

**Natal departure timing from spatially-varying environments is
dependent of individual ontogenetic status**

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Abstract Natal departure timing represents one of the first crucial decisions for juveniles born in spatially-varying environments that ultimately disappear but our knowledge on its determinants is limited. The present study aimed at understanding the determinants of juvenile natal departure by releasing individually tagged juvenile pike (*Esox lucius* L.) with variable body size and trophic position in a temporary flooded grassland. Specifically, we whether natal departure depends on individual competitive status (*‘competition hypothesis’*), physiological tolerance to environmental conditions (*‘physiological hypothesis’*) or individual trophic position and the spatial heterogeneity of trophic resources (*‘trophic hypothesis’*). The results indicated that departure timing was negatively correlated with body size at release, showing that the dominance status among competing individuals was not the main trigger of juvenile departure. A positive correlation between departure timing and individual body size at departure was observed, suggesting that inter-individual variability in physiological tolerance did not explain departure patterns. While individual growth performances were similar irrespective of the timing of natal departure, stable isotope analyses revealed that juveniles with higher trophic position departed significantly earlier than individuals with lower trophic position. Therefore, the trade-off driving the use of spatially-varying environments was most likely dependent upon the benefits associated with energetic returns than the costs associated with inter-individual competition or physiological stress. This result highlighted how ontogeny, and particularly ontogenetic niche shift, can play a central role in juvenile’s decision to depart from natal habitats in a predatory species.

Keywords Temporary waters, dispersion, inter-individual variability, stable isotope analyses, ontogenetic niche shift.

Introduction

The departure of juveniles from their natal environment is a crucial ecological and evolutionary phenomenon for many organisms that directly influences individual survival and population functioning. It represents one of the first bottlenecks in many populations as high mortality rates usually occur at this life stage (Gaines and Bertness 1993; Clobert et al. 2001) and hazardous decisions may be fatal for juveniles born in spatially-varying environments (Chesson and Huntly 1997; Chesson 2000). In many aquatic ecosystems, drought and flood episodes dramatically influence both the availability and the suitability of habitats (Matthews 1998; Humphries and Baldwin 2003). They also generate temporarily flooded habitats located at the interface between terrestrial and aquatic ecosystems that are exploited by a wide range of organisms (Williams 2006). These temporary waters serve, for instance, as critical seasonal habitats for reproduction and juvenile development of many animal species (Magoulick 2000; Schwartz and Jenkins 2000; Jopp et al. 2010).

For those species that cannot cope with the complete drying of temporary waters (Williams 2006), natal departure timing of juveniles from these environments is a crucial decision (Werner and Gilliam 1984; Kramer et al. 1997) since it is associated with important costs (e.g. mortality) and benefits (e.g. growth). Indeed, habitat use interpreted as a trade-off (Morris 2003) may be a useful approach to understanding the departure of juveniles from temporary environments. Such a trade-off occurs when an ecological, behavioural or physiological trait of an organism that confers advantage for performing one biological function simultaneously confers a disadvantage for another function (e.g., Chase and Leibold 2003; Brönmark et al. 2008). The departure of juveniles from temporary environments provides a unique opportunity to help our understanding of habitat selection as a mechanism governed by a trade-off (e.g., Morris 2003; Bronmark et al. 2008). The use of harsh and spatially-varying environments by juvenile fish (i.e., temporary waters) represents one of such

trade-off (Fig. 1) because these habitats provide benefits that could balance associated costs compared to more stable environments (e.g., Schlosser 1987; Matthews and Marsh-Matthews 2003; Brönmark et al. 2008). For instance, physiological stress associated with changes in physical/chemical water conditions such as hypoxia and/or hyperthermia can be balanced by foraging benefits and control immigration to and emigration from temporary waters (Fig. 1). Therefore, temporal and spatial fluctuations of the environment and interactions between individuals can dramatically change the trade-off outcomes, but little is known about the triggers of natal departure for juveniles facing such conflicting demands.

The present study aims at identifying the determinants of natal departure timing from temporary habitats using juvenile pike (*Esox lucius* L.) as a model. Pike is a freshwater top-predatory species and adults commonly use temporary waters such as flooded grassland to spawn (Craig 2008). Pike has a high fecundity and juvenile mortality represents a strong bottleneck in many populations (Casselman 1996; Bry et al. 1995; Craig 2008). After hatching, larvae and juveniles develop in temporary waters in spring, and individuals have to disperse to permanent waters as the water level decreases and the habitat availability and suitability decline in early summer (Craig 1996; Cucherousset et al. 2007a). In parallel with natal departure, juvenile pike also display a strong ontogenetic dietary shift from zooplanktivory toward piscivory (Bry et al. 1995; Craig 2008). Therefore, three mutually exclusive hypotheses were tested to identify the mechanisms triggering natal departure of juvenile pike. (1) The ‘*competition hypothesis*’ assumes that natal departure is driven by individual competitive status (e.g., Nilsson 2006). While facing a progressive decrease in habitat availability caused by a progressing drying out, it is expected that the smallest individuals leave before larger conspecifics, since they are poorer competitors (Fig. 2a). (2) The ‘*physiological hypothesis*’ assumes that natal departure is driven by physiological tolerance to environmental conditions (e.g., Chapman et al. 2002). Because of negative

allometric relationship for mass-specific gill surface area, small-bodied fish have more efficient oxygen exchange with water compared with large ones and, consequently, they are less sensitive to hypoxia (Hugues 1984; Robb and Abrahams 2003). Therefore, it is expected that body-size at departure decreases when environmental conditions deteriorate (Fig. 2b). (3) The ‘*trophic hypothesis*’ assumes that natal departure is driven by individual trophic position and the spatial heterogeneity of trophic resources. Indeed, spawning areas generally do not provide a sufficient abundance of prey fish for individuals shifting their diet toward piscivory. Therefore, it is expected that those individuals that are most advanced in ontogenetic development depart first (Fig. 2c). To test these hypotheses and predictions, we stocked juveniles pike from the same cohort into a temporary habitat that dried out and subsequently monitored departure timing at the individual level. We also measured the consequences of departure timing on individual growth rates.

Materials and methods

Study area

The study was carried out in May and June 2005 in a temporarily flooded grassland of the Brière marsh (France, 47°22’N, 02°11’W, Fig. 3: details about the study area available in Cucherousset et al. 2006). The study site covered 0.47 ha (at the start of the study) and was connected through a unique point to an adjacent 2.13 ha pond. It was selected because it is a typical spawning and nursery habitat and wild juvenile pike were previously captured there (Cucherousset et al. 2007a). Food resources strongly differed between the two habitats: the mean abundance of zooplankton was significantly higher in the flooded grassland than in the adjacent pond ($185.5 \text{ mg.L}^{-1} \pm 94.6 \text{ SD}$ and $104.0 \text{ mg.L}^{-1} \pm 77.9 \text{ SD}$, respectively; Wilcoxon signed rank test, $Z = -1.988$, $P = 0.047$, $n = 10$). Conversely, forage prey fish abundance was

twofold lower in the grassland compared to the pond (0.09 ind.m^{-2} and 0.20 ind.m^{-2} , respectively, Cucherousset 2006). Although mean daily temperature was similar between the two habitats (i.e. $20.0^{\circ}\text{C} \pm 2.48 \text{ SD}$ and $20.6^{\circ}\text{C} \pm 2.41 \text{ SD}$ in the flooded grassland and in the adjacent pond, respectively), daily variability was higher in the flooded grassland than in the adjacent pond (mean daily range = $11.43^{\circ}\text{C} \pm 4.16 \text{ SD}$ and $5.46^{\circ}\text{C} \pm 1.72 \text{ SD}$, respectively; Wilcoxon test, $Z = 5.303$, $P < 0.001$, $n = 37$). Mean daily maximal water temperature was significantly higher in the flooded grassland than in the adjacent pond ($25.50^{\circ}\text{C} \pm 4.71 \text{ SD}$ and $22.9^{\circ}\text{C} \pm 3.55 \text{ SD}$, respectively; Wilcoxon test, $Z = 5.061$, $P < 0.001$, $n = 37$).

Monitoring

A total of 192 individually PIT-tagged pike were released into the study site on 20 May 2005 (Cucherousset et al. 2007b). These individuals were young-of-year juveniles that came from manual fertilization of gametes of adults collected in the wild and were hatchery-reared and fed with zooplankton for 4-5 weeks. Individuals were selected to cover the range of body size and trophic level present in the entire cohort and, consequently, to include individuals with different ontogenetic and trophic position. Indeed, cannibalism often occurs when juvenile pike are reared in hatchery conditions (e.g., Bry et al. 1992), leading to the existence of zooplanktivorous and piscivorous individuals within the same cohort. Before releasing, each individual had been anaesthetized with eugenol (0.04 mL.L^{-1}), measured for fork length to the nearest mm (i.e. body-size at releasing, BS_R , average = $51.1 \text{ mm} \pm 5.2 \text{ SD}$), fin-clipped for stable isotope analyses (SIA) to assess trophic level at release and tagged (Cucherousset et al. 2007b; 2009). Pike departure from the grassland to the adjacent pond was monitored continuously with a fyke net (5 mm mesh) equipped with two wings and arranged in a V-shape directing the fish into the chamber. Another net was set in the opposite direction to monitor potential individuals returning to the grassland. However, no tagged individual was

captured in this fyke net. The nets were checked at least once a day throughout the study period. Recaptured individuals were anaesthetized, checked for tags, measured for fork length (i.e. body-size at departure, BS_D) and fin-clipped again to evaluate their trophic position using SIA. This was performed only for individuals recaptured more than five days after release since the pelvic fin had redeveloped sufficiently to be clipped again and to reflect the food assimilated in the grassland. After recovery, fish were released in the adjacent pond. Trapping was conducted until the total drying out of the grassland (i.e. 16 June 2005, see details in Cucherousset et al. 2007b).

Stable isotope analyses

Stable isotopes of carbon and nitrogen were used to estimate the origin of the carbon source ($\delta^{13}C$) and the trophic level ($\delta^{15}N$) of consumers and their prey (e.g., Fry 2006). Fin clipping of juvenile pike was selected because stable isotope values of fin and muscle tissues closely correlate, allowing non-lethal sampling and, consequently, repeated measurement on the same individuals (Cunjak et al. 2005; Jardine et al. 2005; Syvaranta et al. 2010). Young-of-the-year fish display fast somatic growth and rapid isotopic turnover rate (e.g., Bosley et al. 2002; Weidel et al 2010). Recently grown tissue was fin-clipped on recaptured juvenile pike, so it was assumed that significant ontogenic shifts over the experiment could be detected by means of SIA. SIA were performed for surviving fish that departed after five days post release ($n = 29$ among 37 individuals that emigrated, see Cucherousset et al. 2007b) using the samples collected at release ($\delta^{13}C_R$ and $\delta^{15}N_R$) and at departure ($\delta^{13}C_D$ and $\delta^{15}N_D$). To determine individual trophic position prior to release, samples of zooplankton ($n = 3$), that represented the unique food item given to the juveniles pike, were collected at the hatchery. The main potential prey were also sampled in the flooded grassland on 13 May, just before the fish release: zooplankton (mainly *Cladocera* and *Copepoda*, $n = 3$ pooled samples), macro

invertebrates (amphipoda: *Gammarus* sp. (pooled sample composed of 8 individuals) and juvenile red swamp crayfish (*Procambarus clarkii* Girard, pooled sample composed of 3 individuals)) and forage fish (*Gambusia holbrooki* Girard, pooled sample composed of 3 individuals). All samples were oven dried (60°C for 48h) and ground to a homogeneous powder using a mixer mill (Retsch MM 200), weighed (approximately 0.2 mg) and encapsulated in tin foil. SIA were performed at the Stable Isotopes in Nature Laboratory (SINLAB), University of New Brunswick, Canada.

Data analyses

After inspections of normality, Spearman's correlations were used to test the relationships between departure timing (in days from the release day, $n = 29$) and BS_R , BS_D and trophic level at release ($\delta^{15}N_R$) and at departure ($\delta^{15}N_D$). Significant p-values were corrected for multiple comparisons ($n = 4$) using a Bonferroni procedure ($\alpha = 0.05/4 = 0.0125$).

To further investigate the role of individual trophic position on natal departure, we analysed the stable isotope data using circular statistics (Schmidt et al. 2007). Here, this approach was applied at the individual level to compare *i*) the stable isotope shifts between the release and departure of individuals with different trophic levels at release and *ii*) determine whether these shifts differed from the stable isotope differences of zooplankton between the hatchery and the grassland. Specifically, we calculated the position of each individual pike (using tag number) in the isotopic niche space ($\delta^{15}N$ - $\delta^{13}C$, expressed in polar coordinates), and also the differences between values at release ($\delta^{13}C_R$ and $\delta^{15}N_R$) and at departure ($\delta^{13}C_D$ and $\delta^{15}N_D$). The difference between the positions of any given individual is characterized by an angle and a length. The same procedure was applied to zooplankton samples from the hatchery and from the grassland. To allow comparisons between individuals

with different trophic levels, individuals needed to be regrouped according to their trophic position at releasing. Therefore, we used hierarchical cluster analysis to group individuals into two clusters (hereafter referred to as '*low trophic level*' and '*high trophic level*') according to $\delta^{13}\text{C}_\text{R}$ and $\delta^{15}\text{N}_\text{R}$ values. We then calculated the mean vector of change between releasing and departure, defined by its angle and length, for each trophic level group. Vectors were represented in arrows diagrams where decreasing $\delta^{13}\text{C}$ values correspond to left-directed vectors and decreasing $\delta^{15}\text{N}$ values correspond to bottom-orientated vectors (e.g., Wantzen et al. 2002; Schmidt et al. 2007). Rayleigh's tests were used to assess whether the distribution of the angles of change departed from uniformity, i.e. testing for a significant stable isotope shifts for each group and for zooplankton between the hatchery and the grassland. Afterwards, we used the Watson-William's two-sample test to determine whether those shifts differ between trophic level groups and from the stable isotope differences of zooplankton between the hatchery and the grassland.

Finally, we investigated the consequences of departure timing on individual growth rates. Growth rate (mm.day^{-1}) was calculated for each surviving individuals using the following formula: $\text{growth rate} = (\text{BS}_\text{D} - \text{BS}_\text{R}) / \text{departure timing}$ (Cucherousset et al. 2007b). Then, we performed a cubic-splint analysis (Schulter 1988) to determine the shape of the fitness function (with individual growth rate as a proxy) using a Generalized Additive Model with growth rate as a response variable and departure timing as a predictor. Except circular statistics, which were calculated using Oriana 3.11 (Kovach Computing Services, Anglesey, Wales), all statistical tests were performed using R (R Development Core Team 2007) with $\alpha = 0.05$.

Results

Natal departure was relatively continuous throughout the monitoring period (Fig. 4) with, on average, $1.7 (\pm 1.61 \text{ SD})$ individuals departing from the grassland each day. A negative correlation was found between the departure timing and BS_R (Spearman's correlation, $r_s = -0.77$, $p < 0.0001$, $n = 29$) with the largest individuals at release departing first from the temporary water (Fig. 4a). Body-size of individuals departing from the flooded grassland significantly increased as they departed later (Fig. 4b), i.e. departure timing was positively correlated to BS_D (Spearman's correlation, $r_s = 0.72$, $p < 0.0001$, $n = 29$). The departure timing was significantly and negatively correlated with $\delta^{15}N_R$ and $\delta^{15}N_D$ (Spearman's correlations, $r_s = -0.69$, $p < 0.0001$, and $r_s = -0.57$, $p = 0.0011$, $n = 29$, respectively). Indeed, individuals with the highest trophic level at release and at departure, i.e. individuals the most advanced in their ontogenetic diet shift, departed earlier than individuals with the lowest trophic level at release and at departure (Fig. 4c-d).

Among the individuals analysed for stable isotope at departure and used for a hierarchical cluster analysis, nine individuals belonged to the low trophic level group and twenty individuals belonged to the high trophic level group. Both fish and zooplankton demonstrated significant differences in stable isotope values between the hatchery and the grassland (Table 1, Fig. 5). After release, individually tagged fish from hatchery diluted their stable isotope signatures toward grassland signatures, but dilution patterns differed between the two trophic level groups (Watson-Williams test, $df = 1,27$, $F = 20.546$, $p < 0.001$). Specifically, individuals belonging to the low trophic level group displayed a change similar to the difference in zooplankton isotope values (Watson-Williams test, $df = 1,10$, $F = 0.007$, $p = 0.933$), i.e. zooplanktivorous individuals continued to feed upon zooplankton in the grassland (Fig. 5). In contrast, the change for individuals belonging to the high trophic level group was significantly different from the difference in zooplankton isotope values (Watson-Williams test, $df = 1,21$, $F = 22.585$, $p < 0.001$). Finally, no significant effect of departure

timing on individual growth rates was observed (Generalized Additive Model, $df = 1$, $F = 0.501$, Deviance explained = 1.82%, $p = 0.485$, $n = 29$).

Discussion

The timing of departure from natal habitats is crucial for juveniles of many organisms since it strongly affects population functioning. Some potential causes of inter-individual variations in departure timing have been previously reported, including the role of individual body size and/or growth. In amphibians for instance, departure rate of northern red-legged frogs (*Rana aurora*) from their natal pond and survival are positively correlated with individual body size and the date of metamorphosis (Chelgren et al. 2008). In nesting birds such as tree swallows (*Tachycineta bicolor*), space availability in the nest and food resources decline as nestlings grow, and inter-individual variability in wing length explains variations in the timing of fledging (Michaud and Leonard 2000). In other taxa such as fish, juveniles' decision to depart from natal habitat in brown trout (*Salmo trutta*) can be mostly driven by individual body size and growth rate (Acolas et al. 2012).

The present study, however, gives evidence that body size and individual growth alone may not adequately enlighten the dynamics of natal departure from spatially-varying environments. Individually tagged juvenile pike of different sizes were stocked in a temporary flooded grassland, and departure timing was monitored during the period of drying out. Although significant correlations were found between juvenile body size and departure timing, the patterns observed did not match with current hypotheses on the role of body size on the decision to emigrate. Firstly, the largest juvenile at release departed earlier, i.e. before food resources and habitat availability declined. Assuming that they are dominant over small juveniles (e.g., Nilsson 2006), competition between individuals could not explain juvenile's

decision to leave. Therefore, the competition hypothesis was rejected. Secondly, small-bodied fish are known to have more efficient oxygen exchange with water compared with large ones (Pauly 1981; Hugues 1984; Robb and Abrahams 2003), and should be more tolerant to hypoxia when water temperature gets higher and the temporary habitat dries out. However hypoxic and thermal stresses were likely not a major trigger in juveniles' decision to leave since juveniles that departed later were larger than early emigrants. Therefore, the physiological hypothesis was rejected. Conversely, juveniles that departed earlier were smaller at departure than late migrants and these individuals had already achieved their ontogenetic trophic niche shift toward piscivory. Stable isotope analyses revealed that about two third of the juveniles used in our experiment were piscivorous at release, meaning that they had developed cannibalistic behaviour as commonly reported for such species (e.g., Bry et al. 1992; Juanes 2003; Skov and Koed 2004).

Stable isotope analyses on recaptured individuals leaving the temporary habitat revealed that piscivorous individuals departed earlier than zooplanktivorous individuals, and it is likely that these individuals migrated to the adjacent pond in search of higher abundance of prey fish. Some piscivorous individuals, however, tended to shift back to a zooplankton diet soon after their release in the flooded grassland, as indicated by a slight decrease of $\delta^{15}\text{N}$ values in their tissues (Fig. 5). This shift back to zooplankton diet was likely to be suboptimal with lower benefits and/or higher costs (Fig. 1), and they finally emigrated shortly afterwards. This is in line with laboratory experiments by Galarowicz and Wahl (2005), who demonstrated that energy return ($\text{J} \cdot \text{min}^{-1}$) of large young-of-the-year walleye (*Sander vitreus* Mitchill) was high when feeding on fish and low when feeding on zooplankton. Therefore, the trophic hypothesis is accepted, indicating that the trade-off driving the use of spatially-varying environments is likely to be more dependent upon the benefits associated with energetic returns than the costs associated with inter-individual conflicts or physiological

constraints. This highlights how ontogeny, and particularly ontogenetic niche shift toward higher trophic level, can play a central role in juvenile's decision to depart from natal habitats in a predator species.

As water level decreased, food availability and water quality (higher temperature and lower dissolved oxygen) concurrently declined and the risk of mortality from being trapped in desiccating pools became higher (Capone and Kushlan 1991; Magoulick and Kobza 2003). In our study, however, zooplankton abundance was higher in temporary flooded grassland than in the adjacent pond. Our results illustrated a trade-off between the costs linked to the risk of being stranded and suffering poor water conditions, and the benefits from higher energy returns resulting from higher food abundance and the advancement in the ontogenetic niche shift toward higher trophic level. Interestingly, we did not find any significant effect of natal departure timing on individual growth rate. Contrary to other studies (e.g., Post 2003; Galarowicz and Wahl 2005), an early shift toward piscivory and departure from the temporary grassland did not affect individual growth performance at early life stages in our experiment. Nevertheless, earlier natal departure might be indirectly beneficial to individual survival, since mortality risk was likely to sharply increase in the temporary flooded grassland as water level declined (Kushlan 1976; Capone and Kushlan 1991). As well, early transition to piscivory and departure from the natal temporary habitat might increase subsequent probabilities of surviving to predation during the summer and starvation over the winter (e.g., Sogard 1997; Post 2003). Complementary investigations are now needed to further quantify potential delayed effects of early ontogenetic shift in diet and natal departure timing from spatially-varying environments on the life-history of individuals and their fitness.

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Table 1 Directional statistics quantifying the shift in stable isotope values of zooplankton and the two trophic level groups of juvenile pike between the hatchery (values at release: $\delta^{13}\text{C}_\text{R}$ and $\delta^{15}\text{N}_\text{R}$) and the flooded grassland (values at departure: $\delta^{13}\text{C}_\text{D}$ and $\delta^{15}\text{N}_\text{D}$). Significant p-values are in bold.

Group	n	Main vector		Raleigh's test	
		Direction (SD)	Length	Z	p-values
Zooplankton	3	258.4 (6.14)	0.994	2.97	0.035
Low trophic level	9	257.4 (17.4)	0.955	8.21	< 0.0001
High trophic level	20	235.6 (7.5)	0.991	19.60	< 0.0001

Figure legends

Fig. 1 A conceptual framework of the seasonal changes of (a) the costs (e.g. physiological stress), (b) the benefits (e.g. foraging return) and (c) the trade-off in spatially-varying environments (i.e. temporary waters, dotted line) and more stable environments (i.e. permanent waters, full line). Fish colonisation of and departure from spatially-varying environments are expected to occur when the cost are higher than the benefits, as indicated by the arrows. For instance, increased environmental harshness during drought is likely to induce a shift to more stable habitats (i.e. juvenile departure) when the instantaneous foraging return does not balance the associated physiological stress from hypoxia and hyperthermia in water.

Fig. 2 The three hypotheses tested in this study to identify the mechanisms triggering juvenile pike departure from temporary waters: (a) *Competition hypothesis*: smallest individuals emigrate before larger conspecifics as they are less competitive, (b) *Physiological hypothesis*: largest individuals at releasing emigrate the first because they are less tolerant to hypoxia and hyperthermia, and (c) *Trophic hypothesis*: individuals with higher trophic level (i.e. the most advanced in their ontogenetic diet shift) emigrate first because the natal habitat does not provide enough food resources (see text for additional details).

Fig. 3 Progressive drying out of a typical temporarily flooded grassland in the Briere marsh from spring to summer 2006 (a April 5th, b April 18th, c May 30th, d July 5th).

Fig. 4 Correlations between departure timing (days) of juvenile pike ($n = 29$) from the flooded grassland and (a) body-size at releasing (BS_R , mm), (b) body-size at departure (BS_D , mm), (c) trophic level at releasing ($\delta^{15}N_R$, ‰), and (d) trophic level at departure ($\delta^{15}N_D$, ‰). The continuous lines represent the significant correlations and the dotted lines are the 95% confident intervals.

Fig. 5 Arrow diagram for the isotopic shift of (a) zooplankton from the hatchery to the grassland, (b) individuals belong to the low trophic level group ($n = 20$) and (c) individuals belong to the high trophic level group ($n = 9$). For juvenile pike, each arrow represents a single individual and was calculated using the stable isotope values at the beginning (its release in the grassland) and at the end (its departure from the grassland) of the study. The straight dotted line is the mean vector of change among all individuals and the curved dotted line indicates the 95% confidence interval. Complementary statistics are provided in Table 1.

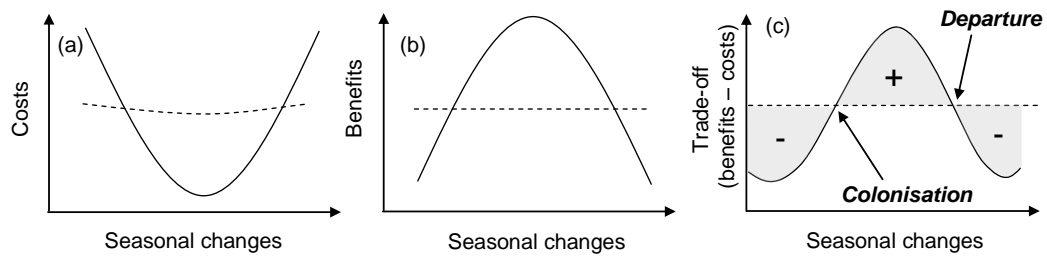


Figure 1

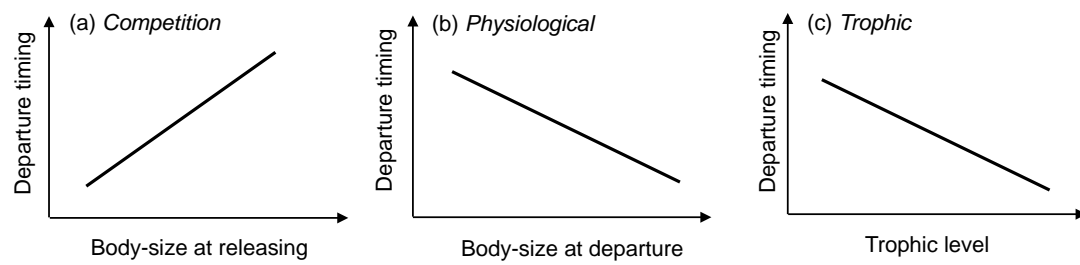


Figure 2

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Figure 3

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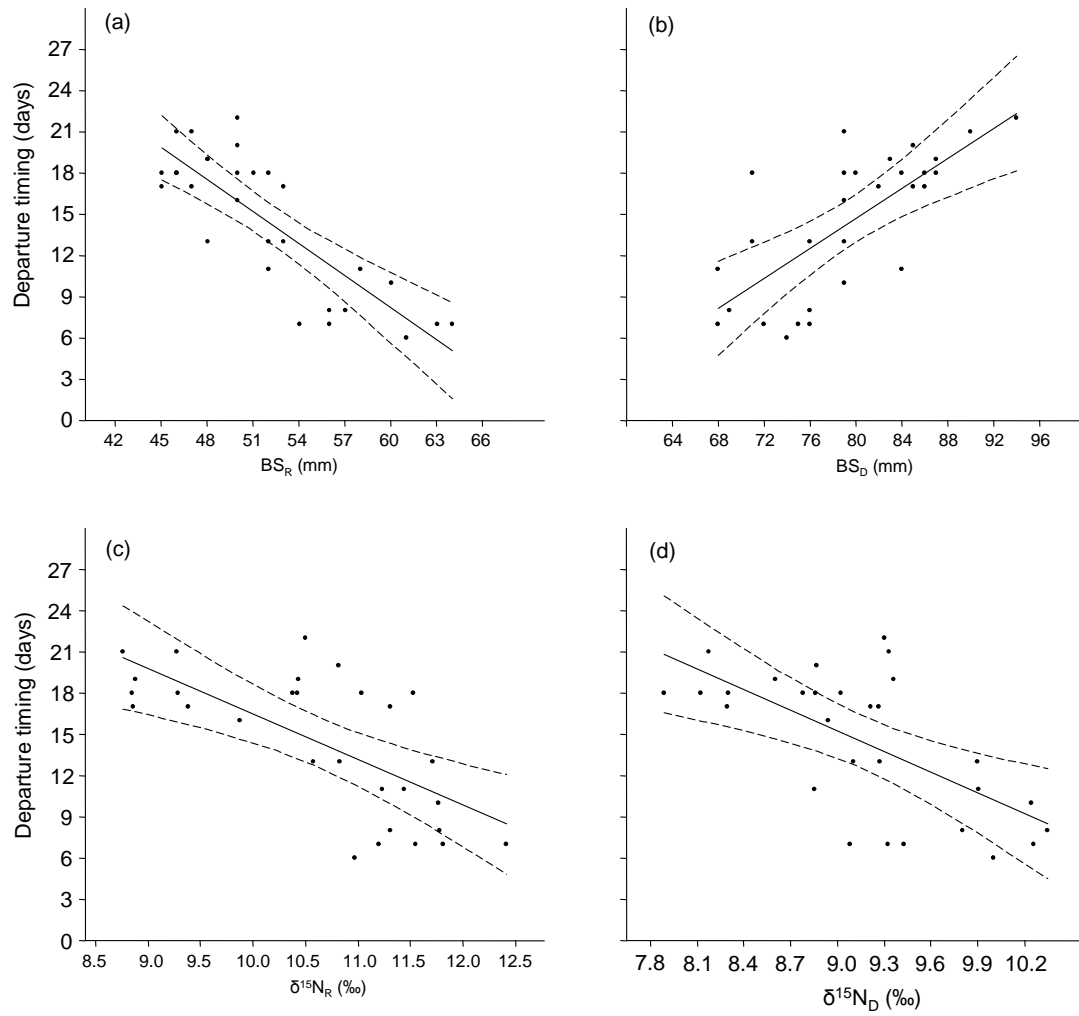


Figure 4

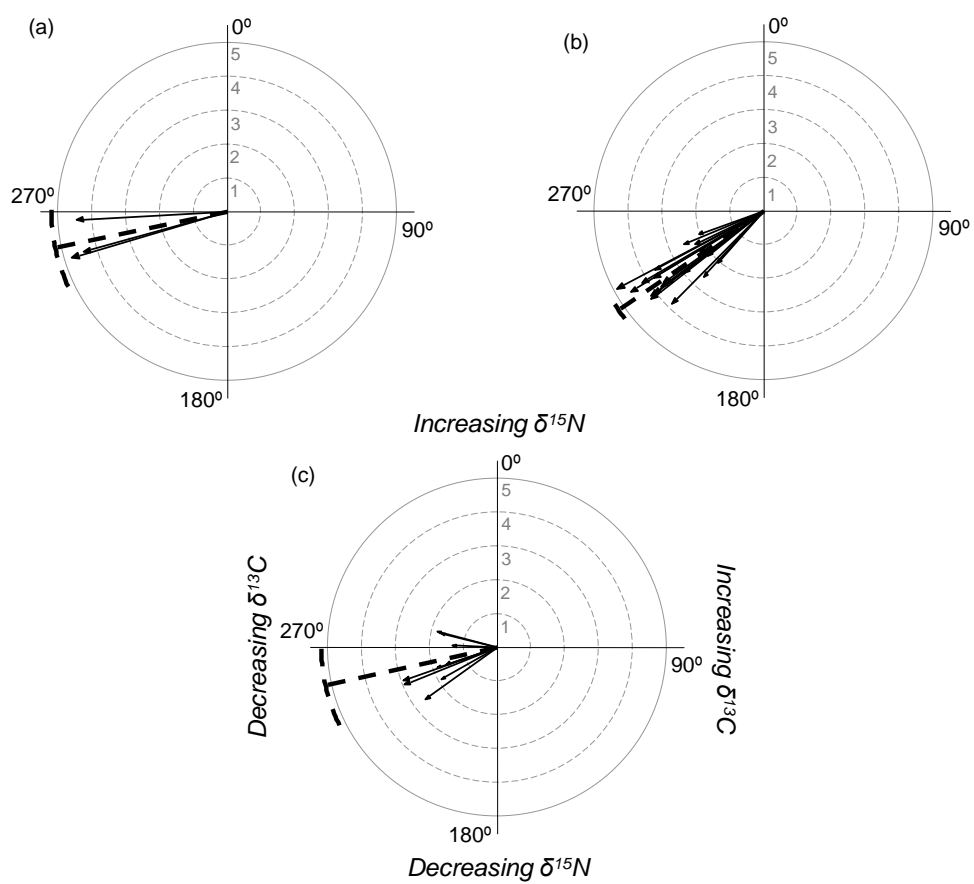


Figure 5