Natural selection by pulsed predation: survival of the thickest

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Abstract. Selective predation can lead to natural selection in prey populations and may alleviate competition among surviving individuals. The processes of selection and competition can have substantial effects on prey population dynamics, but are rarely studied simultaneously. Moreover, field studies of predator-induced short-term selection pressures on prey populations are scarce. Here we report measurements of density dependence in body composition in a bivalve prey (edible cockle, *Cerastoderma edule*) during bouts of intense predation by an avian predator (Red Knot, *Calidris canutus*). We measured densities, patchiness, morphology, and body composition (shell and flesh mass) of cockles in a quasi-experimental setting, i.e., before and after predation in three similar plots of 1 ha each, two of which experienced predation, and one of which remained unvisited in the course of the short study period and served as a reference. An individual's shell and flesh mass declined with cockle density (negative density dependence). Before predation, cockles were patchily distributed. After predation, during which densities were reduced by 78% (from 232 to 50 cockles/m^2), the patchiness was substantially reduced, i.e., the spatial distribution was homogenized. Red Knots selected juvenile cockles with an average length of 6.9 ± 1.0 mm (mean ± SD). Cockles surviving predation had heavier shells than before predation (an increase of 21.5 percentage points), but similar flesh masses. By contrast, in the reference plot shell mass did not differ statistically between initial and final sampling occasions, while flesh mass was larger (an increase of 13.2 percentage points). In this field study, we show that Red Knots imposed a strong selection pressure on cockles to grow fast with thick shells and little flesh mass, with selection gradients among the highest reported in the literature.

Key words: bivalves; competitive release; density dependence; directional selection; foraging; intertidal mudflats; natural selection; phenotypic selection; predator defense; selective predation; shorebirds; soft-sediment habitat.

INTRODUCTION

Predation is a key process in the ecology and population dynamics of prey (Vermeij 1987, Krebs and Davies 1997), and selective predation is an important agent of natural selection due to the removal of specific classes of prey (Endler 1986, Wade and Kalisz 1990), leading to the evolution of predator defense mechanisms (Caro 2005). Furthermore, when prey suffer from density-dependent processes, by thinning prey densities, predation can alleviate competition between surviving individuals (de Roos and Persson 2013). For instance, if individual growth is negatively density dependent, predation reduces competition and thus enhances the growth of surviving individuals. Predation can thus have a major influence on densities, patchiness, size structure, body composition, and potentially the reproductive

output of prey at the population level (Gurevitch et al. 2000, de Roos and Persson 2013).

Although predator–prey interactions have been studied for a long time (Verhulst 1838, Krebs and Davies 1997, Caro 2005), studies that quantify the short-term selection pressures by predators on prey populations are rare, especially in the wild (Endler 1986, Calsbeek and Cox 2010). Here, we report on natural predation by Red Knots *Calidris canutus* on edible cockles *Cerastoderma edule* burrowed at shallow depths in temperate intertidal mudflats without experimental artefacts resulting from predator exclosures. In fact, we utilized the spatial unpredictability in the occurrence of flocks of foraging Red Knots (Folmer et al. 2010) to provide us with predation plots as well a reference plot without predation.

We quantified densities, patchiness, and external morphology (shell length, width, and height), as well as body composition (shell and flesh mass) of cockles in their natural environment. We were able to quantify these variables before and after a two-week pulse of intense predation by Red Knots, as well as in a situation

PLATE 1. A group of foraging Red Knots (*Calidris canutus islandica*) on intertidal mudflats. Some of the birds have found edible cockles (*Cerastoderma edule*) that they are about to swallow whole. Photo credit: Jan van de Kam.

without predation; the latter served as a reference. The comparison of cockles between the predation and the reference plots enabled us to study effects of predators on their prey in this quasi-experimental natural setting. Note that we consider it a *quasi*-experiment because we did not control where the birds foraged. We will show that the cockles suffered from intraspecific competition (negative density dependence), and that Red Knots can have profound effects on the length distribution of cockles, as well as their density, patchiness, and body composition. We calculated selection gradients that were among the highest reported in the literature, and showed that Red Knots imposed strong selection on cockles to grow fast with thick shells and little flesh mass.

METHODS

Background

Red Knots (see Plate 1) are medium-sized shorebirds that during the nonbreeding season live in tidal areas (Piersma 2007, 2012). They are social and foraging groups of up to several thousand individuals are common (Piersma et al. 1993). Over short timescales (weeks) their foraging locations tend to be unpredictable, which is attributed to their strong social attraction (Folmer et al. 2010), mobility (van Gils et al. 2005b), and the large spatial extent of foraging opportunities (Kraan et al. 2009). Within each low-tide period, Red Knots fly

tens of kilometers across exposed mudflats in search of buried hard-shelled mollusks such as edible cockles (Piersma et al. 1993, van Gils et al. 2005b). Because they swallow their prey whole, Red Knots are limited to ingesting cockles smaller than 16 mm (Zwarts and Blomert 1992, Piersma et al. 1993) and constrained by the amount of shell material that they can process (van Gils et al. 2003a). Due to this digestive constraint, Red Knots maximize their energy intake rates by selecting individual cockles with large flesh mass compared to their shell mass (van Gils et al. 2005a).

Cockles are suspension-feeding bivalves that are commonly found in the Dutch Wadden Sea (Beukema et al. 1993). Their spatial distribution is widespread (Kraan et al. 2009), and they can be found in densities of up to several thousand individuals/m^2 (Jensen 1993). Cockle population size, as well as recruitment, greatly varies between years (Beukema et al. 1993). They spawn between May and August, leading to distinct year classes (Beukema et al. 2001). After a planktonic phase of several weeks, they settle on mudflats when they are ~0.3 mm long (e.g., De Montaudouin and Bachelet 1996). Cockles live in mudflats with inundation times ranging from 2 to 12 hours and sediment grain sizes ranging from 75 to 275 μm (Kraan et al. 2010). Nonetheless, cockles prefer mudflats with inundation times between 6 and 8 hours (Kraan et al. 2010). Due to

short siphons, they are limited in their burying depth and are found within a few centimeters of the surface (Zwarts and Wanink 1989). Living close to the surface and within reach of predators (e.g., Red Knots with their 4 cm long bills), cockles rely on predator defenses such as shell thickness (armor). Cockles can grow to a maximum of 50 mm, and generally don't live longer than 5 years (Beukema et al. 1993).

Study design

Our study site was located in the Dutch Wadden Sea on the tidal flats near the uninhabited islet of Griend (53°14.615′ N, 5°15.219′ E; Appendix: Fig. A1). Griend is surrounded by extensive intertidal mudflats that stretch for tens of kilometers. Near Griend, we selected three plots (plots A, B, and C) of 100×100 m each where Red Knots were previously seen foraging on cockles. All plots were visually identical, located at similar distances from Griend (590, 660, and 520 m for plots A, B, and C, respectively), and had similar inundation times (7.6, 7.7, and 6.7 hours for plots A, B, and C, respectively) and sediment grain sizes (182, 182, and 185 μm for plots A, B, and C, respectively; see Compton et al. [2013]). Given the wide range of inundation times (from 2 to 12 hours) and sediment structures (from 75 to 275 μm) that cockles occur at (Kraan et al. 2010), the differences in habitat characteristics between the plots are actually small. In fact, all plots fall within the preferred habitat range of cockles (Kraan et al. 2010). Due to difficulty in predicting where Red Knots would forage within a tide (Folmer et al. 2010), we did not know beforehand at which plot, if any, Red Knots would forage. Two of the three plots were visited by knots (plots A and B), and even though we had seen foraging knots there as well, plot C was not visited by Red Knots during our measurement interval. This allowed us to study the effect of Red Knot predation on cockles in comparison to a reference plot without predation, i.e., a before–after control–impact design. All three plots were sampled intensively over a relatively large spatial scale (1 ha).

Sampling the prey

On 12 and 18 August and on 4 September 2010 we sampled cockle densities in plots A, B, and C, respectively. On 26 August, Red Knots gave up foraging in plots A and B. On 26 August, 2 and 9 September, we resampled cockle densities in plots A, B, and C, respectively. Although ideally we should have sampled all plots simultaneously, logistical limitations prevented us from doing so. Nonetheless, the sampling dates were relatively close together and we have no reason to suspect that factors that vary over time have influenced our results (Zwarts 1991). At each plot we sampled 150 stations, of which 100 sampling stations were placed 10 m apart on a systematic grid, and the remaining 50 sampling stations were randomly placed on grid lines (Bijleveld et al. 2012). This sampling design allowed for precise estimation of mean densities, as well as spatial autocorrelation parameters that were necessary for estimating patchiness and accurate spatial interpolations of cockle densities (Bijleveld et al. 2012).

We marked sampling stations with color-coded PVC tubes (20 mm in diameter) reaching 20 cm above the mudflat. We avoided resampling the exact locations by initially sampling east and finally sampling 10 cm west of the marker. At each sampling station we collected one core ($1/56$ m^2) to a depth of 20–25 cm, which we rinsed over a 1-mm mesh sieve. We collected and froze all cockles before taking them to the laboratory, where their lengths, widths, and heights (as defined by Zwarts and Blomert 1992) were measured to the nearest 0.1 mm. From a subsample of 115 sampling stations (1094 individuals), we determined an individual's body composition by measuring dry mass of the shell (DM_{shell}) and ash-free dry mass of the flesh ($AFDM_{flesh}$) according to the procedure described by Piersma et al. (1993). These body compositional samples were unevenly distributed between plots and sampling occasions. For the first and second sampling occasion we sampled 21 and 0 individuals from plot A, 186 and 72 individuals from plot B, and 214 and 601 individuals from plot C. In order to correct for this uneven distribution, we analyzed the data in mixed-effect analyses with sampling station as random effect (see *Data analyses*).

Spatially autocorrelated cockle densities

Often, animal densities are positively correlated over small distances, and the farther apart, the weaker this correlation. A spatial autocorrelation function describes how spatial autocorrelation changes with distance, and can be used for estimating the average patch size (e.g., Kraan et al. 2009), or for spatial interpolations (Cressie 1993). In order to investigate the effect of predation on the patchiness of cockles, as well as to visualize their spatial distributions, we calculated spatial autocorrelation functions and interpolated cockle densities across each plot. Per sampling core, we counted the number of cockles that were suitable for Red Knots to swallow (<16 mm). We normalized model residuals by transforming the numbers of suitable cockles with the common logarithm ($\log_{10}$). To avoid taking the logarithm of zero, we added one before the data transformation. We calculated a correlogram based on the (transformed) numbers of suitable cockles per sampling core for each plot with a spatial lag of 3 m. We then fitted several commonly used spatial autocorrelation functions to the correlograms and selected the exponential spatial autocorrelation function (van der Meer and Leopold 1995, Bijleveld et al. 2012) that had the lowest Akaike Information Criterion between all plots.

In order to estimate the average cockle patch size within plots, we calculated at what distance the autocorrelation reached the arbitrary value of 0.1 (Kraan et al. 2009). In the presence of spatial autocorrelation, we estimated mean cockle densities

and their standard errors with generalized least squares (Cliff and Ord 1981); otherwise we used ordinary least squares analyses (Bijleveld et al. 2012). For each plot, we spatially interpolated cockle densities with kriging (Cressie 1993). For representation purposes, we back-transformed the density estimates with their 95% confidence interval (CI) and divided these by the surface area of the sampling core to obtain cockle densities in numbers per square meter. Note that as a result of the logarithmic transformations, model results represent geometric means instead of arithmetic means. In order to correct for this bias and obtain the arithmetic means, we multiplied the back-transformed estimates by the antilog of $0.5 \times \log_e(10) \times \sigma^2$ (Rothery 1988).

Sampling predator abundances

In order to estimate densities of foraging Red Knots in the study plots, we video-recorded each plot, in good weather during the daytime, during low tide for as long the plot was studied (between the initial and final prey sampling of each plot). By slowly moving the camera from left to right, each plot could be captured entirely by one camera. In total we video-recorded Red Knots for 15 and 22 hours in plots A and B, and for 0 hours in plot C, as there were no Red Knots present during the short study period. Based on these recordings we estimated that an average of 74 ± 4.9 Red Knots (mean $\pm$ SD) per plot were present in plots A and B for an average duration of 2 hours per tide, and none in plot C.

Data analyses

Due to nonlinearity and heteroscedasticity, the allometric relationships between body composition and length are usually analyzed with linear regressions on a log-log scale. However, due to remaining nonlinearity, we modelled an individual's DM_{shell} and $AFDM_{flesh}$ with length on a log-log scale using nonlinear local regression models (LOESS with local quadratic fitting; Appendix: Fig. A2) (for R-script see Bijleveld et al. 2015). LOESS is flexible and follows the data regardless of any nonlinear patterns. To compare DM_{shell} and $AFDM_{flesh}$ between differently sized cockles, we extracted an individual's residual from the nonlinear LOESS fits, which reflects their relative DM_{shell} and $AFDM_{flesh}$. For representation purposes, we back-transformed these residuals into ratios representing an individual's body composition relative to the expected value for that length. Note that even though shell length is a one-dimensional measure of body size, our results were similar to analyses with three-dimensional measures of size (length $\times$ width $\times$ height). Because length is a more intuitive measure of size than the three-dimensional multiplication and has been used in bivalve studies before (e.g., Armonies 1992, Zwarts and Blomert 1992, Piersma et al. 1995, van Gils et al. 2005b), all our analyses are based on length. In order to select the smoothing parameter of the LOESS fits, we inspected the pattern of model residuals with length. A smoothing

parameter of 0.5 gave the smoothest fits (i.e., removed the size dependence) while still following the structural features of our data (Jacoby 2000). In order to assess the goodness-of-fit, resembling the coefficient of determination r^2, we calculated the ratio of the sum of squares in the LOESS fitted values to the total sum of squares in the dependent variable (Jacoby 2000). The calculated ratios for DM_{shell} and $AFDM_{flesh}$ were 0.99 and 0.98, but note that, in comparison to r^2 values, the interpretation of these ratios is not straightforward (Jacoby 2000).

For the density dependence analyses we included cockles from all plots, but excluded those samples from the final sampling occasions in the predation plots. Density dependence is a result of intraspecific competition that is not limited to specific size classes, i.e., size classes that Red Knots can swallow. We therefore included cockles of all lengths (between 3.6 and 41.6 mm) in the analyses of density dependence. With this subset of data we calculated an individual's relative DM_{shell} and $AFDM_{flesh}$ as described previously, and analyzed these traits in linear mixed-effect models with sampling station as a random effect, and shell length (in millimeters) plus $\log_{10}$-transformed cockle density (in square meters), and their interaction, as explanatory variables. A significant interaction between length and density on an individual's relative DM_{shell} or $AFDM_{flesh}$ would indicate that cockles of different lengths are differentially affected by density dependence (intraspecific competition). In order to avoid computational issues due to collinearity between predictors, we centered length and $\log_{10}$-transformed density by subtracting their means (12.9 mm and 3.07, respectively). By parametric bootstrapping ($n = 1000$), we calculated significance under the null hypothesis that the estimated coefficients are zero.

To analyze the effects of knot predation on an individual's relative DM_{shell} and $AFDM_{flesh}$, we selected cockles from all plots and sampling occasions, but only those of suitable sizes for Red Knots to swallow (length <16 mm, $n = 887$). With this subset of data we calculated an individual's relative DM_{shell} and $AFDM_{flesh}$ as previously described, and analyzed these traits in linear mixed-effect models with sampling station as a random effect, and "sampling occasion" (a factor coding for either initial or final sampling) plus "predation" (a factor coding for either the predation or reference plots), and their interaction, as explanatory variables. Due to the positive correlation between an individual's relative $AFDM_{flesh}$ and DM_{shell} ($r = 0.29$, $P < 0.01$), we also analyzed these data in bivariate mixed-effect models, i.e., a model with $AFDM_{flesh}$ and DM_{shell} simultaneously as response variables. These results were, nevertheless, similar to univariate analyses, and for brevity we present the univariate mixed-effect models. We additionally investigated the effect of predation on the shape of cockle shells by calculating the ratio of both shell height and shell width to length. We analyzed these ratios in

TABLE 1. Mixed-modelling results for the effects of cockle lengths and densities on their relative body composition.

Response variables and random effects	Predictors	Estimates	SE	P
A) Relative DM_{shell}	intercept	−0.000	0.004	1.00
	length	−0.000	0.000	0.69
	density	−0.031	0.011	<0.01
	length × density	−0.002	0.001	0.08
Sampling station		0.023	0.003	<0.01
Residual		0.063	0.001	<0.01
B) Relative $AFDM_{flesh}$	intercept	−0.002	0.008	0.82
	length	0.001	0.000	0.16
	density	−0.057	0.018	<0.01
	length × density	0.006	0.001	<0.01
Sampling station		0.053	0.005	<0.01
Residual		0.063	0.001	<0.01

Notes: The mixed-modelling results for the effects of cockle length (mm) and density (cockles/m^2) on an individual's relative (A) dry mass of the shell (DM_{shell}), and (B) ash-free dry mass of the flesh ($AFDM_{flesh}$). Cockle density was $\log_{10}$-transformed. In order to avoid computational issues due to collinearity, covariates were centered with their mean length (12.9 mm) and $\log_{10}$-transformed density (3.07). The random effect estimates refer to standard deviations. Note that these data included cockles of all lengths (3.6–41.6 mm) and excluded data from the final sampling occasions in the predation plots.

mixed-effect models as explained above, but included cockle length (centered by subtracting its mean) as an explanatory variable in the analyses of the ratio of width to length to correct for its linear increase with shell length (0.008 ± 0.001 mm^{-1}, $P < 0.01$). By parametric bootstrapping ($n = 1000$), we calculated significance under the null hypothesis that the estimated coefficients are zero.

We calculated linear and nonlinear selection gradients (Lande and Arnold 1983, Endler 1986) on length and body composition with multivariate models following Johnson et al. (2012). As collinearity between variables can make these multivariate analyses unreliable, we calculated selection gradients for length in a multivariate model with an individual's relative $AFDM_{flesh}$ and DM_{shell}. The condition numbers of the resulting variance–covariance matrices indicated no problems with collinearity for either the predation ($\kappa = 2.4$) or the reference plot ($\kappa = 1.5$). By parametric bootstrapping ($n = 1000$), we calculated standard deviations and significance of the selection gradients under the null hypothesis that they are zero.

All data analyses were carried out in R v3.1.0 (R Development Core Team 2013) with the packages ncf for calculating correlograms, fields for spatial interpolations, and lme4 for mixed-effect model analyses.

RESULTS

Density dependence

A cockle's relative shell mass (DM_{shell}) and flesh mass ($AFDM_{flesh}$) declined with cockle density (Table 1 and Fig. 1). The interaction between length and density on relative DM_{shell} was nonsignificant (Table 1A). For relative $AFDM_{flesh}$ this interaction was significantly positive (Table 1B), indicating that smaller cockles were proportionally more affected by intraspecific competition than larger ones.

Predation and the patchiness of prey

Before predation the cockles (length <16 mm) were patchily distributed (Fig. 2A, C, and E). This was evidenced by the significant positive autocorrelation at distance zero (b_0) and the decline of autocorrelation with distance (b_1) that we measured in plot A ($b_0 = 0.47 \pm 0.05$ [mean ± SE], $P < 0.01$, and $b_1 = -0.05 \pm 0.01$, $P < 0.01$); plot B ($b_0 = 0.54 \pm 0.12$, $P < 0.01$, and $b_1 = -0.07 \pm 0.02$, $P < 0.01$); and plot C ($b_0 = 0.35 \pm 0.10$, $P < 0.01$, $b_1 = -0.05 \pm 0.02$, $P = 0.03$; Fig. 3A, C, and E). The distance at which autocorrelation dropped below 0.1 (the average patch size) was 31 m for plot A, 25 m for plot B, and 24 m for plot C. Initial cockle densities were on average 186 cockles/m^2 (95% CI [119; 278 cockles]) in plot A, 277 cockles/m^2 (95% CI [210; 362 cockles]) in plot B, and 1230 cockles/m^2 (95% CI [1037; 1457 cockles]) in plot C.

Red knot predation reduced cockle densities by 72% in plot A and 83% in plot B to 52 cockles/m^2 (95% CI [42; 62 cockles]) and 48 cockles/m^2 (95% CI [38; 59 cockles]) respectively (Fig. 2A–D). After predation, the patchiness in cockle densities was substantially reduced (homogenized), as shown by the nonsignificant spatial autocorrelation parameters after predation for both plot A ($b_0 = 0.13 \pm 0.22$, $P = 0.56$, and $b_1 = 0.29 \pm 0.63$, $P = 0.66$) and plot B ($b_0 = -0.06 \pm 0.15$, $P = 0.68$, and $b_1 = -0.07 \pm 0.23$, $P = 0.77$) (Fig. 3B, D). Compared to the initial sampling, mean cockle density in the reference plot was similar to the final sampling (1280 cockles/m^2, 95% CI [1030; 1587 cockles], Fig. 2E, F). There were some differences in the spatial density distribution between the initial and final sampling in the reference plot (Fig. 2E, F), but these probably reflect sampling error. The autocorrelation parameters ($b_0 = 0.41 \pm 0.14$,
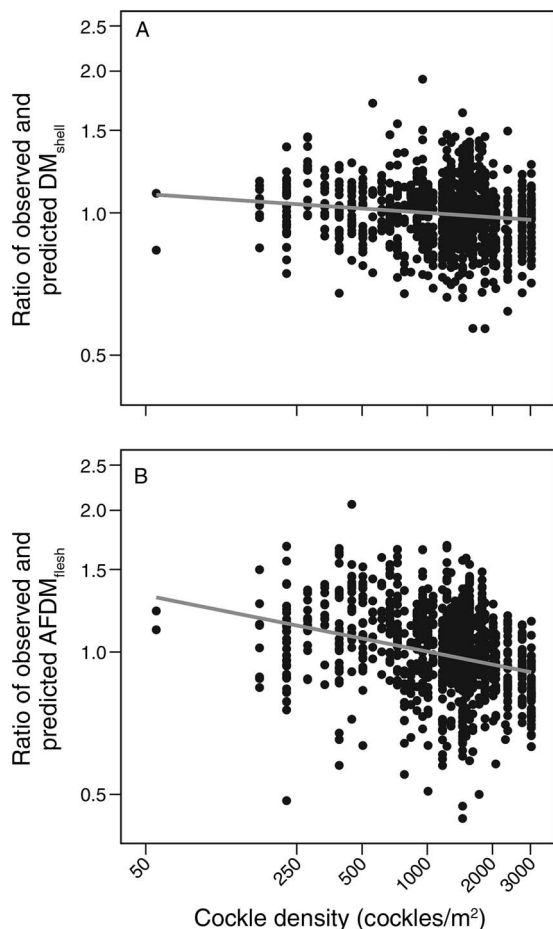
FIG. 1. Negative density dependence in body composition of cockles. An individual's relative (A) dry mass of the shell (DM_{shell}) and (B) ash-free dry mass of the flesh ($AFDM_{flesh}$) were plotted against cockle densities. For representation purposes, we back-transformed relative body composition into ratios representing an individual's body composition relative to the expected value for that length. Note that these data included cockles of all lengths (3.6–41.6 mm) and excluded data from the final sampling occasions in the predation plots. The slope of the regression between relative $AFDM_{flesh}$ and cockle density in panel (B) decreased with cockle length as indicated by the significantly positive interaction between cockle length and density (Table 1). For representation purposes, the regression presented in panel (B) shows the decline in an individual's relative $AFDM_{flesh}$ with cockle density for 6.9 mm long cockles (i.e., mean cockle length eaten by Red Knots).

$P < 0.01$, $b_1 = -0.06 \pm 0.03$, $P = 0.04$), as well as the average patch size (24 m), were similar to those at initial sampling (Fig. 3E, F).

Selective predation and phenotypic traits of the prey

The differences in length distribution and body composition of cockles, before and after predation, were pronounced. Before predation, the mean length of suitable cockles (length < 16 mm) in both plots A and B was 7.4 ± 2.4 mm [mean ± SD]), whereas after predation the mean length increased to 10.4 ± 2.9

mm; Fig. 4A, B). Subtracting the frequency distributions of suitable cockles before and after predation suggests that Red Knots had selected cockles with a mean length of 6.9 ± 1.0 mm. The length distribution of suitable cockles in the non-predation reference plot C did not differ between the initial (10.9 ± 1.8 mm) and final sampling (11.1 ± 1.8 mm, Fig. 4C).

Predation had no effect on the shape of cockle shells, as neither did the ratio of width to length before predation (0.65 ± 0.07 [mean ± SD]) differ from that after predation (0.66 ± 0.08), nor did the ratio of height to length differ between before (0.90 ± 0.05) and after predation (0.91 ± 0.07). In reference plot C, the ratio of cockle width to length did differ significantly (0.01 ± 0.005 [mean ± SE], $P = 0.01$) between the initial (0.66 ± 0.07 [mean ± SD]) and final sampling (0.67 ± 0.05 [mean ± SD]), and the ratio of height to length differed significantly (0.01 ± 0.003 [mean ± SE], $P < 0.01$) between initial (0.89 ± 0.05 [mean ± SD]) and final sampling (0.90 ± 0.04 [mean ± SD]). The changes in shell shape between initial and final sampling in the reference plot were small and similar to the predation plots, as neither did the changes in height-to-length ratios (−0.004 ± 0.007 [mean ± SE], $P = 0.53$), nor the changes in width-to-length ratios (0.02 ± 0.010 [mean ± SE], $P = 0.14$) differ significantly between the predation and reference plots.

Individuals surviving predation had heavier shells, an increase of 21.5 percentage points (95% CI [12.4; 31.2], $P < 0.01$; Fig 5A and Appendix: Table A1), than before predation, indicating that predation affected cockle shell thickness. An individual's relative $AFDM_{flesh}$ did not differ between the initial and final measures (6.4 percentage points higher, 95% CI [−5.1; 19.1], $P = 0.26$; Fig 5B and Appendix: Table A1). In reference plot C, we observed no significant difference in an individual's relative DM_{shell} between initial and final sampling (2.4 percentage points, 95% CI [−3.3; 8.4], $P = 0.42$; Fig 5A and Appendix: Table A1). However, we did observe that an individual's relative $AFDM_{flesh}$ was 13.2 percentage points larger in the final sample compared to the initial sample (95% CI [2.6; 25.1], $P = 0.02$; Fig 5B and Appendix: Table A1).

Selection gradients

In the predation plots, we observed positive linear selection gradients on cockle length and relative DM_{shell}, but we did not find this for an individual's relative $AFDM_{flesh}$ (Table 2). The nonlinear (quadratic) selection gradients on length, and relative DM_{shell} were also significantly positive, and we found that natural selection favored combinations of large lengths and small relative $AFDM_{flesh}$ (Table 2). In the reference plot, we did not find a significant linear selection gradient on an individual's relative DM_{shell}, but those on length and relative $AFDM_{flesh}$ were significantly positive (Table 2). In addition, the nonlinear selection gradient on DM_{shell} was significantly positive, and natural selection favored
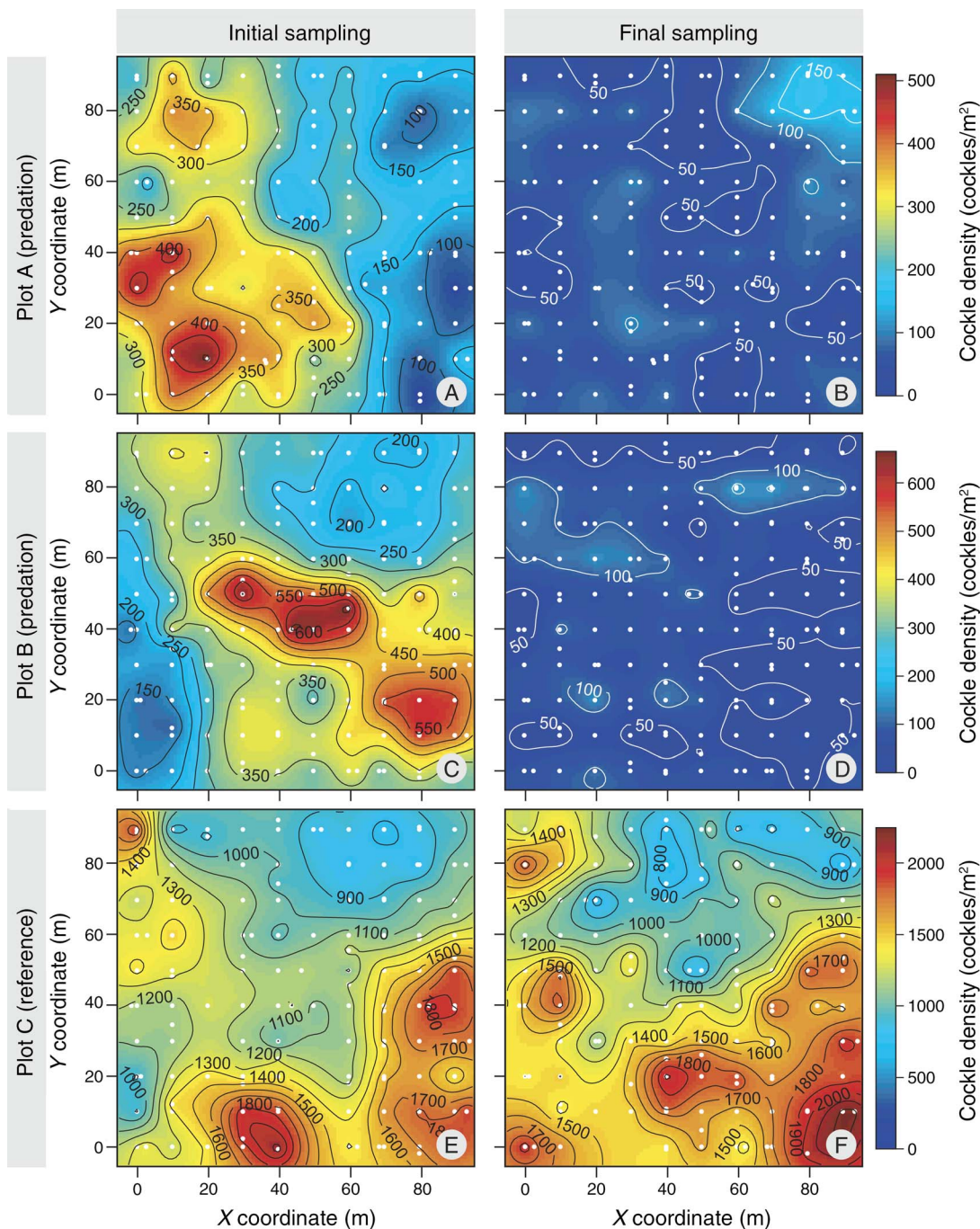
FIG. 2. Spatial density distributions of suitable-sized cockles that are suitable for Red Knots to swallow (length < 16 mm). Rows represent the different plots (respectively plots A, B, and C), and the columns represent the sampling occasion, with the initial sampling shown on the left (panels A, C, and E), and the final sampling shown on the right (panels B, D, and F). The top two rows (panels A–D) show the plots where cockles were fed upon by Red Knots, and the third row (panels E–F) shows the reference plot where Red Knots were not observed foraging. For the spatial representation of final densities (panels B and D) we spatially interpolated densities with the autocorrelation function estimated from the initial sampling. White dots show the sampling stations and the colors represent cockle densities (cockles/m²). Note that the density scales differ between plots.
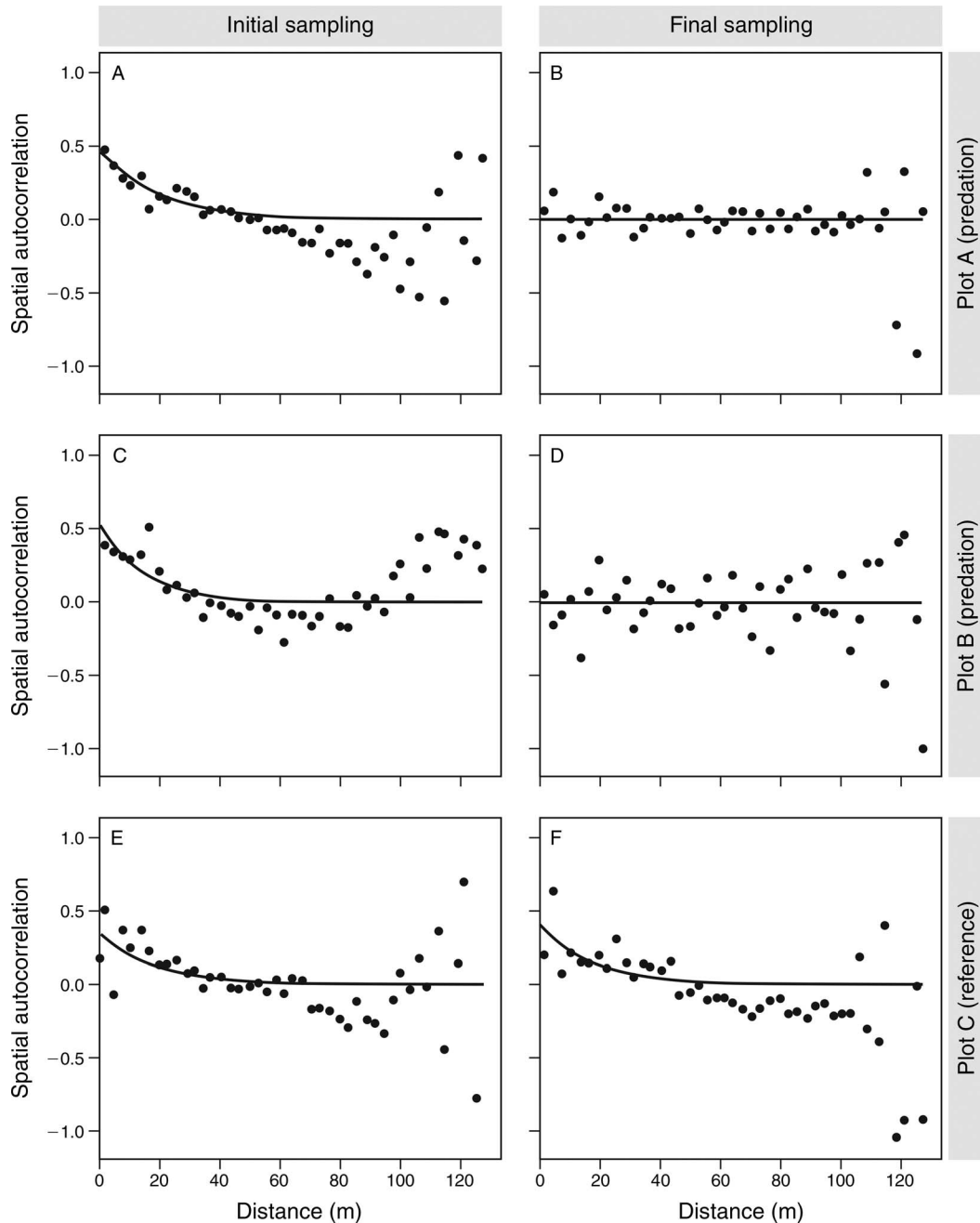
FIG. 3. Spatial autocorrelation functions of the transformed numbers of suitable cockles (length < 16 mm) per sampling core. The rows represent the different plots (respectively plots A, B, and C), and the columns represent the sampling occasion, with the initial sampling shown on the left (panels A, C, and E), and the final sampling shown on the right (panels B, D, and F). Plots A and B were visited by foraging Red Knots, and plot C was a reference plot without Red Knot predation. The initial autocorrelation functions are given by: $y = 0.47e^{-0.05x}$ for plot A, $y = 0.54e^{-0.07x}$ for plot B, and $y = 0.42e^{-0.06x}$ for plot C. The final autocorrelation function for plot C was $0.41e^{-0.06x}$.

combinations of large lengths and large relative $AFDM_{flesh}$ (Table 2).

The significantly positive linear selection gradients on length and $AFDM_{flesh}$ in the reference plot indicated growth between the initial and final sampling period. In order to account for such growth and investigate the net effect of predation on natural selection, we subtracted the linear selection gradients of the reference plot from those of the combined predation plots. These adjusted selection gradients confirmed that predation generated a positive selection gradient on cockle length, a positive selection gradient on relative DM_{shell}, but also revealed a
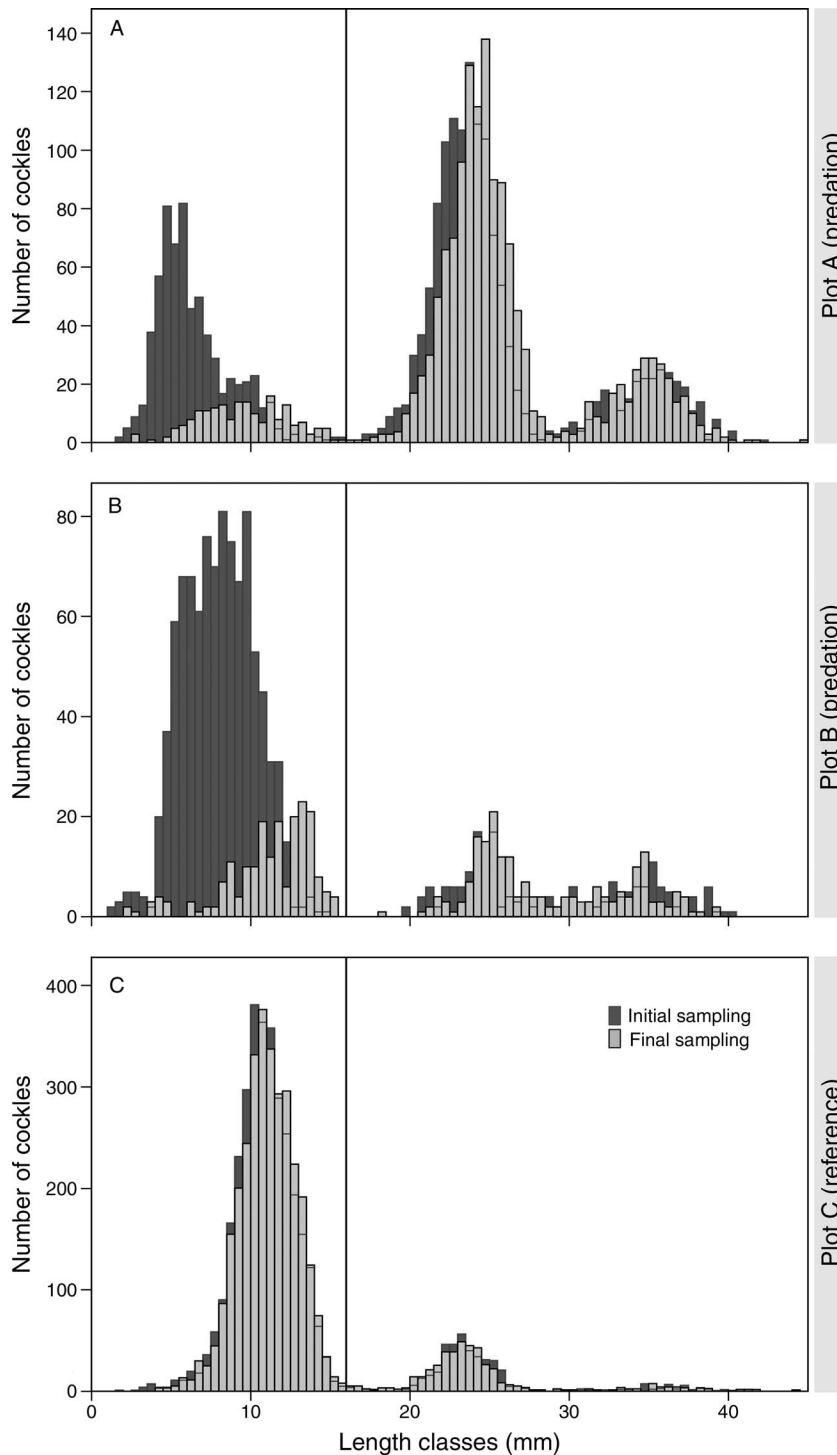
FIG. 4. Effects of predation on the length distribution of cockles. We present the length distributions of cockles at initial and final sampling for (A) predation plot A, (B) predation plot B, and for (C) the reference plot without predation. The vertical lines indicate the upper limit (16 mm) of cockles that Red Knots are able to swallow. When the initial number of cockles was smaller than that of the final number, a short horizontal line indicates the height of the underlying bar. Note the different scales of the *y*-axis.
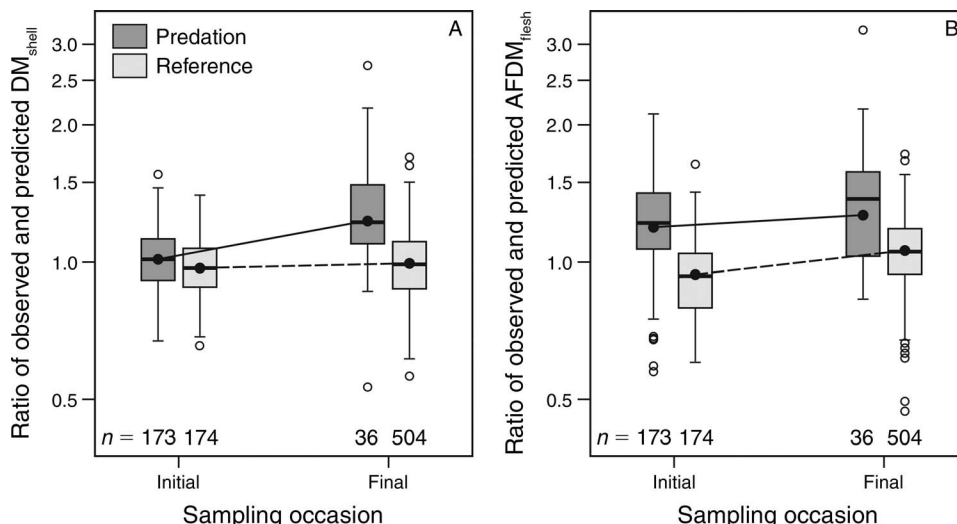
FIG. 5. Effects of predation on cockle body composition. We present an individual's relative (A) dried shell mass (DM_{shell}), and (B) ash-free dry mass of the flesh ($AFDM_{flesh}$) at the initial and final sampling occasion and separated for the predation plots and reference plot. For representation purposes, we back-transformed relative body composition into ratios representing an individual's body composition relative to the expected value for that length. Note that these data were limited to cockles that Red Knots were able to swallow (lengths < 16 mm); n = number of cockles. The boxes indicate the inter-quartile range, the horizontal lines in the boxes indicate the median, the whiskers indicate the 95% data range, and the data points indicate the <5% data range. The circles represent model estimates from the Appendix: Table A1, which are connected within the predation treatment (solid lines) and reference treatment (dotted lines). Note the logarithmic scale on the y-axis.

negative selection gradient on relative $AFDM_{flesh}$ (Table 2).

DISCUSSION

The processes of selection and competition are rarely studied together, and field studies of predator-induced short-term selection pressures on prey populations are scarce. In this quasi-experimental field study, we showed that cockles suffered from intraspecific competition, and that selective predation by Red Knots has profound effects on the density, the patchiness, as well as the length distribution and body composition of their cockle prey. Red Knots ate small cockles with thin shells and proportionally large flesh content, imposing a strong selection pressure on cockles to grow fast and have thick shells with little flesh mass. Before discussing the

ecological implications of our study, we will first address possible caveats in our study design.

Study design and robustness of results

The nature of our field study suggested some problems of sampling design. The predation and reference plots were sampled in sequence (the reference plot was sampled 2–3 weeks after the predation plots). The difference in depletion between the predation and reference plots could therefore be confounded by some (environmental) variable that changed over time causing differential natural mortality or emigration between the predation and reference plots. We do not think this is a realistic concern, as in August–September the environmental conditions in the Wadden Sea, and indeed cockle body condition, tend to be stable (Zwarts 1991). Parada

TABLE 2. Cockle selection gradients imposed by Red Knot predation.

Selection gradient	Trait	Predation			Reference			Difference		
		Est.	SE	P	Est.	SE	P	Est.	SE	P
Linear (β)	length	1.39	0.28	<0.01	0.40	0.09	<0.01	1.00	0.29	<0.01
	DM_{shell}	1.41	0.33	<0.01	0.02	0.09	0.82	1.39	0.34	<0.01
	$AFDM_{flesh}$	−0.41	0.26	0.12	0.65	0.10	<0.01	−1.07	0.28	<0.01
Nonlinear (γ)	length	3.48	1.11	<0.01	0.28	0.20	0.16	3.21	1.13	<0.01
	length × DM_{shell}	0.97	1.25	0.44	−0.05	0.15	0.75	1.02	1.26	0.42
	length × $AFDM_{flesh}$	−2.11	0.96	0.03	0.64	0.19	<0.01	−2.75	0.98	<0.01
	DM_{shell}	4.77	1.76	<0.01	0.36	0.18	<0.05	4.41	1.77	0.01
	DM_{shell} × $AFDM_{flesh}$	−0.06	1.10	0.96	0.12	0.16	0.44	−0.18	1.11	0.87
	$AFDM_{flesh}$	1.44	0.82	0.08	0.38	0.26	0.14	1.06	0.86	0.22

Notes: We estimated cockle selection gradients for the predation and reference plot, and we show their differences. The traits refer to a cockle's length in millimeters, as well as the relative dry mass of the shell (DM_{shell}), and relative ash-free dry mass of the flesh ($AFDM_{flesh}$). Note that we limited these analyses to cockles that Red Knots could ingest (lengths < 16 mm).

and Molares (2008) estimated the natural mortality of cockles at 0.01 cockles/d, which, in our study, would translate into a density reduction of 7% over the course of 14 days. Thus, natural mortality alone cannot explain the observed density changes.

Also cockle emigration rates seem too low to account for the observed density reduction. Only spat up to a size of 3.5 mm is capable of migration in the water column over large distances (Armonies 1992). Larger cockles are capable of crawling over the surface at speeds of 0.6 cm/d (Flach 1996), but speeds of 50 cm/d have also been reported (Mouritsen 2004). Such speeds will correspond to an average linear movement of 0.08 m, and 7 m at the most, during our short study period. These distances fall comfortably within the 1-ha scale of our plots. Like natural mortality, emigration does not seem capable of reducing cockle densities by 72–83%.

In fact, the numbers of Red Knots that we observed in the predation plots are capable of causing the observed depletion. In our plots, Red Knots foraged on average for 2 hours per tide, and selected 6.9 mm long cockles with an average of 1.9 mg AFDM$_{flesh}$ (Appendix: Fig. A2). In order to maintain their energy balance, Red Knots require an intake rate of 0.3 mg AFDM$_{flesh}$/s (Piersma et al. 1995). The average difference of 182 cockles/m^2 before and after predation would thus be capable of sustaining 69 Red Knots per tide throughout our study period of 24 low tides. This estimate is similar to the 74 ± 4.9 Red Knots (mean ± SD) that we observed per tide, which shows that Red Knot predation would indeed cause a depletion of 72–83%.

The absence of true replication of the reference plot leads to the question whether this is a sufficient reference. We argue that the large spatial spread (across 1 ha) of the samples taken within the reference plot should be seen as replication. Nevertheless, there were differences between the predation and reference plot, e.g., cockle abundance, size distribution. In ideal circumstances the two treatments should only differ in predation level. For a field study like this, the habitat differences (e.g., in inundation time, sediment structure) between the predation and reference plot were actually very small (Kraan et al. 2010, but see *Methods*). In fact, the reference and predation plots were all in the preferred habitat range of cockles (Kraan et al. 2010), and all plots contained cockles of suitable sizes to Red Knots. There is nothing to suggest that the differences in depletion between the predation and reference plots would be caused by something other than predation. Moreover, the presence of foraging Red Knots in the reference plot, before and after the experimental observation period, indicated its potential suitability to Red Knots.

The timing between resampling the predation and reference plots was different (14 days for the predation and 5 days for the reference plot). That exposure to potential predation was smaller, does not make the unvisited reference plot less of a valid reference for lack of predation. Nonetheless, the difference in timing might affect the comparison of selection gradients between the predation and reference plots (i.e., the net selection gradients, Table 2). We would argue, however, that our results are robust to this difference in sampling interval for the following reasons. As a consequence of the shorter sampling interval, we underestimated the increase in mean length in the reference plot and consequently overestimated the *net* selection gradient on length. However, the increase in length due to growth (over 14 days) was small compared to the increase in mean length due to the selective removal of small size classes (Fig. 4A, B).

The selection gradient for relative flesh mass was also robust to the difference in sampling interval; in fact, the estimate is conservative. Since the selection gradient on flesh mass in the reference plot would have been larger when given more time, subtracting this from the selection gradient in the predation plot would have resulted in a stronger (more negative) net selection gradient. Note that the selection gradients resulting from predation are as expected based on Red Knot foraging behavior (e.g., van Gils et al. 2003a, 2005a).

Density dependence in the prey

Predation can have profound influences on the population dynamics of species, especially when population processes are density dependent (Gurevitch et al. 2000). For example, by reducing prey numbers, predation can reduce competition and enhance growth (van Gils et al. 2012). This has a major influence on size structure, and potentially on reproductive output at the population level (Beukema et al. 2001, de Roos and Persson 2013). Initially there was debate on whether bivalve suspension feeders, such as cockles, can show negative density dependence, as they are hypothesized to be less susceptible to intraspecific competition for resources (Levinton 1972). However, later empirical studies showed that suspension-feeding bivalves are actually susceptible to competition for space and/or for food at even quite low densities (Peterson and Andre 1980, Jensen 1993, Kamermans 1993). In particular, cockle growth (De Montaudouin and Bachelet 1996), flesh content (Sutherland 1982), reproductive success (Beukema et al. 2001), and survival (Parada and Molares 2008) have been shown to decrease with increased cockle densities. Here, we additionally demonstrate declines in the relative shell and flesh mass of cockles with density. We also show that the smallest cockles were most susceptible to intraspecific competition on flesh mass (as indicated by the significant interaction between length and density on AFDM$_{flesh}$ [Table 1B]).

Depletion of cockle densities and community effects

Predators may substantially impact the densities of their prey. Over the course of four months, for instance, Common Eiders *Somateria mollissima* consumed be-

tween 48% and 69% of their bivalve prey in an area of 6.7 ha (Guillemette et al. 1996). In a study on Red Knots, it was shown that during single low-tide periods they were able to take 25% of the bivalve stock (in this particular case represented by *Mya arenaria*) in small areas (100 m^2; van Gils et al. 2003b). Among the most substantial prey depletion reported in literature is that of a combination of different wader species foraging on chironomid larvae in 100-m^2 plots, which decreased in density by 87% over the course of 13 days (Székely and Bamberger 1992).

Prey depletion is often studied by means of predator exclosures (Sih et al. 1985), artifacts that in intertidal soft-sediment systems tend to alter the physical environment and affect prey behavior, growth, etc. (Wilson 1991). Predator exclosures also suffer the problem of a mismatch of scale between the area covered by exclosures (several square meters) and the much larger extents over which predators forage (Thrush 1999). This study is quite unique in its ability to estimate depletion on a relatively large, and ecologically relevant, spatial scale without experimental artifacts.

The arms race between predators and prey

Natural selection by selective removal of prey can have a profound influence on prey behavior, morphology, and physiology (Genovart et al. 2010, Benkman et al. 2013, Vedder et al. 2014). Under the selection pressures imposed by predators, prey continuously evolve behavioral, morphological, and physiological defense mechanisms (Dawkins and Krebs 1979). In the case of bivalves, they can reduce predation risk either by burrowing deeper into the sediment (Zwarts and Wanink 1989), building armor (Vermeij 1987), or quickly attaining a refuge in size (Paine 1976). Cockle burying depth is limited by their short siphons, and they are found within a few centimeters of the surface (Zwarts and Wanink 1989). This excludes the option to reduce risk via burrowing deeper, and hence cockles need to rely on predator defenses such as fast growth and/or shell thickness (armor). Cockles longer than 16 mm cannot be ingested by Red Knots (Zwarts and Blomert 1992, Piersma et al. 1993) and thus attain a refuge in size (Paine 1976). Indeed, we found that Red Knots mainly foraged on juvenile cockles of 7 mm in length.

Cockles that survived predation by Red Knots had heavier shells, indicating that Red Knots selectively fed upon cockles with a light shell. Alternatively, the observed increase in shell mass might have been an induced predator response (Harvell 1990). Indeed, the intraspecific competitive release due to Red Knot predation could have accelerated a predator-induced increase in shell mass. Nevertheless, given published shell accumulation rates (e.g., Smith and Jennings 2000), the magnitude of the observed increase within two weeks in shell mass, with 21.5 percentage points, seems too large to be accounted for by a plastic predator-induced

response alone. Furthermore, due to their digestive constraint, Red Knots are expected to selectively feed upon on cockles with little shell mass and large flesh mass, thus maximizing their energy intake rates (van Gils et al. 2003a). Our data does suggest that Red Knots are capable of selecting those individuals with little shell mass and large flesh mass (Table 2).

The strength of natural selection

Estimates of natural selection gradients on morphological traits are common, but few are available for body compositional traits (Kingsolver et al. 2012). Compared to the standardized selection gradients reported in the literature (Lande and Arnold 1983, Endler 1986), the ones we found in the present study rank among the highest (Siepielski et al. 2009, Kingsolver and Diamond 2011b). For example, >99% of the linear selection gradients reported in literature are smaller than the ones we found on cockle length and shell mass in the predation plots (Kingsolver and Diamond 2011a). The fact that we observed such strong (nonlinear) selection gradients implies that individual cockles have the potential to increase fitness quite substantially. That this has not happened on the population level (assuming that the traits have a heritable component, e.g., Luttikhuizen et al. [2003]), suggests that cockles are limited in their evolutionary response by, for instance, trade-offs between fitness components, or temporal and spatial fluctuations in natural selection (Kingsolver and Diamond 2011b, Kingsolver et al. 2012).

We have investigated survival without taking reproduction into account. Perhaps, increased survival from predation (investing in armor) comes at the cost of reproduction and competitive ability, thus reducing total fitness. Interestingly, and perhaps indicative of a trade-off between investing in armor or flesh mass, the selection gradients when predators are present show that cockles invested in armor, but when predators were absent cockles invested more in incorporating flesh mass (Table 2). Indeed, it has been found that a large flesh mass increases reproduction in bivalves (Honkoop et al. 1999, Beukema et al. 2001). The population response to selection is an average over space and time (Siepielski et al. 2009). As shown by the fact that only two of the three plots were experiencing predation in this study, Red Knot predation pressure will vary in both space and time (Folmer et al. 2010) and thus create temporal and spatial fluctuations in the direction and strength of natural selection.

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SUPPLEMENTAL MATERIAL

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