) to cold-water (capelin, herring) pelagic prey (Montevecchi and Myers 1996, 1997). This dietary shift occurred during a period of megascale physical and biological change on the Newfoundland and Labrador Shelf. Changes included the extreme cold surface water event of 1991 (Drinkwater 1996), breeding failures of surface-feeding seabirds (Regehr and Montevechi 1997), the southward influx of polar cod (*Boreogadus saida*) as a dominant pelagic species (Frank et al. 1996), and the collapse of groundfish stocks (Hutchings 1996). The shift in the gannets' diet during the 1990s, including the increased consumption of Atlantic salmon, does not appear to be a simple consequence of cold surface water. A major dietary change occurred in 1990, one year before the extreme cold SST event of 1991, and continued after surface water temperatures warmed during the mid-1990s (Drinkwater 1996). In a somewhat parallel finding in the Pacific Ocean, Welch et al. (1998) related a long-term response of sockeye salmon (*Oncorhynchus nerka*) to a short-term oceanographic perturbation. Such a long-term biological change in response to rapid onset, relatively discrete perturbations reflects a large-scale regime shift (sensu Steele 1998).

The increase in salmon in the gannets' diet could be due to any of a number or combination of factors: (*i*) an increase in the abundance of post-smolts, (*ii*) an increase in their relative abundance related to the changing abundances or alternative prey, and (or) (*iii*) an increase in availability due to a change in the salmon's migratory patterns, with higher numbers of post-smolts occupying the southern Labrador Sea during the 1990s. Decreased mackerel abundance in the region could favor greater predation on salmon by gannets that are opportunistic generalist predators on pelagic prey. The mean energy density for major warmwater prey is $7.1\ kJ \cdot g^{-1}$ (mackerel 10.3, squid 4.3, saury 6.8) and $5.7\ kJ \cdot g^{-1}$ for cold-water prey (herring 7.2, capelin 4.2; Montevecchi et al. 1984). Thus, alternative prey were energetically more valuable relative to Atlantic salmon ($4.4\ kJ \cdot g^{-1}$, Cairns 1998) during 1977–1989, the period of warmwater prey, than during 1990–2000, the period of cold-water prey. Moreover, the number of prey per food load increased while the average length of prey decreased over the 24-year sampling period, as gannets shifted from dominant consumption of large pelagic species like mackerel before 1990 to small ones like capelin during the 1990s. As post-smolt salmon in August are substantially larger than capelin, this might also have favored an increase in the gannets' consumption of salmon during the 1990s. It would, however, be unlikely to account for all the change given that mean percentage of salmon in the birds' diets rose by an order of magnitude between 1977–1989 (0.29%) and 1990–2000 (2.53%). Had comparable numbers of post-smolt salmon been present within the gannets' foraging range around Funk Island during the 1970s and 1980s, we expect that more of them would have been found in the birds' regurgitations.

Summer occurrences of post-smolt Atlantic salmon in the Labrador Sea does not preclude their presence elsewhere. Of 420 tags returned from post-smolts that had been marked in rivers in Quebec, the Maritimes, and New England, only 30 (7.6%) were recovered from the Atlantic coasts of New-foundland and Labrador (Ritter 1989; Cairns and Reddin 2000). Return dates from the Labrador Sea and from southern areas ranged from June to September–October, suggesting either a diffuse and asynchronous migration, or one with routes and timing that vary from year to year (Friedland et al. 1999). Research and commercial fishing in the Bay of Fundy and in the northwestern Gulf of St. Lawrence demonstrates also that post-smolt Atlantic salmon can remain in coastal waters during summer and fall (Dutil and Coutu 1988).

Tag recoveries from salmon originating from rivers in New England, the Bay of Fundy, and southwestern Nova Scotia on Funk Island have been interpreted as evidence of a salmon migration route east of Newfoundland (Montevecchi et al. 1988*b*). Tags from these areas have, however, also been recovered in the northern and eastern Gulf of St. Lawrence (Ritter 1989), suggesting that post-smolts from the southern part of the range can also reach the Labrador Sea via the Gulf of St. Lawrence, passing through the foraging ranges of gannet colonies there.

Consumption of Atlantic salmon by gannets

Estimates of seabird consumption are usually derived from deterministic bioenergetic models that yield single-value outputs (e.g., Cairns et al. 1991). We used stochastic model runs to evaluate error in our estimates. Model outputs varied over wide ranges, indicating substantial uncertainty in consumption estimates. Comparisons of estimated consumption by gannets with indirect estimates of post-smolt Atlantic salmon biomass and numbers introduce additional uncertainty (Cairns and Reddin 2000).

These limitations notwithstanding, our data and simulations suggest that gannet predation on post-smolts could influence the population dynamics of Atlantic salmon in the Northwest Atlantic. Some post-smolts are likely to be within the foraging range of gannet colonies for a substantial period between river exit and mid-autumn, when the gannets depart from eastern Canadian waters. Much more extensive dietary sampling at gannet colonies other than Funk Island and at other times is needed to critically assess the potential influences of gannet predation on the population dynamics of post-smolt Atlantic salmon in the Northwest Atlantic.

North American gannet numbers increased 2.4 fold between 1977 and 1999. Growing gannet populations could have consumed increasing numbers of post-smolts since the 1970s. Most of the tags from post-smolt Atlantic salmon recovered in the gannet colony on Funk Island have come from hatchery-reared fish released in the Penobscot River, Maine. Tags could make post-smolts more vulnerable to gannets and other avian predators that prey proportionally more heavily on hatchery-reared fishes than on wild ones. If so, predation on hatchery-reared fish could inflate estimates of predation on wild post-smolts. Salmon vertebrae and ring patterns on scales (Friedland et al. 1999) regurgitated by gannets could help determine relative predation rates of wild and hatchery-released fish. Nevertheless, hatchery fish are a small fraction of the Atlantic salmon post-smolts in the re-

610

Can. J. Fish. Aquat. Sci. Vol. 59, 2002

gion, so their increased susceptibility would have negligible effects on predation opportunities by gannets.

In some restricted environments, marine birds consume small proportions of salmonid numbers and biomass. For example, below a dam on the Columbia River 2% of juvenile Pacific salmon (*Oncoryhynchus* spp.) and steelhead were estimated to be preyed upon by seabirds (Ruggerone 1986). Notably, whereas prey swamping of predators may have occurred, this mortality estimate is lower than some of those generated for predation on post-smolt Atlantic salmon by gannets in the open ocean, where overall predation by birds might be expected to be less intense. Presumably the predation imposed by gannets on Atlantic salmon smolts represents an additive source of mortality.

Atlantic salmon are extremely rare in the diets of Atlantic cod (*Gadus morhua*), common murres (*Uria aalge*), and harp (*Phoca groenlandica*), harbor (*Phoca vitulina*), and grey (*Halichoerus grypus*) seals in the Northwest Atlantic (Cairns and Reddin 2000). Post-smolt salmon may be more vulnerable to gannets than other large marine predators, owing to the gannets' large size and specialized feeding habit of plunge-diving into surface waters (Garthe et al. 2000), the habitat favored by salmon (Dutil and Coutu 1988). The decreasing incidence of post-smolts in gannet diets since 1995 and their absence in 1999 and 2000 could also reflect decreased availability of Atlantic salmon in the region (see Montevecchi and Myers 1995).

Many complexities and controversies surround considerations of the consumption of commercial prey by large predators (Lavigne 1996). Arguments for culls of large marine predators whose diets contain small proportions of commercial prey for portions of the year ignore uncertainties inherent in multispecies and ecosystem interactions (Swain and Sinclair 2000). Wild Atlantic salmon will likely best benefit from the mitigation of human impacts, including aquacultural practices, releases of hatchery fishes, pesticide use, and the damming, pollution, and degradation of rivers (e.g., Gross 1998; Fairchild et al. 1999; Levin et al. 2001) and their cumulative effects. Influences of these cumulative effects are likely reflected in the general inverse relationship between human and Atlantic salmon populations along a North American latitudinal gradient from New England through the Maritime Provinces, Gulf of St. Lawrence, and Newfoundland and Labrador.

Given the precarious state of wild Atlantic salmon and risk to the species' population integrity, understanding of the marine ecology of Atlantic salmon is urgently needed. The use of gannet diets to sample post-smolts, despite its many associated uncertainties, has provided some insight into their marine distribution, movements, abundance, and mortality.

There are many practical implications for integrating seabird studies in multidisciplinary ecosystem and fisheries research. The systematic sampling of gannets' diets at multiple colonies and from June through September can provide an efficient and cost-effective means of obtaining biological and ecological data on post-smolt Atlantic salmon. Research cruises are constrained by high costs, whereas colony-based sampling of gannets' diets can be repeated annually at modest expense, without harm to the birds. The foraging ranges of gannets around breeding colonies in North America cover a substantial portion of the presumed marine distribution of post-smolt Atlantic salmon. Sampling seabird diets could provide samples of salmon tissue for genetic assessments of origins, as well as samples of scales and otoliths that can be used to elucidate individual histories (Friedland et al. 1999). Findings from the gannets' dietary data could be used to help clarify post-smolt migratory movements, growth rates, natural mortality, and food habits.

Acknowledgements

References

Beland, K.F., Kocik, J.F., vandeSande, J., and Sheehan, T.F. 2001. Striped bass predation upon Atlantic salmon smolts in Maine. Northeast. Nat. **8**: 267–274.

Bennett, D.C., and Hart, L.E. 1993. Metabolizable energy of fish when fed to captive great blue herons (*Ardea herodias*). Can. J. Zool. **71**: 1767–1771.

Birt-Friesen, V.L., Montevecchi, W.A., Cairns, D.K., and Macko, S.A. 1989. Activity-specific metabolic rates of free-living northern gannets and other seabirds. Ecology, **70**: 357–367.

Burton, J. 1980. L'alimentation estivale du fou de bassan (*Sula bassana* L.) au Rocher aux Oiseaux, Iles-de-la-Madeleine, Quebec. Nat. Can. (Ottawa), **107**: 289–291.

Cairns, D.K. 1992. Bridging the gap between ornithology and fisheries science: use of seabird data in stock assessment models. Condor, **94**: 811–824.

Cairns, D.K. 1998. Diet of cormorants, mergansers, and kingfishers in northeastern North America. Can. Tech. Rep. Fish. Aquat. Sci. No. 2225.

Cairns, D.K. 2001. An evaluation of possible causes of the decline in pre-fishery abundance of North American Atlantic salmon. Can. Tech. Rep. Fish. Aquat. Sci. No. 2358.

Cairns, D.K., and Reddin, D.G. 2000. The potential impact of seal and seabird predation on North American Atlantic salmon. Can. Stock Assess. Secretariat Res. Doc. 2000/12. (http://www.dfo-mpo.gc.ca/CSAS/CSAS/DocREC/2000/PDF/2000_012e.pdf)

Cairns, D.K., Chapdelaine, G., and Montevecchi, W.A. 1991. Prey exploitation by seabirds in the Gulf of St. Lawrence. *In* The Gulf of St. Lawrence: small ocean or big estuary? *Edited by* J.-C. Therriault. Can. Spec. Publ. Fish. Aquat. Sci. No. 113. pp. 277–291.

Chardine, J.W. 2000. Census of northern gannet colonies in the Atlantic region. Can. Wildl. Serv. Atl. Reg. Tech. Rep. Ser. 361. *Available from* Canadian Wildlife Service, Sackville, NB E4L 1G6.

Dempson, J.B., Reddin, D.G., O'Connell, M.F., Helbig, J., Bourgeois, C.E., Mullins, C., Porter, T.R., Lilly, G., Carscadden, J., Stenson, G.B., and Kulka, D. 1998. Spatial and temporal varia-

tion in Atlantic salmon abundance in the Newfoundland–Labrador region with emphasis on factors that may have contributed to low returns in 1997. Can. Stock Assess. Secretariat Res. Doc. 98/114. *Available from* Department of Fisheries and Oceans, Northwest Atlantic Fisheries Centre, P.O. Box 5667, St. John's, NF A1C 5X1.

Drinkwater, K.F. 1996. Atmospheric and oceanic variability in the northwest Atlantic during the 1980s and early 1990s. J. Northw. Atl. Fish. Sci. **18**: 77–97.

Dutil, J.-D., and Coutu, J.M. 1988. Early marine life of Atlantic salmon, *Salmo salar*, postmolts in the northern Gulf of St. Lawrence. Fish. Bull. **86**: 197–212.

Fairchild, W.L., Swanberg, E.O., Arsenault, J.T., and Brown, S.B. 1999. Does an association between pesticide use and subsequent declines in catch of Atlantic salmon (*Salmo salar*) represent a case of endocrine disruption? Environ. Health Perspect. **107**: 349–357.

Frank, K.T., Carscadden, J.E., and Simon, J.E. 1996. Recent excursions of capelin (*Mallotus villosus*) to the Scotian Shelf and Flemish Cap during anomalous hydrographic conditions. Can. J. Fish. Aquat. Sci. **53**: 1473–1486.

Friedland, K.D., Dutil, J.-D., and Sadusky, T. 1999. Growth patterns in postmolts and the nature of the marine juvenile nursery for Atlantic salmon, *Salmo salar*. Fish. Bull. **97**: 472–481.

Garthe, S., Benvenuti, S., and Montevecchi, W.A. 2000. Pursuit-plunging by northern gannets (*Sula bassana*) feeding on capelin. Proc. R. Soc. Lond. Ser. B Biol. Sci. **267**: 1717–1722.

Gross, M.R. 1998. One species with two biologies: Atlantic salmon (*Salmo salar*) in the wild and in aquaculture. Can. J. Fish. Aquat. Sci. **55**(Suppl. 1): 131–144.

Hutchings, J.A. 1996. Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. Can. J. Fish. Aquat. Sci. **53**: 943–962.

Hutchings, J.A., and Jones, M.E.B. 1998. Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. Can. J. Fish. Aquat. Sci. **55**(Suppl. 1): 22–47.

International Council on the Exploration of the Sea (ICES). 1999. Report of the working group on North Atlantic salmon. ICES CM 1999/ACFM:14.

Kirkham, I.R., McLaren, P., and Montevecchi, W.A. 1985. The food habits and distribution of northern gannets off eastern Newfoundland and Labrador. Can. J. Zool. **63**: 181–188.

Lafleur, Y. 1969. Île Bonaventure 1968. Unpublished report. Université Laval, Quebec City.

Lavigne, D.M. 1996. Ecological interactions between marine mammals, commercial fisheries, and their prey: unravelling the tangled web. *In* Studies of high-latitude seabirds 4: Trophic relationships and energetics of endotherms in cold ocean systems. *Edited by* W.A. Montevecchi. Can. Wildl. Serv. Occas. Pap. No. 91. pp. 59–71.

Levin, P.S., Zabel, R.W., and Williams, J.G. 2001. The road to extinction is paved with good intentions: negative association of fish hatcheries with threatened salmon. Proc. R. Soc. Lond. Ser. B Biol. Sci. **268**: 1153–1158.

Lorenzen, K. 1996. The relation between body weight and natural mortality in juvenile and adult fish: a comparison of natural ecosystems and aquaculture. J. Fish Biol. **49**: 627–647.

Montevecchi, W.A., and Myers, R.A. 1995. Prey harvests of seabirds reflect pelagic fish and squid abundance on multiple spatial and temporal scales. Mar. Ecol. Prog. Ser. **117**: 1–9.

Montevecchi, W.A., and Myers, R.A. 1996. Dietary changes of seabirds indicate shifts in pelagic food webs. Sarsia, **80**: 313–322.

Montevecchi, W.A., and Myers, R.A. 1997. Centurial and decadal oceanographic influences on changes in northern gannet populations and diets in the north-west Atlantic: implications for climate change. ICES J. Mar. Sci. **54**: 608–614.

Montevecchi, W.A., Ricklefs, R.E., Kirkham, I.R., and Gabaldon, D. 1984. Growth energetics of nestling northern gannets (*Sula bassanus*). Auk, **101**: 334–341.

Montevecchi, W.A., Birt, V.L., and Cairns, D.K. 1988*a*. Dietary changes of seabirds associated with local fisheries failures. Biol. Oceanogr. **5**: 153–161.

Montevecchi, W.A., Cairns, D.K., and Birt, V.L. 1988*b*. Migration of post-smolt Atlantic salmon, *Salmo salar*, off northeastern Newfoundland, as inferred by tag recoveries in a seabird colony. Can. J. Fish. Aquat. Sci. **45**: 568–571.

Myers, R.A., Akenhead, S.A., and Drinkwater, K.F. 1990. The influence of Hudson Bay runoff and ice melt on the salinity of the inner Newfoundland Shelf. Atmos. Ocean, **28**: 241–256.

Nelson, J.B. 1978. The gannet. T & AD Poyser, Berkhamsted.

Nettleship, D.N., and Chapdelaine, G. 1988. Population size and status of the northern gannet *Sula bassanus* in North America, 1984. J. Field Ornithol. **59**: 120–127.

Poulin, J.-M. 1968. Reproduction du fou de Bassan (*Sula bassana*), Île Bonaventure (Québec). M.Sc. thesis, Université Laval, Quebec City.

Rail, J.-F., Chapdelaine, G., Brousseau, P., and Savard, J.-P.L. 1996. Utilisation des oiseaux marins comme bioindicateurs de l'écosystème marin de l'estuaire et du Golfe Saint-Laurent. Can. Wildl. Serv. Tech. Rep. No. 254. *Available from* Canadian Wildlife Service, Ste. Foy, QC G1V 4H5.

Reddin, D.G. 1988. Ocean life of Atlantic salmon (*Salmo salar* L.) in the Northwest Atlantic. *In* Atlantic salmon: preparing for the future. *Edited by* D.H. Mills and D.J. Piggins. Croon Helm, London. pp. 483–511.

Reddin, D.G., and Friedland, K.D. 1993. Marine environmental factors influencing the movement and survival of Atlantic salmon. *In* Salmon in the sea and new enhancement strategies. *Edited by* D.H. Mills. Blackwell Scientific, London. pp. 79–103.

Reddin, D.G., and Short, P.B. 1991. Postsmolt Atlantic salmon (*Salmo salar*) in the Labrador Sea. Can. J. Fish. Aquat. Sci. **48**: 2–6.

Regehr, H.M., and Montevecchi, W.A. 1997. Interactive effects of food shortage and predation on breeding failure of black-legged kittiwakes: indirect effects of fishery activities and and implications for indicator species. Mar. Ecol. Prog. Ser. **155**: 249–260.

Ricklefs, R.E., and Montevecchi, W.A. 1979. Size, organic composition and energy content of North Atlantic gannet *Morus bassanus* eggs. Comp. Biochem. Physiol. A Comp. Physiol. **64**: 161–165.

Ritter, J.A. 1989. Marine migration and natural mortality of North American Atlantic salmon (*Salmo salar* L.). Can. Manuscr. Rep. Fish. Aquat. Sci. No. 2041.

Ruggerone, G.T. 1986. Consumption of migrating juvenile salmonids by gulls foraging below a Columbia River dam. Trans. Am. Fish. Soc. **115**: 736–742.

Scheel, D., and Hough, K.R. 1997. Salmon fry predation by seabirds near an Alaskan hatchery. Mar. Ecol. Prog. Ser. **150**: 35–48.

Steele, J.H. 1998. Regime shifts in marine ecosystems. Ecol. Appl. **8**: 533–536.

Swain, D.P., and Sinclair, A.F. 2000. Pelagic fishes and the cod recruitment dilemma in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. **57**: 1321–1325.

Welch, D.W., Ishida, Y., and Nagasawa, K. 1998. Thermal limits and ocean migrations of sockeye salmon (*Oncorhychus nerka*): long-term consequences of global warming. Can. J. Fish. Aquat. Sci. **55**: 937–948.

612

Can. J. Fish. Aquat. Sci. Vol. 59, 2002

Welch, D.W., Ward, B.R., Smith, B.D., and Eveson, J.P. 2000. Temporal and spatial responses of British Columbia steelhead (*Oncorhynchus mykiss*) populations to ocean climate shifts. Fish. Oceanogr. **9**: 17–32.

World Wildlife Fund (WWF). 2001. The status of wild salmon: a river by river assessment. World Wildlife Fund, Washington, D.C.