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### Red knot habits

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Toxin constraint explains diet choice,  
survival and population dynamics  
in a molluscivore shorebird

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**ABSTRACT**

Recent insights suggest that predators should include (mildly) toxic prey when non-toxic food is scarce. However, the assumption that toxic prey is energetically as profitable as non-toxic prey misses the possibility that non-toxic prey have other ways to avoid being eaten, such as the formation of an indigestible armature. In that case, predators face a trade-off between avoiding toxins and minimizing indigestible ballast intake. Here we report on the trophic interactions between a shorebird (red knot, *Calidris canutus canutus*) and its two main bivalve prey, one being mildly toxic but easily digestible and the other being non-toxic but harder to digest. A novel toxin-based optimal diet model is developed and tested against an existing one that ignores toxin constraints on the basis of data on prey abundance, diet choice, local survival and numbers of red knots at Banc d'Arguin (Mauritania) over 8 years. Observed diet and annual survival rates closely fit the predictions of the toxin-based model, with survival and population size being highest in years when the non-toxic prey is abundant. In the 6 out of 8 years when the non-toxic prey is not abundant enough to satisfy the energy requirements, red knots must rely on the toxic alternative.

## INTRODUCTION

Toxic food is better avoided and there is a large literature on how predators learn to avoid toxic prey (Gittleman & Harvey 1980; Alatalo & Mappes 1996; Speed 2000; Endler & Mappes 2004; Greenlees, Phillips & Shine 2010; Halpin & Rowe 2010). Nevertheless, an emerging, alternative view is that predators should not entirely neglect toxic prey as long as this could increase their opportunity to gain energy (Speed 1993; Sherratt 2003; Sherratt, Speed & Ruxton 2004; Barnett, Bateson & Rowe 2007; Skelhorn & Rowe 2007; Skelhorn & Rowe 2010; Barnett *et al.* 2012). Mildly toxic prey species that are not directly lethal upon ingestion could be valuable during times when non-toxic food is in short supply (Lindström *et al.* 2001; Kokko, Mappes & Lindström 2003). There are a number of cases where predators have been reported to consume toxic but not-immediately-lethal prey (Kicklighter, Fisher & Hay 2004; Gray, Kaiser & Green 2010; Beckmann & Shine 2011; Garcia, Sulkin & Lopez 2011; Lincango *et al.* 2011; Williams *et al.* 2011), but the dietary choices (Kicklighter, Fisher & Hay 2004; Gray, Kaiser & Green 2010; Skelhorn & Rowe 2010; Beckmann & Shine 2011; Lincango *et al.* 2011) and subsequent demographic consequences (Garcia, Sulkin & Lopez 2011) remain unexplained in mechanistic and functional terms.

Optimization models may help us to understand how predators should strategically trade off the minimization of toxin ingestion with the maximization of energy gain. Recent state-dependent models predict that the hungrier a predator, the more likely it is to accept toxic prey (Sherratt 2003; Sherratt, Speed & Ruxton 2004), a prediction that was upheld empirically (Barnett, Bateson & Rowe 2007; Barnett *et al.* 2012). Furthermore, through a predator's hunger state, the willingness to include mildly toxic prey should depend on the abundance and availability of non-toxic food, which is a prediction that allows field testing. However, when it comes to field testing, in both the models and the experiments the only difference between prey types was their degree of toxicity, and this may be quite unrealistic.

In nature, prey species differ in many more defense traits than degrees of toxicity. By making it difficult for a predator to detect, capture, ingest or digest prey (Jeschke & Tollrian 2000; Caro 2005), non-toxic and nutritious prey species may escape predation. Predators, therefore, need to deal with multiple constraints and may face much steeper trade-offs between energy gain and toxin avoidance than hitherto assumed. Here we will focus on such a system in which a predator faces the choice between an easy to digest toxic prey and a much harder to digest non-toxic prey. Building upon the existing digestive rate model (DRM) developed by Hirakawa (Hirakawa 1995), which includes a digestive constraint but not a toxin constraint, we have developed a novel toxin-digestive rate model (TDRM) to generate food-density-dependent predictions on optimal diet and maximum energy intake rates for systems where prey differ in toxicity. The predictions of both DRM and TDRM are then put to the test in an 8-year field study on food abundance, diet choice, survival rate and population size in a molluscivore vertebrate predator, the red knot (*Calidris canutus canutus*; hereafter knot), in their nonbreeding area at Banc d'Arguin (Mauritania), characterized by a highly sulfidic environment in which the most abundant mollusc prey is toxic while other prey types are not.

### Study system

The intertidal flats at Banc d'Arguin are densely covered by seagrass (mainly *Zostera noltii*) (Wolff & Smit 1990). Detritus is produced at a high rate, which is degraded anaerobically by sulfate-reducing bacteria (Jørgensen 1982), causing a build-up of high concentrations of hydrogen sulfide (H<sub>2</sub>S) in sediment pore water (Calleja, Marbà & Duarte 2007; van Gils *et al.* 2012). Sulfide is toxic to many organisms as its lipid solubility enables it to freely penetrate biological membranes, eventually slowing down the functioning of mitochondria and the production of ATP (Bagarinao 1992). A specialized group of organisms that can profit from high sulfide concentrations in seagrass beds are Lucinidae (Taylor *et al.* 2011), heterodont bivalves that live in symbiosis with chemoautotrophic bacteria inside their gill structures (Taylor & Glover 2006). These bacteria oxidize sulfide that is provided by the lucinid host to synthesize sugars which fuel both the growth of the lucinid host and its endosymbiotic bacteria (Johnson, Diouris & Le Pennec 1994). The lucinid *Loripes lucinalis* (hereafter *Loripes*) is the dominant bivalve in Banc d'Arguin, with densities of up to 4,000 individuals per m<sup>2</sup> (van der Geest *et al.* 2011; van der Heide *et al.* 2012), and hence Banc d'Arguin can be considered as a chemosynthesis-based ecosystem (Dubilier, Bergin & Lott 2008).

Banc d'Arguin is an important nonbreeding area for Arctic-breeding shorebirds, hosting more than 2 million individuals in winter, with knots being the most abundant molluscivore (Altenburg *et al.* 1982). Knots face a trade-off between feeding on the super-abundant but toxic *Loripes* (Chapter 2) and a much less abundant but non-toxic prey, *Dosinia isocardia* (hereafter *Dosinia*; numerically *Loripes* and *Dosinia* together make up 75% of all molluscs that are ingestible by knots (Honkoop *et al.* 2008) and dominate the diet of knots (Onrust *et al.* 2013). Knots face an additional trade-off: *Loripes* has a very thin shell, whereas *Dosinia* has a thicker armature. As knots ingest their prey whole (Piersma, Koolhaas & Dekinga 1993), they often face a digestive processing constraint (van Gils *et al.* 2003a), which can be alleviated by selecting bivalves that have high flesh-to-shell mass ratios (van Gils *et al.* 2005b). The toxicity of *Loripes* for knots has recently been investigated experimentally (Chapter 2). Captive knots that were given a diet of *Loripes* only quickly developed diarrhea, thereby losing significant amounts of water. Their compensatory water consumption could not prevent a decrease in food intake. When given a diet of non-toxic *Dosinia*, birds recovered within an hour. Intake rates on *ad libitum* available *Loripes* were three times lower than expected on the basis of maximal shell mass processing rates, whereas intake rates on *ad libitum* available *Dosinia* matched the prediction of a model that predicted intake as constrained by the processing of shells. When given the choice between *Dosinia* and *Loripes*, the captive birds included both prey types in their diet, which maximized their energy intake rate as predicted by a model developed for *ad libitum* situations.

### Toxin-Digestive Rate Model (TDRM)

The TDRM is developed for non-*ad-libitum* circumstances, where foragers need to search for their prey. In its most simple form, it assumes that there are just two prey types  $i = 1, 2$ , which can each be characterized by energy contents  $e_i$ , indigestible ballast mass  $k_i$ , toxin

contents  $s_i$ , handling time  $h_i$ , searching efficiency  $a_i$  and density  $D_i$ . The problem is finding the acceptance probabilities  $\mathbf{P} = (p_1, p_2)$  for both prey types which maximize the forager's long-term energy intake rate  $Y$ , the latter is given by the multi-species version of Holling's disc equation (Holling 1959):

$$Y = \frac{p_1 a_1 D_1 e_1 + p_2 a_2 D_2 e_2}{1 + p_1 a_1 D_1 h_1 + p_2 a_2 D_2 h_2} \quad (3.1)$$

In the 'classical prey model' (Stephens & Krebs 1986), which ignores possible digestive and toxin constraints, finding the optimal solution is straightforward. First, rank prey types such that  $e_1/h_1 > e_2/h_2$ . Always accept type 1 ( $p_1 = 1$ ), and accept type 2 ( $p_2 = 1$ ) whenever  $a_1 D_1 e_1 / 1 + a_1 D_1 h_1 \leq e_2 / h_2$ , otherwise reject ( $p_2 = 0$ ). This model, coined the 'contingency model' CM (Belovsky 1984), has been upheld in many diet studies on a variety of foragers (Sih & Christensen 2001), but was refuted in the case of knots (van Gils *et al.* 2005b; Quaintenne *et al.* 2010). As knots face a digestive constraint they should and do take a prey's ballast mass into account when selecting their diet (van Gils *et al.* 2005b).

If ballast intake rate  $X$  for the optimal solution in the CM exceeds digestive constraint  $c$ , then the forager faces a digestive bottleneck, in which case the CM yields a suboptimal solution (Hirakawa 1995). Then the rate-maximizing diet choice can be found using the digestive rate model DRM (Hirakawa 1995). This model can be solved graphically by plotting energy intake rate  $Y$  against ballast intake rate  $X$  for all possible combinations of  $\mathbf{P}$ , including partial preferences for either type (Fig. 3.1A). Then, by drawing digestive constraint  $c$  (vertical bar in Fig. 3.1A), one can work out which diet choice  $\mathbf{P}$  yields the maximum sustainable energy intake rate  $Y$  under constraint  $c$  (asterisk in Fig. 3.1A). For details we refer to the original paper by Hirakawa (Hirakawa 1995) and its first applications in knots (van Gils *et al.* 2005b), for which such an 'all-or-nothing constraint' has explained intake rate (van Gils *et al.* 2003a), prey choice (van Gils *et al.* 2005b; Quaintenne *et al.* 2010), patch choice (van Gils *et al.* 2005c), selection of stopover sites (van Gils *et al.* 2005a) and even digestive organ sizes (van Gils *et al.* 2003a; van Gils *et al.* 2006; van Gils *et al.* 2007). As already mentioned by Hirakawa (Hirakawa 1995), the same graphical procedure can be followed when the forager faces a toxin *rather* than a digestive constraint (replacing ballast intake rate  $X$  by toxin intake rate  $Z$  and ballast contents  $k_i$  by toxin contents  $s_i$ ).

However, a forager's energy intake rate may be bottlenecked by *both* a digestive and toxin constraint. This occurs when, accounting for digestive constraint  $c$  in the DRM (i.e. when  $X > c$  in the optimal CM solution), toxin intake rate  $Z$  in the optimal DRM solution exceeds  $q$ . This can only occur when the highest digestive quality prey (i.e. the one with the highest  $e_i/k_i$ ) is most toxic (i.e. the one with the highest  $e_i/s_i$ ; in our *Loripes-Dosinia* case this condition was always upheld; Table A3.1). Graphically, the optimal solution under both constraints can be found by adding a third axis to Hirakawa's state space (Fig. 3.1B; mind we have added the third axis to the existing two-dimensional plane making reading the details easier, we could have also plotted  $X$ ,  $Y$  and  $Z$  three-dimensionally). Solving the model analytically is equally straightforward and we will refer to it as toxin-digestive rate model TDRM (note that TDRM equals a DRM when only one of both

constraints operates, which in turn equals a CM when none of the constraints is present). First, maximal sustainable ballast intake rate  $X$  is set by digestive constraint  $c$ :

$$X = c \quad (3.2a)$$

which can be written as:

$$\frac{p_1 a_1 D_1 k_1 + p_2 a_2 D_2 k_2}{1 + p_1 a_1 D_1 h_1 + p_2 a_2 D_2 h_2} = c \quad (3.2b)$$

Similarly, maximally tolerable toxin intake rate  $Z$  is set by toxin constraint  $q$ :

$$Z = q \quad (3.3a)$$

which can be written as:

$$\frac{p_1 a_1 D_1 s_1 + p_2 a_2 D_2 s_2}{1 + p_1 a_1 D_1 h_1 + p_2 a_2 D_2 h_2} = q \quad (3.3b)$$

Solving eqs. 3.2b and 3.3b for the two unknown variables  $p_1$  and  $p_2$  yields the optimal acceptance probabilities:

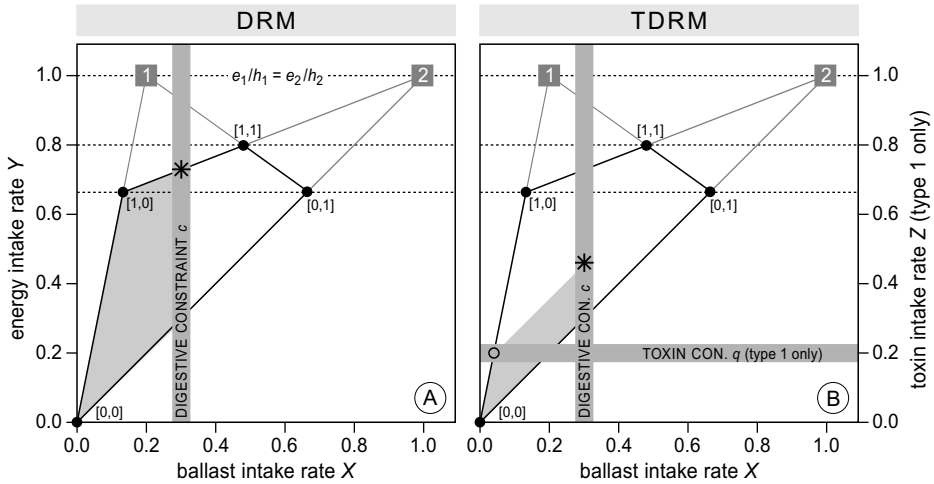
$$p_1 = \frac{s_2 c - k_2 q}{a_1 D_1 (s_2 (k_1 - h_1 c) + s_1 (h_2 c - k_2) + q (h_1 k_2 - h_2 k_1))} \quad (3.4)$$

$$p_2 = \frac{k_1 q - s_1 c}{a_2 D_2 (s_2 (k_1 - h_1 c) + s_1 (h_2 c - k_2) + q (h_1 k_2 - h_2 k_1))} \quad (3.5)$$

## MATERIAL AND METHODS

### Benthos

Our study period spans from 2003-2010, in which we collected 1,024 benthos samples in 13 consecutive expeditions (Dec. 2003 [n = 84], Dec. 2004 [n = 26], Apr. 2005 [n = 39], Dec. 2005 [n = 8], Nov. 2006 [n = 6], Apr. 2007 [n = 229], Aug. 2007 [n = 8], Oct. 2007 [n = 12], Feb. 2008 [n = 142], Apr. 2008 [n = 78], Nov. 2008 [n = 56], Oct. 2009 [n = 224], and Oct. 2010 [n = 112]). Following procedures described elsewhere (van Gils *et al.* 2005b; van Gils *et al.* 2005c; van Gils *et al.* 2012), a benthos sample represented a sediment core ( $\varnothing$  15 cm) taken to a depth of 20 cm and sieved over a 1-mm sieve. Top (0–4 cm) and bottom (4–16 cm) part of the sample were sieved separately in order to distinguish between prey that are accessible and inaccessible to knots (Zwarts, Blomert & Wanink 1992). In the laboratory, each mollusc was identified to species level and shell length was determined ( $\pm$  0.1 mm). The latter allowed us to distinguish between ingestible and non-ingestible prey (knots can ingest all size classes of *Loripes* and *Dosinia*



**Figure 3.1 Graphical solution to find the optimal choice between two prey types which maximizes energy intake rate under one (A) or two (B) constraints.** In both graphs, asterisk denotes the maximum energy intake rate under both constraints, squared symbols give maximum intake rates ( $e/h$ ) at infinite densities of either type 1 or type 2 when there would be no constraints, kite-shaped surface in between the black solid lines gives feasible intake rates under (given) finite prey densities, grey area within the kite shape gives feasible intake rates under the acknowledgement of (A) a digestive constraint and (B) both a digestive and a toxin constraint. Numbers in squared brackets give diet choice as  $[p_1, p_2]$ . (A) Accounting only for a digestive constraint, the digestive rate model (DRM) ranks prey types on the basis of digestive quality ( $e/k$ ) and predicts for this case that the high-quality prey (type 1) should be fully accepted ( $p_1 = 1$ ), while the poor-quality prey (type 2) should only be partially selected ( $0 < p_2 < 1$ ). (B) Accounting for both constraints, the toxin-digestive rate model (TDRM), predicts partial preference on both prey types ( $0 < p_1 < 1$  and  $0 < p_2 < 1$ ). Maximum intake rate is found by drawing a line parallel to the lower line of the kite shape (this line is parallel because toxin intake rate  $Z$  is kept at  $q$  across this line), starting where toxin constraint  $q$  crosses the left-most line of the kite shape (open dot) until it hits digestive constraint  $c$  (asterisk). Note that the scenario plotted here mimics our study qualitatively (the only toxic prey is the type with the highest  $e/k$  ratio), but not quantitatively (parameter values have been chosen arbitrarily).

< 13.2 mm). By drying (3 d at 60°C), weighing ( $\pm 0.1$  mg), and incinerating (5 h at 550°C) flesh and shell separately we determined individual flesh ash-free dry mass  $AFDM_{\text{flesh}}$  and shell dry mass  $DM_{\text{shell}}$  from subsamples. The relationships of  $AFDM_{\text{flesh}}$  and  $DM_{\text{shell}}$  with shell length were used to predict missing values for those prey items that were not weighed. Next, numerical density ( $D$  in eqs. 3.1–3.5),  $AFDM_{\text{flesh}}$  ( $e$  in eq. 3.1) and  $DM_{\text{shell}}$  ( $k$  in eq. 3.2b) were averaged per year per species (available items only, i.e. those accessible and ingestible) and were used to calculate available biomass densities and as input variables in the two digestive rate models (Table A3.1; toxin contents  $s$  was equated to flesh contents  $e$  in case of *Loripes* since toxin constraint  $q$  is expressed in terms of *Loripes* flesh intake). Further parameter values used were searching efficiency  $a = 4 \text{ cm}^2/\text{s}$  (Piersma *et al.* 1995; van Gils *et al.* 2012), handling time  $h = 1 \text{ s}$  (van Gils *et al.* 2012), toxin constraint  $q = 0.1 \text{ mg } AFDM_{\text{flesh}}/\text{s}$  (Chapter 2; *Loripes* only), and gizzard mass = 10 g (van Gils *et al.* 2005a), resulting in digestive constraint  $c = 5 \text{ mg } DM_{\text{shell}}/\text{s}$  (van Gils *et al.* 2003a).



All samples were taken in the vicinity (< 5 km) of Iwik, Banc d'Arguin (19°53'N, 16°18'W). Samples collected in 2003, 2004 and 2006 were taken closer to Iwik (0–3 km) than in other years (1–5 km). Spatial differences at this scale might have had only little influence. Yet, smaller scale spatial parameters such as distance to gullies, affecting the presence of seagrass (Folmer *et al.* 2012), might have had a larger effect. *Loripes* is mostly found in seagrass, whereas *Dosinia* is almost as abundant in bare as in seagrass habitat (Honkoop *et al.* 2008), and differences in prey densities between years may thus in part be due to differences in spatial design (on average, seagrass covers 80% of the intertidal surface at Banc d'Arguin; Wolff & Smit 1990). We tested potential biases for both spatial scales by comparing our 2004 data (0–3 km to Iwik) with those of an independent study also from 2004 by Honkoop *et al.* (2008), who sampled mudflats 1–5 km away from Iwik and took an equal number of samples in bare and in seagrass habitat. 2004 was a notable year in which *Dosinia* was more abundant than *Loripes* (1142.7 vs. 23.9 m<sup>-2</sup> in our study and 216.6 vs. 198.2 m<sup>-2</sup> in the study by Honkoop *et al.*, after correcting their stratified data for the 80% seagrass-coverage of the intertidal flats and for the species-specific availability fractions, 0.73 for *Dosinia* and 0.70 for *Loripes* [van Gils *et al.* 2012]). We repeated all analyses by replacing our 2004 benthos data by those of Honkoop *et al.*, which revealed that neither the outcome of the survival analyses, nor the outcome of the diet comparisons were sensitive to our spatially inconsistent sampling program (see Appendix 3.1).

### Diet composition

During 6 out of the 13 expeditions we collected 77 faecal samples (2003 [n = 21], 2004 [n = 6], Apr. 2007 [n = 8], Oct. 2007 [n = 14], Feb. 2008 [n = 11] and 2009 [n = 17]), samples usually containing 40–60 droppings. Samples were sorted using standard methodology (Dekinga & Piersma 1993), which has recently been calibrated for knots feeding on *Dosinia* and *Loripes* (Onrust *et al.* 2013). In short, after drying (3 days at 60°C), shell fragments that retained on a 300-µm sieve were sorted out and weighed per species, yielding species-specific estimates of ingested DM<sub>shell</sub> (after correcting for 35% of DM<sub>shell</sub> not being retained on the sieve; Onrust *et al.* 2013). Next, hinges were assorted to species and their heights were determined in order to reconstruct ingested size-distributions. The latter was needed to express a species' relative diet contribution in terms of total AFDM<sub>flesh</sub> consumed, since AFDM<sub>flesh</sub>/DM<sub>shell</sub> ratios are size-dependent (Dekinga & Piersma 1993). Relative diet compositions were logit-transformed before calculating the annual averages (Warton & Hui 2011).

### Annual survival rates

Survival estimates were based on capture/resighting data of a total of 1,595 individually marked knots. The birds were captured and resighted during annual three-week expeditions in November/December 2002–2010 (Leyrer *et al.* 2012), yielding annual survival estimates for 7 consecutive years (2003–2009; because survival rate cannot be separated from resighting probability for 2010 when modeled with time-dependence). The birds were aged upon capture (Prater, Merchant & Vuorinen 1977), distinguishing hatch-year

birds (juveniles) from older birds (adults). Apparent (or local) survival ( $\Phi$ ) and recapture probabilities ( $p$ ) were estimated from live encounter data using Cormack-Jolly-Seber (CJS) models (Lebreton *et al.* 1992). As benthos and diet data were collected throughout the entire study area we pooled the data of the two sites in our study area, Abellgh Eiznaya and Baie d'Aouatif (Leyrer *et al.* 2006; Leyrer *et al.* 2012). Based on knowledge gained from earlier analyses, we made some *a priori* assumptions to reduce the number of parameters in order to increase the precision of the survival estimates: it has been shown that a time-since-marking effect (tsm) explained most of the variation in annual survival (Leyrer *et al.* 2012), and we thus considered tsm-effects to account for transients or handling effects on survival in the first year after capture ( $\Phi^1$ ) vs. subsequent years ( $\Phi^{2+}$ ). It has further been shown that age at capture (adult vs. juveniles) explained a significant part of the variation in survival (Leyrer *et al.* 2012), and we thus included age at capture in our models. Note that knots were treated as adults after their first year (>12 months of age), and consequently no age differences existed within the  $\Phi^{2+}$  category. As we were interested in which of the two diet models best explained the annual variation in survival rate, we included intake rates predicted by the TDRM and DRM, respectively, as continuous variables in the models. Additionally, to test for survival differences between years we included time as a factor (time), but also tested whether there was a linear trend in survival rate over time (Time) since an earlier analysis indicated a decline in knot survival over time (Leyrer *et al.* 2013). In all models, resighting probability  $p$  was modeled as a function of time (again as a factor) and site, as observation effort differed between the two sites and logistic improvements suggested resighting efforts differed between years (Leyrer *et al.* 2012). Both adults and juveniles forage on open mudflats during low tide and assemble at roosts during high tide and we had no reason to expect  $p$  to differ between age classes.

The global model was  $\Phi_{\text{age*tsm+time}} p_{\text{site+time}}$  and we tested the goodness of fit using the median- $\hat{c}$  (c-hat) test implemented in the MARK software (ver. 6.0; White & Burnham 1999). The level of overdispersion was estimated at  $\hat{c} = 1.05 \pm 0.00$ . Models were constructed and run in R (ver. 2.15.0) using the RMark package (Laake 2012; ver. 2.1.4) as an interface for program MARK (White & Burnham 1999). We used model averaging to calculate survival and resighting probability and present parameter estimates as  $\hat{\theta} \pm 1$  SE. Model selection was based on Akaike's Information Criterion corrected for small sample size and overdispersion ( $\hat{c}$ ) (QAICc). Based on the assumptions mentioned above, the candidate model set consisted of all biologically and ecologically plausible combinations of parameterizations for  $\Phi$  and  $p$  (Table A3.2).

### Estimating and predicting population dynamics

Each year between 2002 and 2010 we carried out a single count of all knots roosting in the Iwik study region. This took place during a daytime spring high tide in November/December. Birds were counted using telescopes by two or three groups of observers, each counting a subsection of our study area.

We modeled the population trend for 2002–2010 using adult and juvenile survival rates estimated by the most parsimonious model (i.e. survival model 1 in Table A3.2). In

this statistical model, TDRM energy intake rates  $Y$  served as input, which were predicted on the basis of eq. 3.1 using (1) the observed densities of both *Loripes* and *Dosinia*, and (2) the observed densities of *Loripes* only, and (3) the observed densities of *Dosinia* only. These latter two hypothetical scenarios allow us to hypothesize how much knot population dynamics depend on the presence of either *Loripes* or *Dosinia*. As applied before when modeling knot population dynamics (Baker *et al.* 2004), we used a two-dimensional matrix population model, in which fecundity ( $f$ ; equal to 0 for juveniles and  $0.14 \text{ yr}^{-1}$  for adults [van den Hout *et al.* 2014]), juvenile survival ( $\Phi_{\text{juv}}$ ) and adult survival ( $\Phi_{\text{ad}}$ ) determine how the number of juveniles ( $N_{\text{juv}}$ ) and adults ( $N_{\text{ad}}$ ) in year  $t$  affect the number of juveniles and adults in year  $t + 1$ :

$$\begin{bmatrix} N_{\text{juv}} \\ N_{\text{ad}} \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & f \\ \Phi_{\text{juv}} & \Phi_{\text{ad}} \end{bmatrix}_t \begin{bmatrix} N_{\text{juv}} \\ N_{\text{ad}} \end{bmatrix}_t \quad (3.6)$$

The 2002 count was used as the initial population size in the model.

## RESULTS

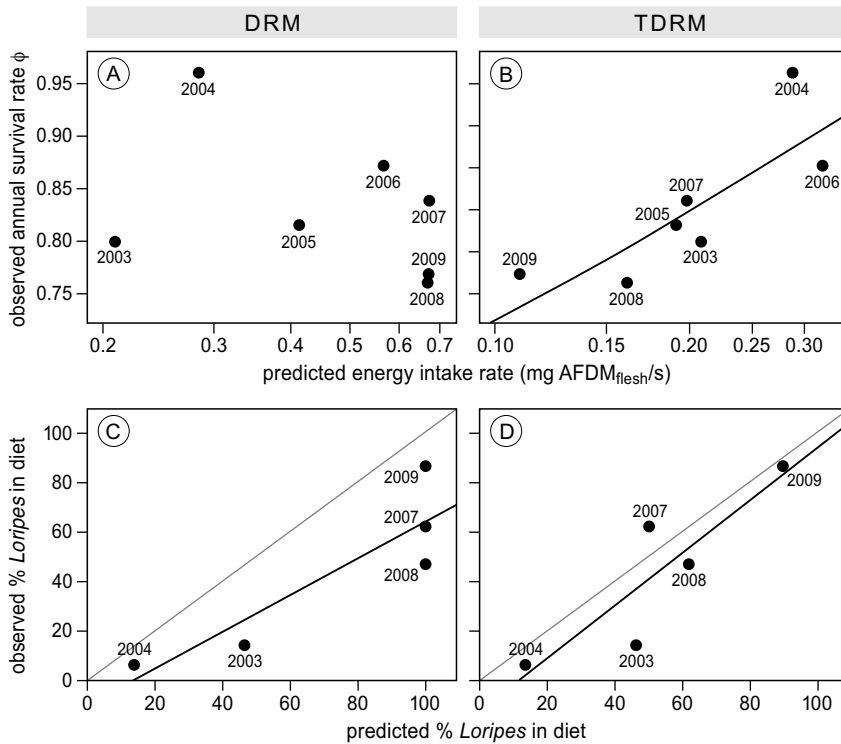
### Annual survival rate

TDRM models were substantially better supported than models including DRM intake rates (accumulated QAICc weight: 0.38 for models including TDRM intake rates, and 0.00 for models including DRM intake rates; Table A3.2; Figs 3.2A-B). Although models including annual variation as explanatory factor (i.e. factor time) scored high in the model selection process (accumulated QAICc weight: 0.48; Table A3.2), they added extra parameters (complexity) to the models and should thus be less favored. There was no evidence for a time trend in survival (i.e. models including Time; accumulated QAICc weight: 0.14; Table A3.2). Furthermore, there was no support for adult survival being different in the first year after marking, compared to subsequent years (model 2 vs. model 3,  $\Delta\text{QAICc} = 0.34$ ). Model averaged survival estimates can be found in Table A3.3.

### Diet composition

The observed contribution of *Loripes* to the diet was less than predicted by the DRM (Fig. 3.2C;  $t = -3.44$ ,  $df = 4$ ,  $P = 0.03$ ). For 3 out of 5 years for which we had diet data available, the DRM predicted that knots should fully ignore *Dosinia* (Fig. 3.2C). In those three years (2007, 2008, 2009), the abundance of *Loripes* was so high that, even if knots would feed on *Loripes* only —the prey with the highest flesh-to-shell mass ratio—, their gizzard would not be able to achieve the required shell mass processing rate; i.e. knots would face a digestive constraint. Hence, only a proportion of encountered *Loripes* should have been accepted (Table A3.4; note that this is different from conceptual Fig 3.1A where, for reasons of visual clarity, we assumed that even maximum ballast intake rates on prey type 1 (i.e.  $k_1/h_1$ ) are below digestive constraint  $c$ ).

In contrast, diet compositions predicted by TDRM matched the observed diets (Fig. 3.2D;  $t = -1.26$ ,  $df = 4$ ,  $P = 0.28$ ). In 3 out of 5 years the intake rate on *Loripes* would have



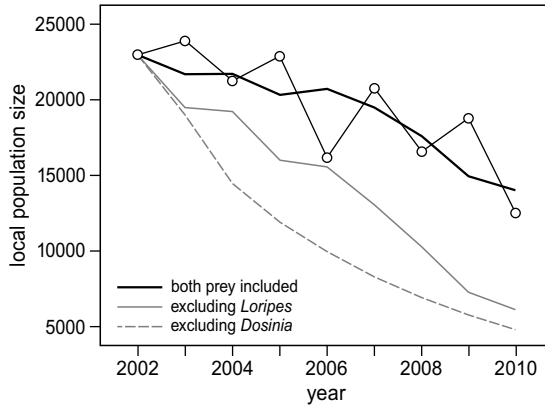
**Figure 3.2** Year-specific adult survival rate as a function of DRM and TDRM predicted intake rate (estimated by model 2 in Table A3.2; year runs from Nov/Dec of the previous year to Nov/Dec of the plotted year). Year-specific adult survival rate does not correlate with DRM-predicted intake rate (A), but correlated positively with TDRM predicted intake rate (B). Line gives model fit (model 1 in Table A3.2). (C) Observed amounts of *Loripes* in the diet (relative to *Dosinia*) are lower than predicted by the DRM, (D) but match with TDRM-predictions. Dashed lines represent  $y = x$  lines, and solid lines are significant regression lines.

exceeded the toxin constraint if all encountered *Loripes* were accepted. Hence, only a proportion of the encountered *Loripes* should have been accepted for this reason (Table A3.4). In those years, knots following the TDRM could accept all encountered (ingestible) *Dosinia* as the occurrence of the toxic constraint kept required shell mass processing rates low and thereby prevented a digestive constraint. Only in the year that *Loripes* was less abundant than *Dosinia* (2004), the TDRM predicts a digestive rather than a toxin constraint. In 2004 knots should thus have accepted all encountered *Loripes* and only a fraction of the encountered (ingestible) *Dosinia* (Table A3.4).

### Predicted and observed population dynamics

Predicted knot population size declined over time, with the decline being steepest if *Dosinia* would have been removed from the system (−79% from 2002 to 2010), followed by the scenario when *Loripes* would have been removed (−74%). However, even with both

prey included in the diet, knot numbers were predicted to decrease over time ( $-39\%$ ; Fig. 3.3). This last model agreed best with the observed decline in knot numbers from 22,859 in 2002 to 12,465 in 2010 ( $-45\%$ ; Fig. 3.3).

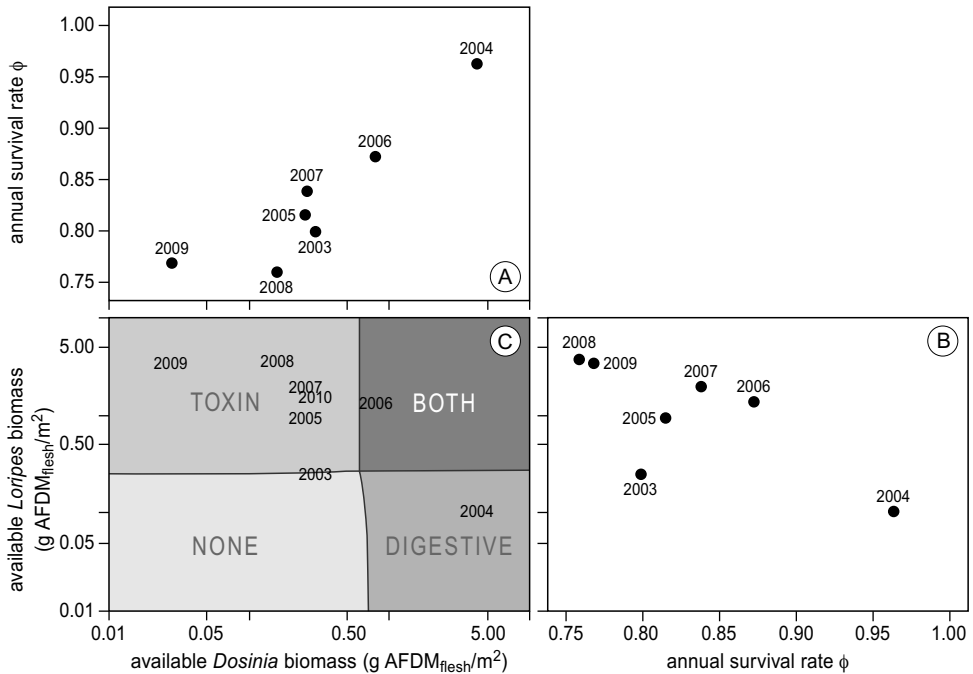


**Figure 3.3 Predicted population dynamics of red knots** in the presence of both prey (thick solid black line), in the absence of *Loripes* (solid grey line), and in the absence of *Dosinia* (dashed grey line). Observed population size (squares connected by thin line) follows predicted population decline based on both prey.

## DISCUSSION

Knot annual survival rates correlated strongly with annual variations in *Dosinia* abundance (Fig. 3.4A; Pearson's  $r = 0.91$ ), but showed no trend with *Loripes* abundance (Fig. 3.4B; Pearson's  $r = -0.72$ ). This strongly suggests that knots need non-toxic *Dosinia* to survive and cannot rely on *Loripes* only, even though *Loripes* is much more abundant and has a much higher flesh-to-shell ratio. The reasoning for this dependency is rather simple: in order to prevent lethal intoxication, knots can ingest *Loripes* up to a rate that is only half of their required intake rate (Chapter 2), and they need prey such as *Dosinia* to meet their energy demands. On the other hand, *Dosinia* was not abundant enough for knots to fully rely on them as an energy source.

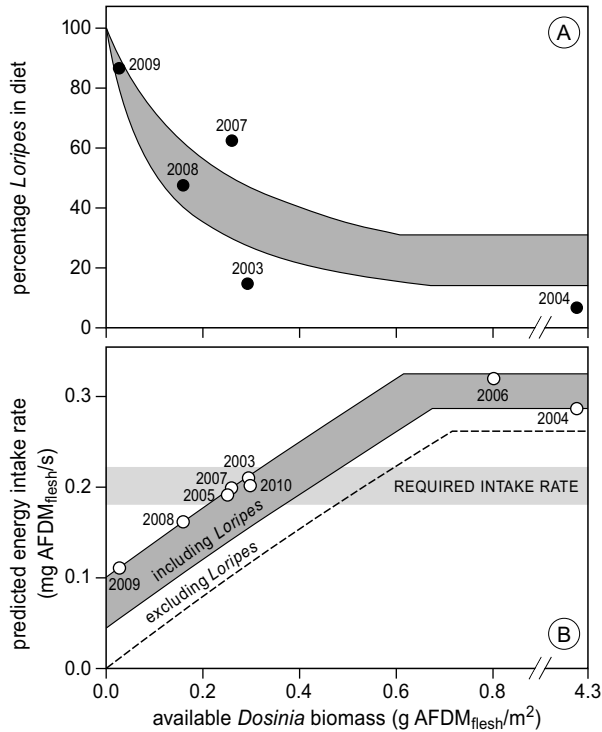
The TDRM optimization model, which seems to capture the essence of the knots' dietary problem, assumes the following strategy: accept toxic but energy-rich *Loripes* until the toxin constraint is met, then add bulky *Dosinia* until the digestive constraint is met. According to our calculations, knots faced both constraints only in 2006 when both prey species occurred in high densities (Fig. 3.4C; for details see Appendix 3.2). In most years (6 out of 8; Fig. 3.4C) however, *Dosinia* was not abundant enough for the birds to become digestively constrained, while the presence of *Loripes* was usually high enough to meet the toxic constraint (Fig. 3.4C). This explains the negative correlation between the *relative* amount of *Loripes* in the diet and the available density of *Dosinia* (Fig. 3.5A): whereas the *absolute* rate at which *Loripes* was eaten was likely to be constant each year (equal to toxic



**Figure 3.4 Year-specific adult survival rate as a function of prey density** (estimated by model 2 in Table A3.2). Adult survival rate does correlate with the available biomass density of *Dosinia* (A), but not with *Loripes* density (B). These prey densities themselves correlate negatively (C). Grey shading in the background indicates whether knots would either face a toxin constraint, a digestive constraint, both constraints, or none of both. For details behind these calculations see Appendix 3.2.

constraint  $q$ ), the *absolute* rate at which *Dosinia* was eaten increased with the available *Dosinia* density as long as birds were not digestively constrained (this would occur at a *Dosinia* density of 0.6–0.7 g AFDM<sub>flesh</sub>/m<sup>2</sup>). A recent study showing year-round changes in *Dosinia* and *Loripes* densities also suggests that the relative contribution of *Loripes* to the diet of knots increased as *Dosinia* stocks became depleted throughout winter (Ahmedou Salem *et al.* 2014).

In Banc d’Arguin, knots need an average energy intake rate of c. 0.2 mg AFDM<sub>flesh</sub>/s in order to maintain body mass (van Gils *et al.* 2009). In a normal year, knots would only achieve half of this rate if they would fully neglect *Loripes* and only accept *Dosinia* as their prey. By adding *Loripes* to their diet knots would just meet their required energy demand. A plot of the predicted intake rate with (grey band; Fig. 3.5B) and without (dashed line; Fig. 3.5B) *Loripes* on the available *Dosinia* densities, shows that energy intake rate without accepting *Loripes* would be insufficient for subsistence in 6 out of 8 years (also see Table A3.4). Only in 2004 and 2006 knots would have been able to achieve their minimum energetic requirements on *Dosinia* alone (Table A3.4; although we modeled knots as ‘intake rate-maximizers’, they could just as well have featured as ‘sulfide minimizers’ in these two years by fully ignoring *Loripes*; however the diet data available for 2004 suggest they did not – Fig. 3.5B).



**Figure 3.5 Predicted red knot diet as a function of available *Dosinia* biomass.** (A) How the amount of *Loripes* in the diet (relative to *Dosinia*) relates to the available density of *Dosinia*, both theoretically (TDRM) and empirically. Theoretical predictions are given by the grey band, with lower line representing a poor *Loripes* density ( $0.1 \text{ g AFDM/m}^2$ ) and upper line a higher *Loripes* density ( $\geq 0.25 \text{ g AFDM/m}^2$ ); as knots face a toxin constraint at *Loripes* densities of at least  $0.25 \text{ g/m}^2$ , diet composition becomes independent of *Loripes* abundance above such densities). Diet composition becomes independent of *Dosinia* density when the digestive constraint is met, i.e. above *Dosinia* densities of  $0.6\text{--}0.7 \text{ g/m}^2$ . (B) TDRM functional response to variations in *Dosinia* density. Grey band as in (A) shows that most variation in intake rate is due to density variations in *Dosinia* rather than in *Loripes*. Nevertheless, without *Loripes*, intake rates would be substantially lower (dashed line) and often below the level required for subsistence. Dots denote year-specific predictions based on *Loripes* and *Dosinia* densities.

Note that rate-maximization *whilst* feeding allows for the minimization of *daily* feeding time if a fixed amount of daily energy is required (Schoener 1971). Minimizing daily feeding time can be beneficial if foraging comes at a cost, such as for example enhanced predation risk (McNamara & Houston 1994). This justifies our approach to analyze survival as a continuous function of intake rate rather than as a simple step function of whether metabolic demands are met. Note further that in poor *Dosinia* years, notably in 2009 (Fig. 3.5B, Table A3.4), knots would not even have been able to survive on the combination of *Loripes* and *Dosinia* alone and would have needed to include other prey types in their diet (which knots indeed did, especially in 2009; Onrust *et al.* 2013).

With *Loripes* and *Dosinia* being by far the most abundant available bivalves at Banc d'Arguin (Honkoop *et al.* 2008), there are not many alternative mollusc prey to include in

the diet. This notion, and the fact that the last years of our study period have not shown high densities of *Dosinia* (Fig. 3.4C), may explain why the local knot population has declined during especially the second half of our study period (Fig. 3.3). However, TDRM energy intake rate showed no trend over time ( $r = 0.51$ ;  $F_{1,6} = 2.07$ ;  $P = 0.20$ ). In addition, also in 1980s, when knot numbers were 40–50% times higher than nowadays (Hagemeijer *et al.* 2004), *Dosinia* and other non-toxic alternatives were never very abundant (Wolff *et al.* 1993). Being a migratory species, it may thus very well be that the carrying capacity of the population is set elsewhere outside Banc d'Arguin (van Gils *et al.* 2009), for example in the Wadden Sea southward staging area where commercial fisheries led to impaired (re)fuelling opportunities (Kraan *et al.* 2010).

It is yet unclear what determines the probability of high densities of *Dosinia*, but the negative correlation between annual averages of *Dosinia* and *Loripes* densities is remarkable (Fig. 3.4C;  $r = -0.76$ ,  $F_{1,6} = 8.30$ ,  $P = 0.03$ ). As has been suggested elsewhere (van Gils *et al.* 2012), this indicates some form of competition between the two species. Alternatively, there may be differences in environmental conditions among years that steer the negative correlation. For example, observed dynamics in seagrass abundance may underlie this correlation (Folmer *et al.* 2012; Leyrer *et al.* 2012), with *Loripes* more strongly linked to seagrass habitat than *Dosinia* (Honkoop *et al.* 2008).

It is exciting to hypothesize about how defense strategies in one prey may have been selected for given the defense strategy in another prey. For example, is the bulkiness of *Dosinia* an evolutionary response to the toxicity of *Loripes*? The comparison between the DRM and the TDRM allows us to hypothesize along these lines: it suggests that toxicity of *Loripes* might have increased predation pressure on *Dosinia*, inducing, on an evolutionary time scale, extra armature in *Dosinia*. The reason behind this is that intake rates on *Dosinia* are much higher in TDRM than in DRM, especially in years of high *Loripes* abundance (Table A3.4). Under DRM, that treats *Loripes* as if it was non-toxic, knots can reach their digestive constraint on *Loripes* only, leaving no room to add bulky *Dosinia*. In contrast, under TDRM, many *Dosinia* can be added to the diet since intake rates on *Loripes* are reduced because of the toxicity constraint.

At the same time the evolution of thick-shelled armature in *Dosinia* may have led to increased predation pressure on *Loripes*, which in turn may have increased *Loripes*' toxicity. Namely, if *Dosinia* would have been relatively thinner shelled than *Loripes* (i.e. when  $e_D/k_D > e_L/k_L$ ), knots would be unable to add *Loripes* if they faced their digestive constraint on *Dosinia* only (i.e. which would happen in *Dosinia*-rich years). Note that the mechanism of enhanced predation pressure on one prey type as a consequence of induced anti-predator defense in the other prey type proposed here is a classic example of 'trait-mediated indirect interactions' (TMII), which have received renewed attention in the ecological literature (Bolker *et al.* 2003; Werner & Peacor 2003; Yamauchi & Yamamura 2005).

With the chemoautotrophic-fuelled *Loripes* being the top most abundant bivalve in the system, Banc d'Arguin can be classified as a chemosynthesis-based ecosystem (Dubilier, Bergin & Lott 2008). In contrast to Banc d'Arguin, most chemosynthesis-based ecosystems, such as deep-sea vents and seep systems, are renown for the their lack of predators



(Carney 1994; Bergquist *et al.* 2003; Kicklighter, Fisher & Hay 2004). Possibly, such systems lack predators because of the overwhelming densities of toxic prey while non-toxic alternatives are not at hand (Tunncliffe 1991). The presence of a suitable non-toxic prey may explain why predators are able to thrive at Banc d'Arguin. Hydrothermal vents and deep-sea cold seeps are geographically more isolated than seagrass beds, and also more hostile because of the limited availability of dissolved oxygen in the deep sea. Their isolated positions makes it costly for predators to switch between "phototrophic" and "chemotrophic" prey, which could be the reason that such systems are frequented little by predators originating from photosynthetic communities (Carney 1994; MacAvoy *et al.* 2008; Cordes, Becker & Fisher 2010). By contrast, in seagrass beds the difference between the anaerobic sulfidic and the aerobic non-toxic environment is just a matter of meters in a horizontal direction (bare versus seagrass mosaics [Honkoop *et al.* 2008; van der Heide *et al.* 2010]), or even centimeters when considered vertically (sulfide concentrations strongly increase in the first 12 cm of the sediment layer [van Gils *et al.* 2012]). This allows predators to "make the best of both worlds" by adding toxic prey to their non-toxic diet as long as toxin levels do not exceed a given threshold. This mimics the problems recognized long ago for terrestrial herbivores, in which diet selection (Schmidt 2000; Dearing, Foley & McLean 2005), habitat use (Moore & Foley 2005), and fitness and population processes (DeGabriel *et al.* 2009) are governed by the occurrence of toxins in the form of secondary plant metabolites or as products from endosymbiotic relationships (Saikkonen *et al.* 1998; Verstraete *et al.* 2011). Our work seems to be the first to make similar problems apparent in a system with predators and prey rather than herbivores and plants.

### **ACKNOWLEDGEMENTS**

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### APPENDIX 3.1. Figure 3.4C explained

This section explains the theoretical basics underneath figure 3.4C, with *Loripes* being denoted by prey type 1 and *Dosinia* by prey type 2.

#### Minimal *Loripes* density ( $D_q$ ) at and above which toxin constraint $q$ is achieved

Toxin intake rate  $Z$  is given by:

$$Z = \frac{a_1 D_1 s_1 + a_2 D_2 s_2}{1 + a_1 D_1 h_1 + a_2 D_2 h_2} \quad (\text{A3.1a})$$

Since type 2 is not poisonous in our case (i.e.  $s_2 = 0$ ) eq. A3.1a simplifies to:

$$Z = \frac{a_1 D_1 s_1}{1 + a_1 D_1 h_1 + a_2 D_2 h_2} \quad (\text{A3.1b})$$

Toxin constraint  $q$  is met when:

$$Z = q$$

Solving eqs. A3.1b and A3.2 for  $D_1$  yield type 1's density  $D_q$  at and above which  $q$  is reached:

$$D_q(\text{type 1}) = \frac{D_2 a_2 h_2 q + q}{a_1 (s_1 - h_1 q)} \quad (\text{A3.3})$$

Note that  $D_q$  increases slightly with an increase in  $D_2$  (solid line in Fig. A3.1), which is due to increasing time loss to handling type 2, which goes at the expense of available search time and thus hampers the intake rate on type 1 at a given density  $D_1$ .

#### Minimal density ( $D_c$ ) of *Loripes* or *Dosinia* at and above which digestive constraint $c$ is achieved

Ballast intake rate  $X$  is given by:

$$X = \frac{a_1 D_1 k_1 + a_2 D_2 k_2}{1 + a_1 D_1 h_1 + a_2 D_2 h_2} \quad (\text{A3.4})$$

Digestive constraint  $c$  is met when:

$$X = c$$

Solving eqs. 3.4 and 3.5 for  $N_1$  yields type 1's density  $N_c$  at and above which  $c$  is reached:

$$D_c(\text{type 1}) = \frac{D_2 a_2 h_2 c - D_2 a_2 k_2 + c}{a_1 (k_1 - h_1 c)} \quad (\text{A3.6})$$

Vice versa,  $D_c$  can also be expressed for type 2 by solving eqs. A3.4 and A3.5 for  $D_2$ :

$$D_c(\text{type 2}) = \frac{D_1 a_1 h_1 c - D_1 a_1 k_1 + c}{a_2 (k_2 - h_2 c)} \quad (\text{A3.7})$$

Note that  $D_c$  decreases with an increase in  $D_1$  (dashed line in Fig. A3.1), which is because the more of type 1 is ingested, the less of type 2 needs to be ingested in order to reach the digestive constraint.

### Minimal densities of *Loripes* ( $D_1^*$ ) and *Dosinia* ( $D_2^*$ ) at which both constraints $q$ and $c$ are met

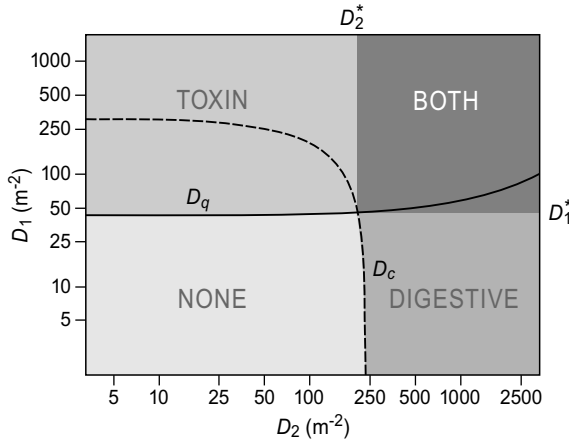
These densities are found by equating eq. A3.3 with eq. A3.6 and solving for  $D_1$  and  $D_2$ , yielding:

$$D_1^* = \frac{k_2 q}{(a_1 k_2 - a_1 c h_2) s_1 + (a_1 h_2 k_1 - a_1 h_1 k_2) q} \quad (\text{A3.8})$$

$$D_2^* = \frac{c s_1 - k_1 q}{(a_2 k_2 - a_2 c h_2) s_1 + (a_2 h_2 k_1 - a_2 h_1 k_2) q} \quad (\text{A3.9})$$

### Density 'regions' with or without constraint(s)

As visualized in Fig. A3.1, both constraints operate when  $D_1 > D_1^*$  and  $D_2 > D_2^*$ . Only the toxin constraint operates when  $D_1 > D_q$  and  $D_2 < D_2^*$ . Only the digestive constraint acts when  $D_1 < D_1^*$  and  $D_2 > D_c$ . None of the constraints act when  $D_1 < D_q$  and  $D_2 < D_c$ . Note that within these larger regions there are two interesting 'subregions'. First, there is a subregion where  $D_1$  is high enough for the digestive constraint to be met – however the



**Figure A3.1** The basis underlying Fig. 3.4C in the paper, showing how we derived critical density thresholds above which the toxin and the digestive constraints operate (for the average year, i.e. by taking as inputs the means of  $e_L$ ,  $e_D$ ,  $k_L$ , and  $k_D$  listed in the last row of Table A3.3). Note that axes are log-transformed, making  $D_q$  and  $D_c$  curved instead of straight lines.

existence of the toxin constraint precludes this. This is where  $D_1 > D_c$  and  $D_2 < D_2^*$ . Second, there is subregion where the existence of the digestive constraint makes the toxin constraint being faced at a lower density than  $D_q$ , which happens because the slowing down effect of handling type 2 prey has disappeared due to digestive constraint  $c$  setting a limit to the handling frequency. This is where  $D_1 < D_q$  and  $D_1 > D_1^*$  (where by definition  $D_2 > D_2^*$ ).

### APPENDIX 3.2. Sensitivity analysis with respect to benthos sampling

Here we explore whether our conclusion that the TDRM is the best-supported model has been affected by our spatially inconsistent sampling program. We do so by replacing our benthos data collected in 2004 by those from an independent study by Honkoop *et al.* (2008), also carried out in 2004 in our study area. Honkoop *et al.* sampled stratified with respect to habitat, and found lower densities in bare (219.4 and 60.0 m<sup>-2</sup> for *Dosinia* and *Loripes*, respectively) than in seagrass habitat (316.1 and 338.9 m<sup>-2</sup> for *Dosinia* and *Loripes*, respectively). Correcting these densities for species-specific availability fractions (0.73 in *Dosinia* and 0.70 in *Loripes*; van Gils *et al.* 2012) and for the fact that on average at Banc d'Arguin bare-seagrass habitat occurs in a 20–80% ratio (Wolff & Smit 1990), leads to the following available densities of *Dosinia* and *Loripes*: 216.6 and 198.2 m<sup>-2</sup>. Assuming the same values for  $e_1$ ,  $e_2$ ,  $k_1$  and  $k_2$  as we found in our study in 2004 (Table A3.3) predicts that knots would face both their toxin and their digestive constraint in 2004 at an energy intake rate  $Y$  of 0.45 (DRM) and 0.33 mg AFDM<sub>flesh</sub>/s (TDRM; compared to 0.29 mg AFDM<sub>flesh</sub>/s for both DRM and TDRM when using our own 2004 benthos data; Table A3.4).

The outcome of the survival analyses is hardly affected by this data replacement (Table A3.5). There is an even stronger support for the models including TDRM (accumulated QAICc weight: 0.63), and again no support for the DRM models (accumulated QAICc weight: 0.00). Also the models including time as a categorical factor (accumulated QAICc weight: 0.29) and time as a continuous variable (accumulated QAICc weight: 0.08) found little support.

Also the outcomes of the diet statistics were unaffected. DRM still overestimated the proportion of *Loripes* in the diet ( $t = -4.70$ ,  $df = 4$ ,  $P = 0.01$ ), while TDRM diets still matched the observed diets ( $t = -1.61$ ,  $df = 4$ ,  $P = 0.18$ ).

**Table A3.1 List of all candidate models tested for estimating apparent annual survival  $\Phi$  and resighting probability  $p$ .** Factors included in models were age (adult/juvenile), time (year as categorical variable), Time (year as continuous variable), tsm (time-since-marking), site (Abelgh Eiznaya/Baie d'Aouatif), TDRM (energy intake rate predicted by TDRM) and DRM (energy intake rate predicted by DRM). Model statistics listed are quasi-likelihood adjusted Akaike's Information Criterion corrected for small sample size, number of parameters (np), QDeviance,  $\Delta\text{QAICc}$  and QAICc weight.

No.	Model	np	QDeviance	$\Delta\text{QAICc}$	QAICc weight
1	$\Phi_{\text{age+TDRM}} p_{\text{site+time}}$	12	941.44	0.00	0.23
2	$\Phi_{\text{age+time}} p_{\text{site+time}}$	18	929.33	0.01	0.23
3	$\Phi_{\text{age*tsm+time}} p_{\text{site+time}}$	19	927.65	0.35	0.19
4	$\Phi_{\text{age*tsm+TDRM}} p_{\text{site+time}}$	13	941.05	1.63	0.10
5	$\Phi_{\text{age+Time}} p_{\text{site+time}}$	12	943.72	2.28	0.07
6	$\Phi_{\text{age*tsm+Time}} p_{\text{site+time}}$	13	942.20	2.77	0.06
7	$\Phi_{\text{time}} p_{\text{site+time}}$	17	934.13	2.78	0.06
8	$\Phi_{\text{TDRM}} p_{\text{site+time}}$	11	946.50	3.05	0.05
9	$\Phi_{\text{Time}} p_{\text{site+time}}$	11	949.67	6.21	0.01
10	$\Phi_{\text{age+DRM}} p_{\text{site+time}}$	12	949.69	8.25	0.00
11	$\Phi_{\text{age*tsm+DRM}} p_{\text{site+time}}$	13	948.87	9.45	0.00
12	$\Phi_{\text{DRM}} p_{\text{site+time}}$	11	957.21	13.76	0.00
13	$\Phi_{\text{age}} p_{\text{site+time}}$	11	967.03	23.57	0.00
14	$\Phi_{\text{age*tsm}} p_{\text{site+time}}$	12	967.00	25.56	0.00
15	$\Phi_{\text{constant}} p_{\text{site+time}}$	10	973.76	28.30	0.00

**Table A3.2 Parameter estimates obtained by model averaging.** Presented are estimate, standard error (SE), and upper and lower 95% confidence interval (CI) for apparent survival  $\Phi$  ( $\Phi^1$  = adult survival in year after capture,  $\Phi^{2+}$  = adult survival in subsequent years,  $\Phi^{juv}$  = juvenile survival in the year after capture) and recapture probability  $p$  (subscript A for site Abelgh Eiznaya and B for site Baie d'Aouatif).

	year	estimate	SE	lower CI	upper CI
<b>apparent survival</b>					
$\Phi^{2+}$	2004	0.92	0.05	0.77	0.98
$\Phi^{2+}$	2005	0.83	0.03	0.76	0.88
$\Phi^{2+}$	2006	0.88	0.03	0.80	0.93
$\Phi^{2+}$	2007	0.83	0.02	0.78	0.87
$\Phi^{2+}$	2008	0.78	0.03	0.72	0.83
$\Phi^{2+}$	2009	0.76	0.03	0.69	0.81
$\Phi^1$	2003	0.82	0.05	0.72	0.90
$\Phi^1$	2004	0.92	0.05	0.76	0.98
$\Phi^1$	2005	0.82	0.03	0.75	0.87
$\Phi^1$	2006	0.87	0.04	0.78	0.93
$\Phi^1$	2007	0.82	0.03	0.76	0.87
$\Phi^1$	2008	0.77	0.03	0.69	0.83
$\Phi^1$	2009	0.75	0.04	0.67	0.81
$\Phi^{juv}$	2003	0.77	0.06	0.64	0.87
$\Phi^{juv}$	2004	0.89	0.07	0.68	0.97
$\Phi^{juv}$	2005	0.76	0.05	0.67	0.84
$\Phi^{juv}$	2006	0.83	0.05	0.71	0.91
$\Phi^{juv}$	2007	0.77	0.05	0.66	0.85
$\Phi^{juv}$	2008	0.70	0.04	0.61	0.78
$\Phi^{juv}$	2009	0.68	0.05	0.57	0.78
<b>resighting probability</b>					
$p_A$	2003	0.30	0.04	0.23	0.38
$p_A$	2004	0.34	0.03	0.29	0.40
$p_A$	2005	0.47	0.03	0.41	0.52
$p_A$	2006	0.50	0.03	0.45	0.56
$p_A$	2007	0.56	0.03	0.50	0.60
$p_A$	2008	0.52	0.03	0.47	0.57
$p_A$	2009	0.65	0.03	0.60	0.71
$p_B$	2003	0.24	0.04	0.18	0.32
$p_B$	2004	0.28	0.03	0.21	0.35
$p_B$	2005	0.40	0.04	0.32	0.47
$p_B$	2006	0.43	0.03	0.37	0.50
$p_B$	2007	0.48	0.03	0.42	0.55
$p_B$	2008	0.44	0.03	0.39	0.50
$p_B$	2009	0.58	0.03	0.52	0.65

**Table A3.3 Year-specific input parameters used in the diet models.** Listed are available numerical density ( $D$ ;  $m^{-2}$ ), AFDM<sub>flesh</sub> ( $e$ ; mg) and DM<sub>shell</sub> ( $k$ ; mg) of available *Loripes* (subscript  $L$ ) and *Dosinia* (subscript  $D$ ). Since the toxin constraint is defined in terms of maximally tolerable flesh mass intake rate, we expressed toxin contents  $s_L = e_L$  and  $s_D = 0$ . Last row gives overall averages of  $e_L$ ,  $e_D$ ,  $k_L$  and  $k_D$ , which have been used to generate theoretical predictions in Figs 3.4C and 3.5.

Year	$D_L$	$D_D$	$e_L (= s_L)$	$e_D$	$k_L$	$k_D$
2003	68.0	46.5	3.7	6.3	28.1	119.4
2004	23.9	1142.7	4.4	3.7	32.9	72.5
2005	93.5	223.3	9.8	1.1	74.8	22.9
2006	141.5	235.8	9.6	3.4	73.3	67.4
2007	376.3	98.7	5.2	2.6	39.4	52.9
2008	563.0	59.3	6.7	2.7	50.7	53.1
2009	725.5	8.3	4.6	3.4	35.2	63.4
2010	357.2	375.4	4.5	0.8	34.1	17.0
Average			6.1	3.0	46.1	58.6

**Table A3.4 Output from the two diet models for each of the study years.**  $p$  refers to the probability that a prey item is accepted upon encounter for *Loripes* (subscript  $L$ ) or *Dosinia* (subscript  $D$ ),  $Y$  giving the predicted energy intake rate (mg AFDM<sub>flesh</sub>/s),  $Y_L$  and  $Y_D$  giving the absolute contributions of respectively *Loripes* and *Dosinia* to  $Y$ ,  $X = c$  indicating whether the digestive constraint is met (y) or not (n), and  $Z = q$  indicating whether the toxin constraint is met or not.

Year	DRM						TDRM						
	$p_L$	$p_D$	$Y$	$Y_L$	$Y_D$	$X = c$	$p_L$	$p_D$	$Y$	$Y_L$	$Y_D$	$X = c$	$Z = q$
2003	1.00	1.00	0.21	0.10	0.11	n	1.00	1.00	0.21	0.10	0.11	n	n
2004	1.00	0.16	0.29	0.04	0.25	y	1.00	0.16	0.29	0.04	0.25	y	n
2005	1.00	1.00	0.41	0.33	0.09	n	0.30	1.00	0.19	0.10	0.09	n	y
2006	1.00	0.21	0.57	0.51	0.06	y	0.20	0.74	0.32	0.10	0.22	y	y
2007	0.99	0.00	0.67	0.67	0.00	y	0.14	1.00	0.20	0.10	0.10	n	y
2008	0.50	0.00	0.67	0.67	0.00	y	0.07	1.00	0.16	0.10	0.06	n	y
2009	0.58	0.00	0.67	0.67	0.00	y	0.08	1.00	0.11	0.10	0.01	n	y
2010	1.00	0.53	0.58	0.53	0.05	y	0.18	1.00	0.20	0.10	0.10	n	y

**Table A3.5** As Table A3.1, but having our 2004 benthos data replaced by those from Honkoop *et al.* (2008).

Model	np	QDeviance	$\Delta$ QAICc	QAICc weight
$\Phi_{\text{age+TDRM}} \rho_{\text{site+time}}$	12	939.39	0.00	0.38
$\Phi_{\text{age*tsm+TDRM}} \rho_{\text{site+time}}$	13	938.89	1.52	0.18
$\Phi_{\text{age+time}} \rho_{\text{site+time}}$	18	929.33	2.06	0.14
$\Phi_{\text{age*tsm+time}} \rho_{\text{site+time}}$	19	927.65	2.40	0.12
$\Phi_{\text{TDRM}} \rho_{\text{site+time}}$	11	944.81	3.41	0.07
$\Phi_{\text{age+Time}} \rho_{\text{site+time}}$	12	943.72	4.33	0.04
$\Phi_{\text{age*tsm+Time}} \rho_{\text{site+time}}$	13	942.20	4.83	0.03
$\Phi_{\text{time}} \rho_{\text{site+time}}$	17	934.13	4.83	0.03
$\Phi_{\text{Time}} \rho_{\text{site+time}}$	11	949.67	8.26	0.01
$\Phi_{\text{age+DRM}} \rho_{\text{site+time}}$	12	952.20	12.81	0.00
$\Phi_{\text{age*tsm+DRM}} \rho_{\text{site+time}}$	13	951.64	14.27	0.00
$\Phi_{\text{DRM}} \rho_{\text{site+time}}$	11	958.99	17.59	0.00
$\Phi_{\text{age}} \rho_{\text{site+time}}$	11	967.03	25.62	0.00
$\Phi_{\text{age*tsm}} \rho_{\text{site+time}}$	12	967.00	27.61	0.00
$\Phi_{\text{constant}} \rho_{\text{site+time}}$	10	973.76	30.35	0.00



