

FLEXIBLE GROWTH RATES IN FORK-TAILED STORM-PETRELS: A RESPONSE TO ENVIRONMENTAL VARIABILITY

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ABSTRACT.—We examined the degree that growth in Fork-tailed Storm-Petrel (*Oceanodroma furcata*) chicks varies among individuals and years. Data on wing chord length and body mass were collected on 10 or more chicks per year on the Barren Islands, Alaska, during seven years over two decades. In contrast to the apparently uniform growth rates in other storm-petrels (e.g. Leach's Storm-Petrel [*Oceanodroma leucorhoa*] and British Storm-Petrel [*Hydrobates pelagicus*]), Fork-tailed Storm-Petrel chicks on the Barren Islands displayed a two-fold variation in both wing growth and mass gain. Variation in growth rate was apparent both within and among years. Correlations between wing growth and mass gain were significant in only four of seven years, a finding we interpret as indicative of the importance of changes in food quality and quantity on growth. The decadal changes in growth rate of this species between the 1980s and 1990s are consistent with the regulating role that environmental variation appears to play in the growth and survival of storm-petrels. We suggest that the wide range of observed growth rates among individuals, years, and between decades is a response to environmental variability. Received 7 November 1996, accepted 9 June 1997.

PROCELLARIIFORM CHICKS grow extremely slowly, and parents can raise only one chick at a time. Yet, excess calories beyond those needed for growth are stored as fat, and chicks normally weigh more than their parents at fledging (Boersma et al. 1980, Warham 1990). Several hypotheses have been advanced to explain this apparent conundrum. Food availability or delivery rates may constrain chick development (Lack 1968). The time available to feed chicks also may be constrained (Dunn 1980). Nearly all storm-petrels are nocturnal at the nesting colony, returning to feed their chick only after dark (Boersma et al. 1980, Boersma and Groom 1993). Particularly at high latitudes, daylight hours encompass more than 80% of the day, leaving only a few hours within which parents can return to their nest (Boersma et al. 1980). Chick growth may be limited by essential nutrients that naturally are scarce in the diet (Ricklefs et al. 1987). Developmental, physiological, or genetic limitations may play a role in causing tissue growth to be slow. Obviously, at some developmental point tissue growth can proceed no faster (Ricklefs 1968, 1979; Dunn 1980; Ricklefs et al. 1980). For example, Ricklefs (1979) suggested that constraints such as DNA and protein synthesis limit growth of the leg or pectoral muscles.

Environmental or ecological control of growth rate versus developmental control are not mutually exclusive hypotheses but represent extremes along a continuum. If growth most commonly is controlled by environmental factors, then the tissue-growth threshold value (i.e. where tissue grows no faster) should be high, allowing for maximal growth in years when food is abundant (Fig. 1A). If food quantity is the limiting parameter, tissue growth rate and mass gain should covary directly. However, if food quantity is a poor predictor of food quality, then rate of mass gain may not necessarily mirror tissue growth (Fig. 1B). Assuming that differences exist in annual food availability and parental foraging efficiency or preference, the quantity and quality of food available to chicks will vary among individuals, as well as among years. Thus, growth rates of individual chicks should reflect both environmental and parental quality and may be highly variable in years of abundant food. We predicted that if environmental variables are important in controlling growth: (1) tissue growth rate should be highly variable among individuals; (2) annual growth rate should be highly variable among years; (3) maximum growth rate should be reached only rarely; and (4) tissue growth rate and mass gain should not necessarily be correlated.

If seabird growth is limited by developmental constraints, then the tissue-growth thresh-

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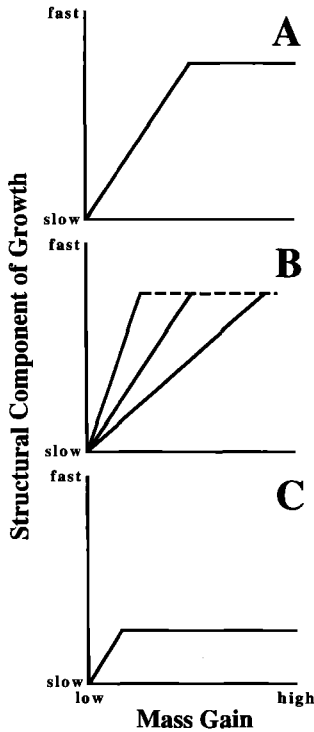


FIG. 1. Theoretical relationships between rate of tissue growth and mass gain in seabirds. (A) Growth rate primarily is environmentally controlled; only in years with abundant food will the threshold of tissue growth be reached. (B) Regardless of the point of tissue-growth maximization, the relationship between tissue growth and mass gain will be influenced by food quality. (C) Growth rate primarily is developmentally controlled; in most years the tissue-growth threshold will be reached, and tissue growth and mass gain will be independent.

old value should be relatively low (Fig. 1C). That is, in most years food and/or nutrient supplies should exceed the processing ability of the chick such that tissue growth rate will be maximized. Birds limited by developmental constraints should always grow at about the same rate; only the most food-deprived individuals should grow more slowly. Thus, the amount of variation in chick growth within and among years should be small. In "normal" to better years, tissue growth would remain fixed at a constant (i.e. maximum) level, but mass gain would increase when chicks shunted extra intake into lipid accumulation (Fig. 1C). In exceptionally poor food years (i.e. growth rates below the threshold), tissue growth and mass gain would be correlated, variance in growth

rate would largely reflect parental foraging ability, and environmental regulation would be indistinguishable from developmental regulation. We predicted that if developmental constraints mainly control growth there would be: (1) less variation in tissue growth rate among individuals; (2) little variation in tissue growth rate among years; and (3) in most years, mass gain would be independent of tissue growth rate.

We examined the degree to which growth of Fork-tailed Storm-Petrels (*Oceanodroma furcata*) is controlled environmentally versus developmentally by comparing mass gain and wing growth in known-age chicks on East Amatuli Island, Alaska, from 1980 to 1982 and again from 1990 to 1993. Wing growth reflects the structural component of growth, whereas mass gain includes a storage component (i.e. fat). We compared variability in growth parameters among individuals within a single season, among seasons, and, to a limited extent, between decades.

METHODS

Study area.—Located at the mouth of Cook Inlet, the Barren Islands (58°55'N, 120°10'W) are part of the Alaska National Maritime Wildlife Refuge system and are uninhabited. The archipelago supports 15 species of seabirds, including storm-petrels, cormorants, gulls, kittiwakes, and a variety of alcids (Bailey 1976). Fork-tailed Storm-Petrels are the most abundant seabird in the archipelago, with an estimated 300,000 birds found principally on East Amatuli Island (Bailey 1976).

Fork-tailed Storm-Petrels arrive on the island in March or April, and eggs usually are laid from May to June. Incubation length is variable, lasting 36 to 70 days (Boersma et al. 1980). Incubation stints are two to five days, and parents often neglect their eggs for several days (Boersma and Wheelwright 1979, Boersma et al. 1980, Boersma 1982). At hatching, chicks are brooded for an average of 5.3 days, at which time they attain thermal independence (Wheelwright and Boersma 1979, Boersma et al. 1980). Chicks remain in the burrow until fledging, when their wings and tail feathers have reached adult size and their body mass is below a critical threshold that allows them to fly.

Monitoring protocol.—Storm-petrel chicks from permanently staked and numbered burrows on East Amatuli Island were weighed and measured through each breeding season. We followed the timing and progression of breeding from before a chick hatched until a chick died or fledged, or we left the island.

Burrows were checked every three days. After hatching, chicks were removed from burrows only after adults were absent, usually two to five days after hatching. Chicks were aged by classifying feather tracts on the back from youngest to oldest (small dots, large dots, lines), color of back skin (red, pink, white/gray), and tarsus color (white to gray) relative to the amount of time the chick had been brooded as well as the number and persistence of stars and/or pips on the egg (Boersma unpubl. data). Hatching day was considered age zero. Field tests of these criteria (i.e. blind tests on chicks of known age) showed that we could accurately estimate age to ± 1 day. We measured chick mass (± 1 g with a Pesola scale) and wing chord length (± 1 mm with Vernier calipers) on every visit. Wing chord was defined as the distance, on an unstretched wing, from the carpal joint to end of the bone, down, shaft, and/or feather as they appeared during chick growth. Additional measures of structural growth such as tarsus and bill length were taken in the field but dropped from the final analysis because the additional amount of variation in growth explained was less than 10% (Boersma unpubl. data). If chicks died or disappeared, death was assumed to have occurred on the date the burrow was last checked (confirmed death) or the date the burrow was found empty (disappearance).

Data management and analysis.—Growth parameters were calculated only for chicks that fledged or were healthy (operationally defined as >80 g; average adult mass is 56 g; Boersma unpubl. data) at the end of the field season. Wing chord measurements were transformed into growth rates following Ricklefs' (1967) logistic formula and presented as the time, in days, it took for the chick to grow from 10% (ca. birth) to 90% of adult wing chord (i.e. $WC-T_{10-90}$), where adult wing chord was set at 162 mm. Wing chord growth was only calculated for chicks that lived to 40 or more days old and had a wing chord >90 mm by the last sampling date. Below this age and size, logistic curves fitted to the data did not accurately reflect wing growth and consistently overestimated time to 90% of adult wing chord (as assessed by performing logistic regressions on truncated measurements of older chicks).

Because Fork-tailed Storm-Petrel chicks characteristically gain and then lose mass before fledging (Boersma et al. 1980), it is harder to fit mass data to a standard growth equation. Therefore, we extracted several relevant variables out of the mass data. First, we smoothed the raw data with a three-point running average to reduce the effect of variation in the time lag between when the chick was last fed and when we weighed it. For chicks that reached ≥ 60 g and had been measured ≥ 5 times, we calculated the maximum instantaneous rate (g/day) at which chicks gained mass (i.e. $WT-IGR_{max}$). Smoothed data were fit by least squares to a Type III functional response logistic approximator; $WT-IGR_{max}$ is the slope

calculated at the inflection point. Graphically, this can be visualized as a line tangent to the steepest point in the mass curve. Because maximal mass gain is not sustained, we also calculated the time in days for each chick to reach 80 g directly from the smoothed mass curves (i.e. $WT-T_{80}$). Finally, we calculated a proportional estimate of body mass, the fatness index (FI), directly from the raw mass data. We defined FI as the number of days the chick weighed 80 g or more divided by the total number of days the chick was visited after it first reached 80 g. For instance, if a chick was weighed eight times after reaching 80 g, and weighed >80 g on six of our visits, FI would be 0.75. Only chicks that were weighed at least four times after reaching 80g were used in the FI calculation. Chicks that reached 80 g and never dropped below that threshold were analyzed separately to minimize non-normality. FI ($<100\%$) was arcsine square-root transformed to correct for non-normality.

In all years, our field seasons ended before the majority of the chicks had fledged, and often before they had attained maximum mass. Therefore, we were unable to reliably calculate maximum mass for most of the chicks. However, for each year we calculated all growth parameters (i.e. both wing and mass) from annual curves where each point represented the mean value of all chicks at a given age (in days) that eventually fledged. Therefore, for the yearly mass curves, we were able to calculate a theoretical maximum mass by fitting the curve to a quadratic equation [$Mass = A + B(age) + C(age)^2$] and then solving for Y_{max} (i.e. WT_{max}).

RESULTS

Hatching-date effects.—Mean hatching date varied significantly among years (one-way ANOVA, $F = 433.65$, $df = 6$ and 293 , $P < 0.001$; Fig. 2, Table 1). In 1991 and 1993, mean hatching dates were more than 20 days later than in 1980 and 1981. Because average chick growth may vary seasonally, we divided chicks into quartiles by hatching date within year, and examined the effect of hatching date on $WC-T_{10-90}$, $WT-IGR_{max}$, and $WT-T_{80}$. For these analyses, the middle two quartiles were combined, (i.e. early, middle, and late treatment levels). During the 1980s wing growth in earlier-hatching chicks was significantly faster than in later-hatching chicks (1980: $F = 21.41$, $df = 2$ and 57 , $P < 0.001$; 1981: $F = 13.95$, $df = 2$ and 92 , $P < 0.001$; 1982: insufficient sample sizes). Mass gain showed no such seasonal pattern. In the 1990s, earlier-hatching chicks took significantly longer to reach 80 g relative to later-hatching

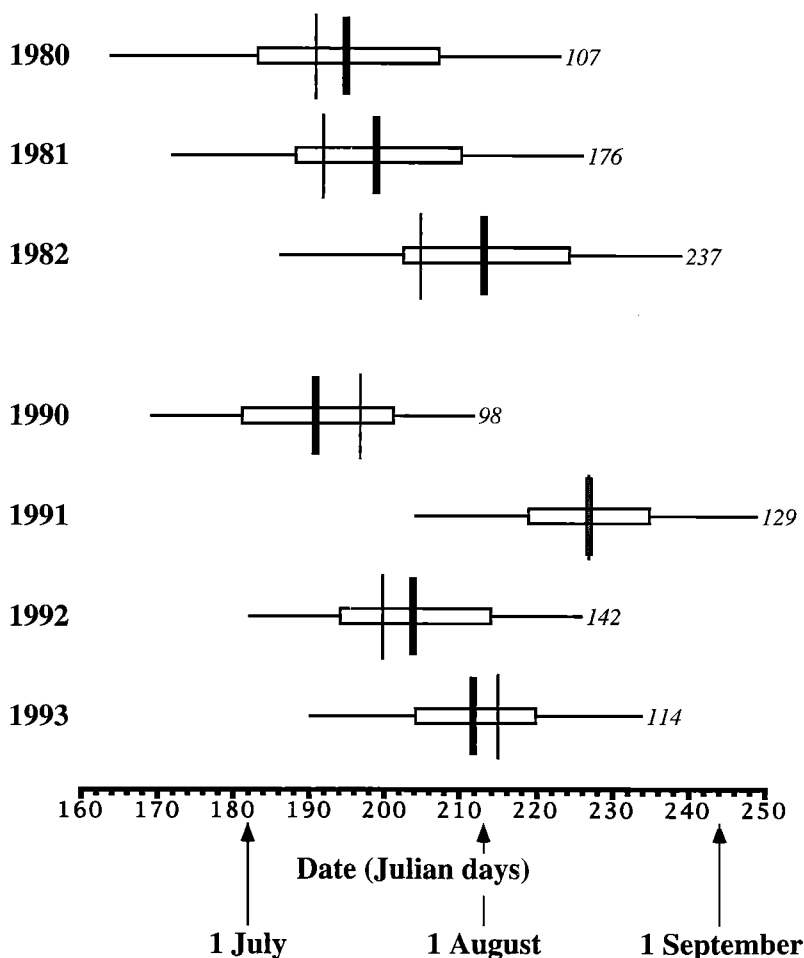


FIG. 2. Annual hatching dates of Fork-tailed Storm-Petrel chicks on the Barren Islands, Alaska. Vertical lines are means, shaded vertical lines are medians, boxes are standard deviations, and whiskers are ranges. Sample sizes are in italics to the right of each whisker.

TABLE 1. *A posteriori* contrasts among years in hatching date, wing chord growth rate ($WC-T_{10-90}$), instantaneous mass gain ($WT-IGR_{max}$), and time to reach 80 g ($WT-T_{80}$) for Fork-tailed Storm-Petrel chicks. Statistics based on chicks hatched in the middle two quartiles (see Methods). Within columns, different letters denote significant differences at $P < 0.05$.

Year	Hatching			
	date	$WC-T_{10-90}$	$WT-IGR_{max}$	$WT-T_{80}$
1980	A	A	B	B, C
1981	A	A, B	A	B, C
1982	C	B	B	A
1990	B	E	C, D	B
1991	E	C, D	B	—
1992	B	D, E	D	C
1993	D	B, C	C	A, B

chicks (1990: $F = 8.52$, $df = 2$ and 12 , $P = 0.005$; 1992: $F = 2.30$, $df = 2$ and 33 , $P = 0.116$; 1993: $F = 9.28$, $df = 2$ and 21 , $P = 0.001$; 1991: insufficient sample sizes), and wing growth showed no seasonal pattern. Because the interaction between hatching date and growth varied among years, we conducted the remainder of the analysis on chicks that hatched in the middle of the season (i.e. quartiles two and three based on hatching date) to minimize the effect of hatching date on our data.

Chick-specific growth.—All individual-specific measures of growth ($WC-T_{10-90}$, $WT-IGR_{max}$, and $WT-T_{80}$) varied significantly among years ($F = 26.64$, $df = 6$ and 207 , $P < 0.001$; $F = 34.92$, $df = 6$ and 256 , $P < 0.001$; $F = 5.35$, $df = 6$ and

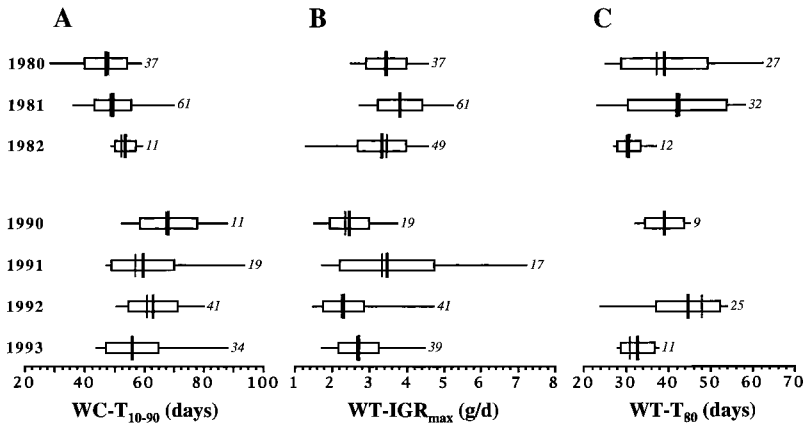


FIG. 3. Annual growth parameters for Fork-tailed Storm-Petrel chicks born in the middle two quartiles (see text) on the Barren Islands, Alaska. (A) Wing chord growth rate, expressed as the time needed to reach 90% of adult wing chord (162 mm) from birth; (B) maximum instantaneous mass gain (see text for details of calculation); and (C) time to reach 80 g. Components as in Figure 2.

110, $P < 0.001$, respectively; Figs. 3A–C, Table 1). In general, chicks grew faster in the 1980s relative to the 1990s. In 1980, chicks reached 90% of wing chord in an average of 46.6 days and gained mass at a maximum rate of 3.4 g/day. By contrast, in 1990 chicks did not reach 90% of wing chord until 68.1 days, almost half again as long, and maximal mass gain was only 2.5 g/day.

In three of seven years, $WT-IGR_{max}$ was a good predictor of $WC-T_{10-90}$ (Table 2, Fig. 4), although it never explained more than 30% of the variation. Apparently, other factors influenced tissue growth and mass gain. Figure 4 depicts the yearly fit between these two growth parameters, where data from each year are represented by an ellipse drawn to estimate an 80% confidence region on the sample (Wilkinson 1989). The slope of the major axis is indicative

of the predictive value of the relationship, and shape and size of the ellipse indicate variance within years (sample sizes as in Table 2). Because $WC-T_{10-90}$ is expressed in days, a low value indicates fast growth; therefore, we inverted the axis as in Figure 1. The relationship between $WC-T_{10-90}$ and $WT-IGR_{max}$ was strongest in the 1990s (Table 2, Fig. 4). Years in which $WT-IGR_{max}$ was not a significant predictor of $WC-T_{10-90}$ tended to have higher average wing chord growth (e.g. 1980 and 1982), suggesting that chicks had reached a tissue-growth threshold.

$WC-T_{10-90}$ and $WT-IGR_{max}$ were not significantly related to how much mass chicks gained (WT_{max}), how many days it took to reach 80 g (WT_{80}), or what percentage of the time chicks reaching 80 g stayed above that mass (FI). Chicks reached 80 g fastest in 1982 and 1993 and slowest in 1981 and 1992 (Fig. 3C; 1991 excluded because of low sample size). However, the chick population exceeded 90 g only in 1991 and 1993 (Table 3), years in which $WC-T_{10-90}$ and $WT-IGR_{max}$ were intermediate (Figs. 3A, B). FI varied from 46.6% in 1981 to 57.7% in 1982, both years in which $WC-T_{10-90}$ and $WT-IGR_{max}$ were high (Figs. 3A, B). Taken together, these data suggest that mass gain is a complex process not easily quantified by a single parameter, and that the absolute amount of mass gained is not necessarily related to the rate of gain.

Decadal patterns.—Our growth-rate data in-

TABLE 2. Mass gain as a predictor of wing growth, by year, in Fork-tailed Storm-Petrel chicks. Sample sizes are number of chicks for which we had measures of wing chord growth and instantaneous mass gain.

Year	<i>n</i>	β_1	<i>t</i>	<i>P</i>	R^2
1980	37	-1.04	-0.47	0.642	0.000
1981	61	-5.33	-4.58	0.000	0.250
1982	11	-3.59	-1.62	0.140	0.139
1990	10	-10.15	-2.22	0.058	0.303
1991	11	-3.89	-1.43	0.187	0.094
1992	40	-8.24	-3.98	0.000	0.275
1993	33	-6.28	-2.38	0.023	0.128

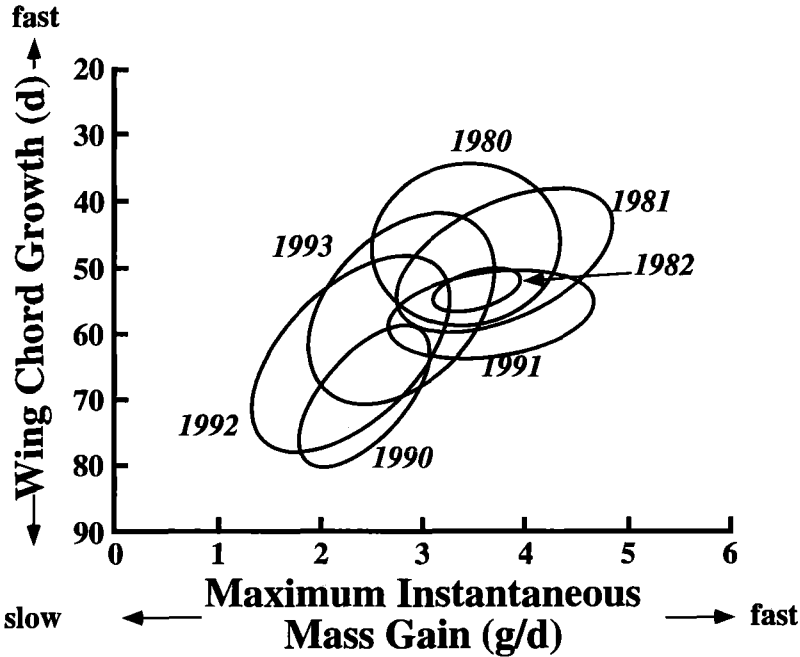


FIG. 4. Fork-tailed Storm-Petrel chick wing chord growth rate ($WC-T_{10-90}$) as a function of maximum instantaneous mass gain ($WT-IGR_{max}$) for each year. Note that the Y-axis has been inverted to follow the presentation in Figure 1. Each ellipse is centered on the mean value for that year and estimates an 80% confidence region on the sample (Wilkinson 1989). For normally distributed data, this would mean that 80% of the data points would fall within the ellipse.

dicating a possible change in the pattern of growth between the early (1980 to 1982) and late (1990 to 1993) years (Figs. 3 and 4). The 1980s were characterized by faster growth, although not necessarily fatter chicks, whereas the 1990s were characterized by slower, more variable growth (cf. 1990 and 1993). Other data collected prior to the chick period corroborate

this difference (Fig. 5). Burrow occupancy and hatching success were higher in the 1980s (burrow occupancy: $\chi^2 = 591.4, v = 6, P < 0.001$; hatching success: $\chi^2 = 177.1, v = 6, P < 0.001$; Fig. 5). Mortality of chicks less than 20 days old was lower ($\chi^2 = 72.4, v = 6, P < 0.001$; Fig. 5). The latter measure is sensitive to parental ability and foraging efficiency, because young chicks (<20 days old) have limited storage capacity and need to be fed on a more regular basis. Combined with an increase in chick mortality, the decline in burrow use and hatching success suggests a directional and long-term change in food availability for Fork-Tailed Storm-Petrels in the northern Gulf of Alaska.

TABLE 3. Mass parameters for Fork-tailed Storm-Petrel chicks using all known age-specific mass data for surviving chicks that hatched in the middle two quartiles (see Methods). Average adult mass in mid-June (before hatching) is about 56 g. Theoretical maximum mass (WT_{max}) within years calculated by fitting mass data to a quadratic equation and solving for Y_{max} .

Year	R ²	WT _{max}
1980	0.839	90.2
1981	0.797	79.2
1982	0.871	89.5
1990	0.583	79.6
1991	0.776	94.1
1992	0.730	83.0
1993	0.784	95.6

DISCUSSION

On the Barren Islands, growth of Fork-tailed Storm-Petrel chicks appears to be controlled largely by environmental factors. In contrast to the uniform growth rates exhibited by Leach's Storm-Petrels (Ricklefs et al. 1980, 1985, 1987) and British Storm-Petrels (Bolton 1995), wing

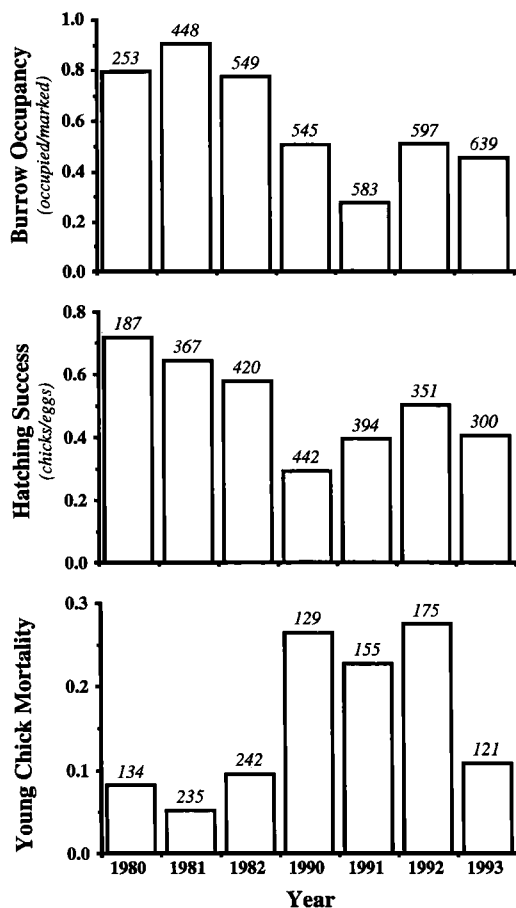


FIG. 5. Population-level parameters for Fork-tailed Storm-Petrels breeding on the Barren Islands, Alaska. % burrow occupancy (upper), % hatching success (middle), and mortality of young (<20 days of age) chicks (lower). Numbers above each bar are sample sizes (burrows, eggs, and chicks, respectively).

growth and mass gain in Fork-tailed Storm-Petrels fluctuated broadly among individuals and among years (Figs. 3 and 4). Ricklefs and Schew (1994) suggested that fat accumulation in storm-petrel chicks is an overfeeding response by the parents in an attempt to minimize undernourishment caused by environmental stochasticity. Chaurand and Weimerskirch (1994) found significant changes in mass gain of foraging Blue Petrel (*Halobaena caerulea*) parents, which they attributed to shifting resource availability within years. Our data suggest that changes in environmental quality, both within and among years, result in differential annual

growth rate of Fork-tailed Storm-Petrel chicks. In some years, chick growth was rapid (i.e. "good" years), suggesting that a tissue-growth threshold was reached. In most years, the range of mass gain was large, regardless of whether tissue growth was fast or slow. Finally, the rate at which chicks gained mass was not a good predictor of maximum mass, or of how long chicks remained above an 80-g threshold.

Several pieces of evidence suggest that chick growth is adjusted to resource availability. Average annual $WC-T_{10-90}$ varied by nearly 50% (a span of 30 days) among the seven years. For "poor" years, wing growth and mass gain were more strongly correlated, suggesting that environmental conditions limited growth; in "good" years, the correlation between wing growth and mass gain was weaker (Fig. 4, Table 2). The average range of wing chord growth rates was 37 days (SD = 9.6, $n = 7$), suggesting broad differences in parental foraging ability and consequent adjustment in chick growth rate. Such a wide range in growth rates indicates that chicks responded to environmental variability, at least up to some threshold value.

Using a partially overlapping data set, Boersma (1986) found a significant relationship between variability in food load and wing growth, indicating that chicks can respond to short-term changes in food availability. Chicks that received bigger but less frequent meals grew faster than those that got smaller but more regular meals (Boersma 1986). Our other measures of growth, which addressed chick fatness, were not correlated with either wing chord growth rate or mass gain. Chicks do not necessarily get fat in years when they grow rapidly (e.g. 1981). Although they may get fat in a year of slow mass gain (e.g. 1993), they don't always do so (e.g. 1990). Ainley et al. (1990) found a similar pattern for Ashy Storm-Petrel (*Oceanodroma homochroa*) chicks on the Farallon Islands: in years when chicks had lower growth rates they also had higher maximum masses.

The range of mass increase and fat accumulation (assessed indirectly as WT_{max} and FI), and the lack of a relationship between these variables and wing chord growth, suggest that changes in food quantity alone are not a sufficient explanation for variability in chick growth. Food quality also could have a significant influence on the tissue growth-mass gain

relationship, where quality can be thought of as the ratio of protein to lipid in the chick diet. In years when maximal protein is delivered, tissue growth rate should be high (given enough energy to process the food), but chicks would not necessarily put on extra mass unless the amount of food exceeded the chick's processing capabilities. In years when minimal protein is delivered, chicks still may gain mass if the food is high in fat. In essence, this mirrors Ricklefs' (1979) energy-sink hypothesis. Thus, truly "good" years are those in which food quantity and quality are maximized, and in which the ceiling of maximum wing chord growth is approached. "Bad" years are those in which food quality is poor and food quantity is low. Intermediate years may describe an inversely related range in quantity versus quality. Differences in the decadal pattern of growth may be explained by changes in food quality. A rigorous assessment of Fork-tailed Storm-Petrel diet, as well as some indication of prey availability, would be needed over several years to determine whether fluctuations in food quantity and quality are responsible for the patterns in chick growth that we observed.

Our data indicate that changes in food availability (whether quantity or quality) may have happened between the early 1980s and the early 1990s. On a regional scale, the northern Gulf of Alaska (55°N and above) experiences 15-to-20-year reversals in sea surface temperatures spanning approximately 3°C (Royer 1989, 1993). This cycle started in the mid-1970s, gradually warming the Gulf of Alaska waters through 1989 (Royer 1989). Alternating cycles of warm and cool water have been correlated with the recruitment of groundfish stocks in the North Pacific, where cold water equaled high recruitment (Hollowed and Wooster 1991). Changes in how rapidly chicks grew in the 1980s compared with the 1990s, and reversal in growth patterns with early chicks growing faster in the 1980s and slower in the 1990s, suggest that prey composition and/or availability also changed between decades. Whether these subtle, long-term changes in the physical oceanography of the system are responsible for the apparent patterns of Fork-tailed Storm-Petrel chick growth through the obvious mechanism of changes in food supply is unknown. However, evidence suggests that seabird diet and forage fish availability has changed sub-

stantially over the last several decades. Piatt and Anderson (1996) found changes in mid-water species composition and abundance, seabird diet, seabird population size, and the frequency of seabird wrecks—all of which indicated that conditions were better for seabirds in the late 1970s to early 1980s than a decade later.

High-latitude environments may have warmed several degrees over the last decade (Keeling et al. 1996), suggesting that large-scale climatic change is an important causal agent in changes in marine productivity. Moreover, climatic variation has been more common in the last 20 years than in previous decades as indicated by the increased frequency of El Niño-Southern Oscillation events (Trenberth and Hoar 1996). Evidence from a well-studied system indicates that climate, phytoplankton, zooplankton, fish, and productivity of birds are tightly correlated (Aebischer et al. 1992). Our data suggest that Fork-tailed Storm-Petrels are well suited to changes in the marine environment and thus are reflectors of climatic changes in the northern Gulf of Alaska.

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