Growth, fledging success and post-fledging survival of juvenile Oystercatchers *Haematopus ostralegus*

MARCEL KERSTEN[1] & ALEX BRENNINKMEIJER[1,2]

[1] *Zoological Laboratory, University of Groningen, Postbox 14, 9750 AA Haren, The Netherlands*
[2] *Institute for Forestry and Nature Research, Postbox 23, 6700 AA Wageningen, The Netherlands*

We studied the consequences of differences in growth rate on the subsequent survival of Oystercatcher *Haematopus ostralegus* chicks. Fledging success increased sharply with growth rate, from zero in chicks growing at less than 6 g per day to about 85% in chicks growing at more than 10 g per day. The age at which chicks fledged varied from 27 to 52 days. Chicks which fledged at an early age displayed a much faster growth rate than later fledging chicks. Although slow growth resulted in a considerable prolongation of the period before fledging, slow-growing chicks fledged at a smaller size and with a lower body-weight than fast-growing chicks. After fledging, all chicks remained almost completely dependent on their parents up to an age of 3 months and often longer.

Almost 40% of the fledglings eventually returned to the breeding area. This figure probably reflects post-fledging survival. Age and size at fledging had no effect on a chick's probability of return. Body-weight at fledging had a small positive correlation with the return probability, but this was not statistically significant. We conclude that although slow growth severely reduces a chick's chance of fledging, it probably does not result in irreversible damage causing an increased risk of mortality during the first years after fledging. Apparently, any possible disadvantage associated with small size or low body-weight could be compensated for after fledging.

Unlike most other shorebird species, Oystercatcher *Haematopus ostralegus* chicks rely entirely on their parents for food (Dircksen 1932, Lind 1965). Hence, the chick's growth rate is under control of the parents and depends critically on the amount of food they deliver. Since starvation was identified as the main source of mortality, especially among older chicks in the population under study (Ens *et al.* 1992), many parents apparently failed to meet the minimal food requirements of their offspring. Such a failure was observed exclusively in pairs occupying 'leapfrog territories', where the nesting and feeding areas were separated and food for the chicks had to be transported over a distance of several hundred metres. Chick starvation could not be demonstrated in pairs occupying 'resident territories', where the chicks were able to follow their parents onto the feeding area (Ens *et al.* 1992).

Starvation is the ultimate result when food provisioning falls short of the minimum requirements. Chicks which suffer from more moderate reductions in food supply, which do not directly result in their death, will undoubtedly grow at a reduced rate. This paper deals with the consequences of slow growth. We have investigated how growth rate affects (1) fledging success, (2) the duration of the period until fledging and (3) the size of the fledglings. We analyse which fledglings survived and later returned to the breeding area and address the question whether slow growth in early life has any long-lasting effect on the bird's fitness.

METHODS

The study was conducted between 1985 and 1991 on a saltmarsh on the island of Schiermonnikoog (53°26′N, 6°13′E) in the Dutch Wadden Sea. The vegetation in the grazed area consisted mainly of *Puccinellia maritima, Festuca rubra, Suaeda maritima* and *Artemisia maritima*. Starting in 1983, adult Oystercatchers were captured while incubating and marked with a unique combination of colour rings. From 1986 onwards, all birds breeding in the 13-ha study area could be identified individually with the use of a telescope.

From late April until the end of July, the study area was thoroughly searched for new nests approximately every 4 days. Since virtually all nests were discovered before clutch completion and incubation lasts, on average, 27 days after the last egg is laid, we were able to forecast the hatching date of each clutch. The nidifugous chicks were marked at hatching with rhodamine or picric acid on the white underparts to allow easy identification in the field and to ensure that the age of each chick was known with an accuracy of 1 day. At least once a week, from two observation towers on the edge of the marsh, we checked which chicks were still alive. During these sessions we also attempted to recapture as many chicks as possible. To this end, the observers in the towers had radio contact with people in the field and guided them to the sites where chicks were hiding. Recaptured chicks were weighed to the nearest gram. We

Table 1. *Biomass (mg ash-free dry weight) of prey species taken by Oystercatchers*

Size class[a]	Large bivalves[b]	Macoma balthica	Nereis diversi-color	Arenicola marina
1	29	29	10	20
2	49	49	20	40
3	68	68	35	144
4	85	85	67	244
5	149	117	111	350
6	282	—[c]	167	517
7	536	—	236	690
8	1016	—	319	900
9	1926	—	415	1200

[a] Size classes are arbitrary units for molluscs (see Methods); in worms, two times the size class gives length (cm) except for *Arenicola* where size classes 1 and 2 refer to broken off tails.
[b] Includes *Mytilus edulis, Cerastoderma edule, Mya arenaria.*
[c] Did not occur.

Figure 1. Survival of Oystercatcher chicks from hatching ($n = 548$) until fledging (left-hand axis, logarithmic scale). The shaded area shows the frequency distribution of age at fledging (right-hand axis). The daily survival rate increased from 0.9335 per day over the first 12 days to 0.9765 per day among chicks that were older than 21 days.

also measured lengths of leg (tarsus plus toe) and wing to the nearest millimetre, as well as bill-length (exposed culmen) and length of head plus bill to the nearest 0.1 mm. Just before fledging, chicks were colour ringed. Fledging date was defined as the first day when wing-length exceeded 180 mm. Chicks with such a wing-length were able to fly at least 100 m and accompanied their parents to better feeding areas outside the breeding territory farther downshore.

Measurements of the time budget and food intake of chicks during low water were conducted by continuous observation from the observation towers using telescopes. During high tides, both adults and chicks were inactive almost all of the time and did not feed. The chick's behaviour was classified into one of the following categories: (1) being brooded by one of the parents, (2) inactive, usually in a sheltered spot, (3) preening, (4) aggression, (5) following parent and begging for food, (6) feeding on its own and (7) handling food items. Food items were easily identified as either marine worms, mainly *Nereis diversicolor* and a few *Arenicola marina*, or bivalve molluscs, mainly *Macoma balthica* and some *Mytilus edulis* and *Cerastoderma edule.* In the case of worms, prey size was scored in 2-cm classes with reference to the bill-length of adult birds (on average 7 cm in males and 8 cm in females; Hulscher 1985). In the case of bivalves, the shells were always opened and only the flesh was ingested. The size of flesh particles was scored in arbitrary size classes from 1 to 9, where size class 4 referred to a flesh particle roughly the size of the colour ring. All data on activity and food intake were stored in an event recorder and transferred later to a personal computer for subsequent analysis. Prey size was translated into biomass (ash-free dry weight) using the conversions given in Table 1. Independent checks demonstrated the reliability of this procedure.
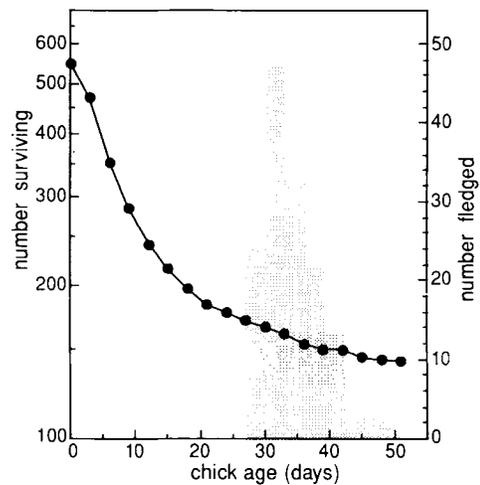
Fledglings which returned to the study area were identi-

fied from their colour rings. Each year, several thousand ring readings were obtained from the observation towers on the edge of the marsh and from a large tower on 5 m of scaffolding on the mudflats about 400 m downshore. Most of these observations were of adult birds, but occasionally a young bird, previously reared in the study area, was discovered. In the course of the study, it became apparent that returning juveniles were most likely to be encountered in the flocks of non-breeding birds in the immediate vicinity of the study area, and from 1988 onwards we devoted special attention to these flocks. In order to avoid inflation of the data due to incorrect readings, we accepted a bird as having survived and returned only if at least two independent observations of this bird were available in the same year.

RESULTS

Chick growth and fledging success

Fledging success was low; on average only one out of four hatchlings fledged successfully. Mortality was highest among young chicks (Fig. 1). Only 44% of 548 chicks survived until they were 12 days old. Older chicks survived better; 77% of 184 chicks that were still alive at an age of 21 days fledged.

There was considerable variation in the age at which chicks actually fledged, ranging from 27 to 51 days (Fig. 1). Chicks which fledged at an early age grew much faster than did later fledging chicks. This was true not only for body-weight but also for wing-length, leg-length and head-length (Fig. 2). Except for the day of hatching, chicks which fledged within 31 days were always significantly heavier and larger than chicks which took more than 38 days to fledge (Student
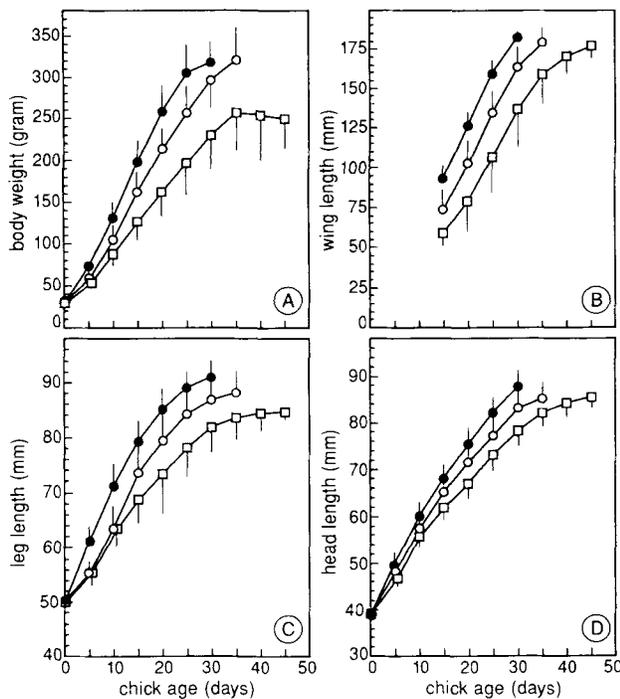
Figure 2. Increase of (A) body-weight, (B) wing-length, (C) leg-length and (D) head-length (head + bill) with age in juvenile Oystercatchers. Chicks were separated into three categories according to fledging age: dots, 27–30 days (n = 33); open circles, 31–37 days (n = 54); open squares, 38–53 days (n = 18). Vertical bars represent one s.d.

Figure 3. The probability of fledging of Oystercatcher chicks in relation to their growth rate between 5 and 25 days of age (dots, left-hand axis, curve fitted by eye). The shaded area shows the frequency distribution of growth rates (right-hand axis).

t-tests, $P < 0.05$ in all cases). Body-weight and structural dimensions of chicks which fledged at 31–38 days of age always were intermediate to those in the extreme categories.

Beintema and Visser (1989) suggested that structural dimensions may be used to estimate the age of a chick and presented nomograms to estimate age from bill-length in Lapwing *Vanellus vanellus*, Redshank *Tringa totanus* and Black-tailed Godwit *Limosa limosa*. The large variation in structural dimensions at any age, illustrated in Figure 2, clearly shows that such an age estimate would be imprecise for the Oystercatcher. For instance, a head-length of 70 mm may belong to a 16-day-old chick which is growing fast, but the same head-length may also refer to a 23-day-old chick growing slowly.

In order to quantify the effect of growth on fledging success, we determined for as many chicks as possible the average rate of body-weight increase when they were between 5 and 25 days of age. During any 1 day, a chick's body-weight varied considerably, depending on whether it had just received food or not. These random variations in body-weight sometimes amounted to 10 g (M. Kersten & A. Brenninkmeijer, pers. obs.), which is of the same order of magnitude as the daily weight increase. To reduce the impact of these random variations on the estimated growth rate,
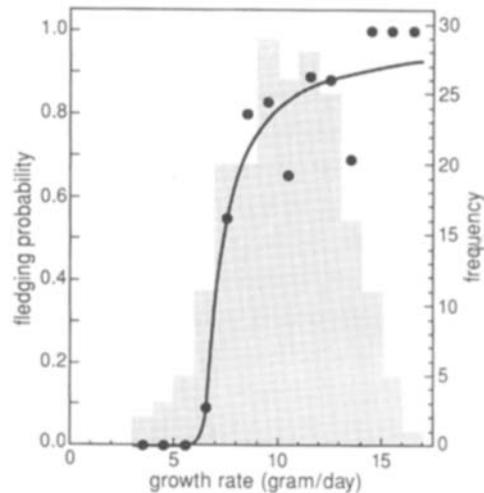
we decided to select those data where at least 10 days elapsed between the first and last measurements of body-weight. Consequently, all chicks which died before the age of 15 days had to be excluded from the analysis. The remaining data show that growth rate had a dramatic effect on a chick's chance to survive until fledging (Fig. 3). A growth rate of at least 6 g per day is the minimum requirement for even a minor chance to fledge successfully. Chick survival increased sharply to about 75% when the growth rate increased from 6 to 9 g per day.

The growth pattern of unsuccessful chicks shows that death was preceded by a period of declining body-weight (Fig. 4). This suggests that slow growth as such was not a direct cause of mortality. These chicks did not succumb while growing at a slow rate but at the end of a period of negative growth. Slow-growing chicks seem more likely to enter a period of negative energy balance. The time interval which elapsed between peak body-weight and death was surprisingly long (up to 15 days) and was positively correlated with the peak body-weight (Fig. 4, inset). If chicks are able to recover from a period of declining body-weight, heavy chicks have a selective advantage because they are able to survive a longer period of negative energy balance. Experimental supplementation of food to a starving chick showed that such a chick may indeed recover from a very low body-weight and eventually fledge (Fig. 4).

Prolongation of the pre-fledging period by slow-growing chicks compensated only partially for the reduced growth rate; final body-weight at fledging was significantly and negatively correlated with the age at fledging. Other, more structural, dimensions such as leg-length, bill-length and head-length were affected in the same way (Fig. 5). This resulted in slow-growing chicks fledging at an older age, with lower body-weight and at a smaller size.
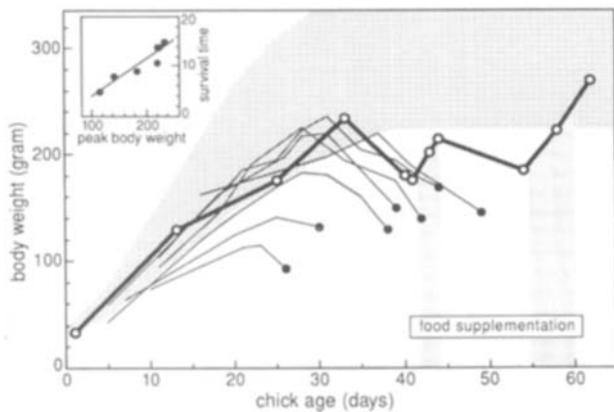
Figure 4. Growth of Oystercatcher chicks which died before fledging. Only those chicks for which at least four measurements of body-weight were available are shown. Large dots represent the last measured body-weight when still alive; all seven chicks died within 3 days after this measurement. The shaded area shows the range of body-weights of chicks which fledged successfully (from Fig. 2A). Also given is the body-weight of one chick which escaped from early death by experimental food supplementation (open circles). The inset shows that the time interval between peak body-weight and actual death increases with peak body-weight: y (days) = $0.075x$ (grams) $-$ 3.5 (r^2 = 0.90, P < 0.05).

Post-fledging survival

The chicks fledged throughout July and August but continued to be dependent on their parents for a considerable period of time. Even 2 months after fledging, the young spent most of their time following a parent and still received more than 90% of their food from the parents (Fig. 6). Although the rate of food provisioning by the parents declined over time, it was still twice as high as the intake rate from self-feeding 6 weeks after fledging. The frequency with which fledglings visited areas farther downshore, where feeding conditions presumably were better, increased with time. Since we were not able to measure food intake in these distant areas, it is impossible to determine when the fledglings became totally independent. Occasional observations of adult Oystercatchers still feeding fully grown fledglings in November indicated that this is a matter of months. This has also been reported by Norton-Griffith (1969), who mentioned nine pairs which were still feeding chicks that were 6 months old.

Most, if not all, fledglings left the island after they had become independent. Four birds which died during the first winter following fledging were recovered from areas to the southwest, along the North Sea coast as far as northwestern France. Five other birds were observed alive elsewhere in
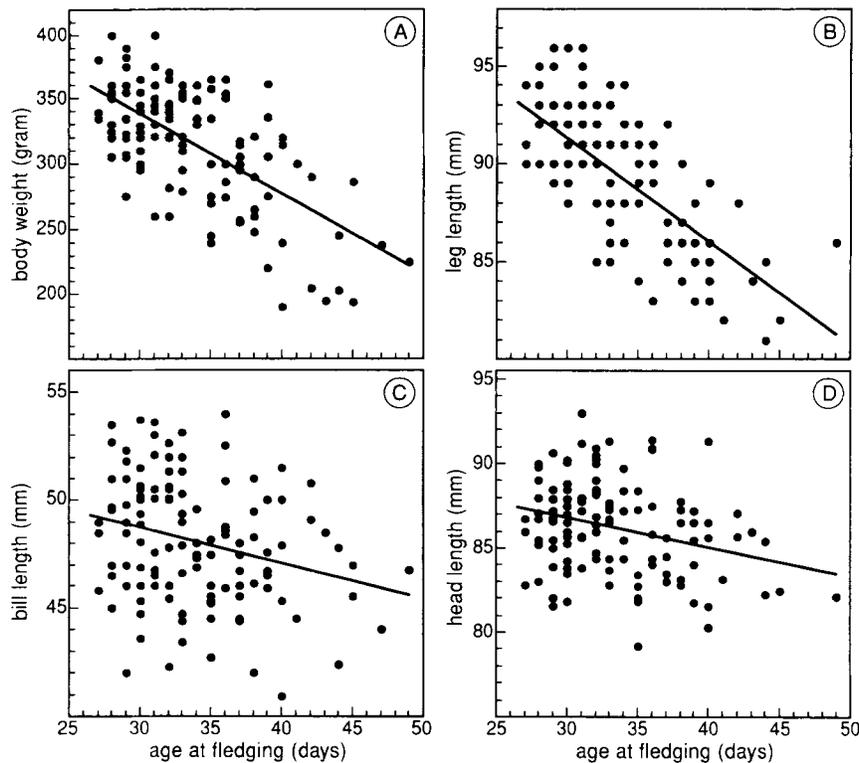

Figure 5. (A) Body-weight, (B) leg-length, (C) bill-length and (D) length of head + bill of Oystercatcher chicks at fledging in relation to the age at which they fledged. All four variables decreased significantly with age at fledging (body-weight, y = 519 $-$ 6.03x, r^2 = 0.39, P < 0.001; leg-length, y = 107.0 $-$ 0.525x, r^2 = 0.48, P < 0.001; bill-length, y = 53.5 $-$ 0.161x, r^2 = 0.07, P < 0.01; head-length, y = 92.0 $-$ 0.174x, r^2 = 0.08, P < 0.001; n = 123 in each case).
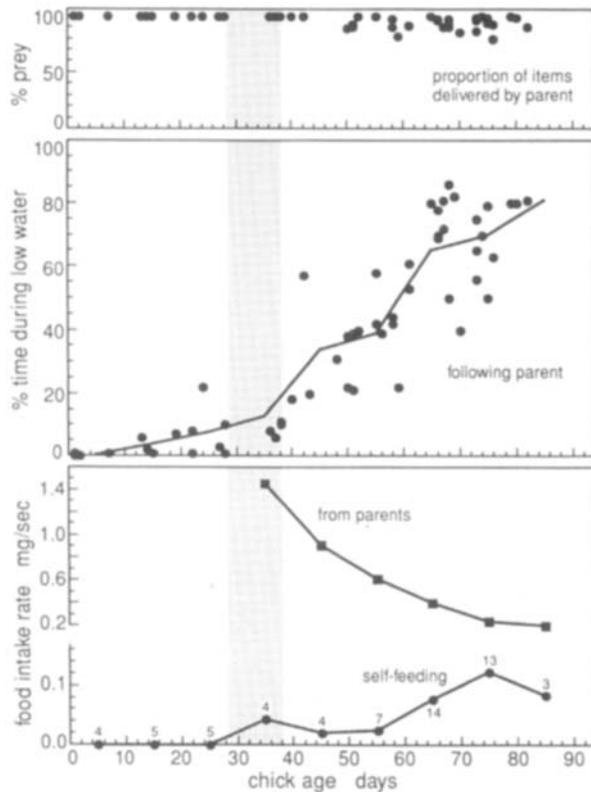
Figure 6. Dependency of Oystercatcher chicks on their parents before and after fledging. Data were collected on seven chicks from five different broods. Hatched area indicates the age at which these chicks fledged. (top) The proportion of prey items delivered by the parents; (centre) Proportion of time during a low water period which a chick spent following one of its parents; line connects average values per 10-day period; (bottom) Average intake rate (ash-free dry weight) per 10-day period while chicks fed for themselves (dots) or while they followed a parent (squares). Figures indicate the number of hours that chicks were observed in the territory. Each symbol is based on data of at least three different chicks except for the age-class 80–90 days when data were available for only two chicks. Note the different scales on the y-axis for 'self-feeding' and 'from parent'.

the Wadden Sea when 1 year old. A total of 46 out of 120 marked fledglings eventually returned to the study area; all but three did so before they were 3 years old (Table 2). The three exceptions were chicks born in 1985 and they may have escaped our observations in 1987, i.e. before we intensified the survey for marked birds in flocks of non-breeding birds. Therefore, we expect that all young birds which return to the study area do so before they are 3 years old.

Neither age (Table 3) nor date (Table 4) at which a chick fledged affected its probability to return to the study area. Similarly, fledgling weight had no significant effect on the probability to return (Table 5). Since the data suggested a slight tendency for heavy chicks to be more likely to return, we also calculated the logistic regression of the probability to return on fledgling weight (Fig. 7), but again the effect was not significant ($T = 1.30$, n.s.). Therefore, we conclude that fledgling weight had little or no effect on post-fledging survival. Birds which fledged with a very low body-weight (about 200 g) still had a fair chance to return to their natal area in later years. Leg-length, bill-length and head-length at the time of fledging had no effect on the probability to return (Kolmogorov-Smirnov tests, n.s. in each case).

Circumstantial evidence suggests that the number of fledglings that return to the study site provides a fairly accurate estimate of post-fledging survival. Five fledglings were observed alive elsewhere in the Wadden Sea when about 1 year old. Since all five birds subsequently returned to the study area, it seems unlikely that an appreciable proportion of young birds emigrate to other breeding areas.

DISCUSSION

Maximum growth rate

The fastest growing chicks in our study had a growth rate comparable with that of chicks raised in the laboratory with food ad libitum (average: 13.1 ± 1.8 g/day, n = 4; M. Klaassen, pers. obs.). In the African Black Oystercatcher Haematopus moquini, the fastest growth rate was 15.6 g per day (Hockey 1984). Adults of this species are slightly larger than European Oystercatchers, weighing on average 694 g (Hock-

Table 2. Number of Oystercatcher chicks that returned to the study area

Year of hatching	No. marked	Year first seen (no.)							Total returned	
		1986	1987	1988	1989	1990	1991	1992	n	%
1985	17	1	4	3[a]	0	0	0	0	8	47
1986	41	—	0	4	0	0	0	0	4	10
1987	19	—	—	6	4	0	0	0	10	53
1988	19	—	—	—	6	7	0	0	13	68
1989	24	—	—	—	—	6	5	0	11	46
Total	120	1	4	13	10	13	5	0	46	38

[a] These birds probably were missed in 1987 (see text).

Table 3. *The relation between age at fledging and post-fledging survival in Oystercatchers. Age had no effect on survival (D = 0.065, n.s., Kolmogorov-Smirnov test)*

Age at fledging (days)	Number marked	Number returned	Percentage returned
27–29	22	8	36%
30–32	38	18	47%
33–35	26	9	35%
36–38	19	6	32%
>38	12	4	33%

Table 5. *The relation between weight at fledging and post-fledging survival in Oystercatchers. Weight had no effect on survival (D = 0.115, P > 0.2, Kolmogorov-Smirnov test)*

Body weight at fledging (g)	Number marked	Number returned	Percentage returned
≤240	5	1	20%
241–270	9	1	11%
271–300	17	5	29%
301–330	33	17	52%
331–360	34	12	35%
>360	14	7	50%

ey 1981) compared with 530 g among the adult birds in our study. Maximum growth rate of the American Black Oystercatcher *Haematopus bachmani* is intermediate to that of the other two species; about 14 g per day (Webster 1942, Groves 1984). Presumably, these values represent the maximum growth rate which is delimited by physiological constraints.

Drent and Daan (1980) assembled data on the growth rate of altricial raptors and sub-precocial seabirds. Their predictive equation, $y = 0.202x^{0.74}$, where y is growth rate in g per day during the period of rapid weight gain and x is adult body-weight in grams, revealed that the growth rates of both raptors and seabirds were on average only 50% of that of passerines (Ricklefs 1968, 1976). Oystercatchers grow even more slowly. Compared with the Drent and Daan equation, the maximum growth rates of the African Black Oystercatcher (15.6 instead of 25.6 g/day) and the European Oystercatcher (13.1 instead of 21.4 g/day) are both only 61% of the predicted value. Other shorebird species were shown to have low growth rates as well (G.H. Visser, unpubl. PhD thesis, University of Utrecht), but a functional explanation for the phenomenon is not obvious.

According to Ricklefs (1973, 1979), slow growth is associated with a precocial mode of development, which he proposed might be due to the incompatibility of simultaneous growth and mature functioning of tissues. This explanation is attractive in the sense that it is entirely causal and does not require a functional counterpart; slow growth is the inevitable consequence of a precocial mode of development, and when a species cannot afford to grow slowly, precociality

Table 4. *The relation between date of fledging and post-fledging survival in Oystercatchers. Date had no effect on survival (D = 0.071, Kolmogorov-Smirnov test)*

Fledging date	Number marked	Number returned	Percentage returned
1–10 July	28	10	36%
11–20 July	41	14	34%
21–31 July	30	16	53%
1–10 August	11	1	9%
>10 August	8	3	38%

is not an available option. There is some evidence that growth and mature functioning are indeed negatively correlated (Ricklefs & Webb 1985, G.H. Visser, unpubl. PhD thesis, University of Utrecht). However, an essential requirement for this explanation to be correct is that the difference in growth rate is indeed due to altricial chicks having more proliferating, and consequently less mature functioning, tissue; a more active proliferating tissue in altricial chicks, where cell division proceeds at a faster rate, would not do the trick. Unfortunately, no one has quantified the amount of proliferating tissue in altricial and precocial chicks. Consequently, the correctness of Ricklefs's hypothesis remains speculative.

Flexibility of growth rate

The majority of the chicks in the field had a growth rate well below the maximum recorded. Fledging success of slow-growing chicks was reduced, but even some of the chicks with a 50% reduced growth rate eventually fledged successfully. This illustrates that growth in the Oystercatcher is remarkably flexible. Ricklefs's (1973) contention that "most species grow at some physiologically maximum rate" implicitly ignores that there is much environmentally induced, intraspecific variation in growth rate. Our data indicate that, although fast growth increases the probability of surviving until fledging, most Oystercatcher chicks grow at a reduced rate. The observed growth rate probably reflects merely the restricted availability of food rather than a species-specific growth strategy.

Intraspecific variation in growth rate is not restricted to Oystercatchers or other species with a (sub)precocial mode of development. Data presented in the literature for both passerines (Florida Scrub Jay *Aphelocoma coerulescens* [Woolfenden 1978], Carrion Crow *Corvus corone* [Richner 1989], Least Flycatcher *Empidonax minimus* [Briskie & Sealy 1989], Blackbird *Turdus merula* [Magrath 1991]) and non-passerines (Sparrowhawk *Accipiter nisus* [Newton 1986], Coot *Fulica atra* [Visser 1974], American Black Oystercatcher [Groves 1984], Sandwich Tern *Sterna sandvicensis* and Common Tern *Sterna hirundo* [Klaassen et al. 1992]) show considerable variation in growth rate. In all these studies, the extreme growth
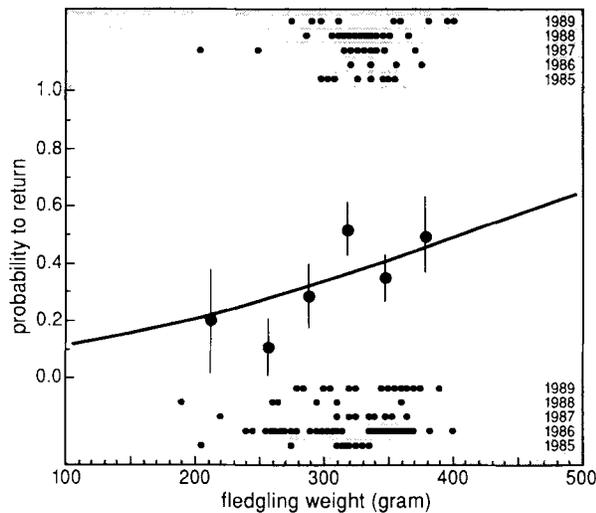
Figure 7. The probability of Oystercatcher fledglings returning to their natal area in relation to their body-weight at fledging. The dots show for each year the body-weights of fledglings that returned (top) and those that disappeared (bottom). The curve shows the relation for all years combined according to the logistic regression equation, $P = \exp(ax + b)/(1 + \exp[ax + b])$, where x is body-weight at fledging (g) and a and b are fitted parameters: $a = 0.0064502$, $b = -2.6220$. The increased return probability at higher fledging weight is not statistically significant ($T = 1.30$, n.s.). Large dots indicate the proportions returning per weight class as given in Table 5. Vertical bars denote one s.e. of the mean.

rates of successful fledglings differed by a factor of two or more.

There can be little doubt that differences in growth rate as observed in this study were the result of considerable variation in food consumption. Among Oystercatchers, the amount of food available to a chick is essentially under control of the parents, which have to provide all the food until well after fledging. It is also affected by the number of siblings in the brood which compete for the same food supply (Ens et al. 1992). The data presented in Figure 2 show that chicks which take a long time to fledge experience a reduced growth rate early in their lives. This indicates that they are subjected to a submaximal food supply at an early age, i.e. long before their requirements become maximal. Since slow-growing chicks fledge at a much lower body-weight than do fast-growing chicks, their maximum food requirements will also be reduced. From the point of view of the parents, this is clearly an advantage, as it reduces the amount of food that they have to deliver on any one day. From this perspective, it is possible that most variation in growth rate of young chicks reflects a parental strategy to adjust the forthcoming maximal energy requirements of the chicks to the maximal amount of food that they are able to deliver.

Post-fledging survival

Differences in growth rate resulted in completely different fledglings. At the time of fledging, slow-growing chicks were

older, lighter and smaller compared with fast-growing chicks (Fig. 5). However, these features had little, if any, effect on post-fledging survival. Similarly, fledgling weight did not affect subsequent survival in Sparrowhawks (Newton 1986), Florida Scrub Jays (Woolfenden 1978), Ipswich Sparrows Passerculus sandwichensis (Ross & McLaren 1982), Dark-eyed Juncos Junco hyemalis (Wolf et al. 1988) and Yellow-eyed Juncos Junco phaenotus (Sullivan 1989). On the other hand, several studies reported that nestlings with a relatively low body-weight were less likely to be recovered later (Perrins 1965, Dhondt 1971, Garnett 1981, Coulson & Porter 1985, Krementz et al. 1989, Smith et al. 1989, Tinbergen & Boerlijst 1990, Hochachka & Smith 1991, Magrath 1991). However, those studies which addressed the timing of juvenile mortality invariably showed that the dependence of survival on nestling weight disappeared not long after the young had become independent. Thus, survival from winter until breeding of juvenile Great Tits Parus major was not related to their body-weight as nestlings (Tinbergen & Boerlijst 1990). Nestling Song Sparrows Melospiza melodia with better nutritional condition were more likely to survive until independence, but recruitment into the breeding population was not related to nestling condition (Hochachka & Smith 1991). Differential mortality according to nestling weight of juvenile Blackbirds continued until 1 month after fledging; birds which survived this period had a random chance of breeding (Magrath 1991).

This indicates that slow growth does not necessarily result in irreversible damage. Apparently, any disadvantage associated with small size or low body-weight at the time of fledging can be compensated for during a later phase. Since fledglings of precocial species still have to grow considerably before they reach adult size (Beintema & Visser 1989), there is plenty of room for such compensatory growth. In Oystercatchers, for instance, fledgling weight ranged from about 200 to 400 g, which is well below the average weight of 495 g of first-year birds in early winter (Swennen & Duiven 1983). Compensatory growth has been documented in both birds and mammals (Wilson & Osbourn 1960). Among birds, this is not restricted to precocial species, as it has been observed also in Song Sparrows (Smith & Arcese 1988) and Tree Swallows Tachycineta bicolor (Wiggins 1990), although it is not always totally effective (Rofstad 1988, Cooch et al. 1991). An extreme case of compensatory growth has been reported in young Domestic Chickens Gallus domesticus. On a deficient diet, the chicks were maintained at a physiological age of 10 days for months. This had little subsequent effect on their final body size and egg production (McRoberts 1965).

The most important factor determining post-fledging survival of juvenile Oystercatchers is probably the weather conditions during their first winter. In most years, some 50% of the first-year birds survive and return to their natal area (Table 2) compared with an annual survival rate of 95% among adult birds (Hulscher 1989). In some years, however, severe winter weather causes mass mortality. This happened in January 1987 when a cold spell in northwestern Europe reduced adult survival in the study population to 74%

(Hulscher 1989). The effect on first-year birds was even more catastrophic: post-fledging survival of chicks born in 1986 was reduced to a mere 10% (Table 2).

Although age, weight and size at fledging did not affect post-fledging survival, it is still possible that light fledglings are at a disadvantage when it comes to recruitment into the breeding population. In Pied Flycatchers *Ficedula hypoleuca* and Carrion Crows, small birds were excluded from territory acquisition (Altalo & Lundberg 1986, Richner 1989). This also may hold true for the Oystercatcher. On the other hand, fledging weight of Razorbills *Alca torda* and Guillemots *Uria aalge* which returned to the breeding colony did not differ from that of chicks which did not (Lloyd 1979, Hedgren 1981, Harris *et al.* 1992). Unfortunately, we are not yet able to present comparable data since Oystercatchers do not commence breeding until they are several years old. On Skokholm, the modal age at first breeding was 5 years (Safriel *et al.* 1984). In our study population, the birds may start breeding at an even later age. Up to the breeding season of 1991, only 4 of the 46 marked fledglings which returned had managed to establish breeding territories for themselves. Although this sample is too small to allow a firm conclusion, these four were not all exceptionally fast-growing chicks. In addition, since Oystercatcher chicks continue to grow after fledging (see above), it is by no means sure that fledgling size is a good predictor of their final size as adults.

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