Journal of Sea Research 92 (2014) 115–124

Contents lists available at ScienceDirect

Journal of Sea Research

journal homepage: www.elsevier.com/locate/seares

Trophic resource partitioning within a shorebird community feeding on intertidal mudflat habitats☆

Pierrick Bocher [a,*], Frédéric Robin [a], Jessica Kojadinovic [a], Philippe Delaporte [b], Pierre Rousseau [b], Christine Dupuy [a], Paco Bustamante [a]

[a] Laboratory Littoral Environnement et Sociétés (LIENSs), UMR 7266 CNRS-Université de La Rochelle, 2 rue Olympe de Gouges, 17000 La Rochelle France

[b] Réserve Naturelle Nationale de Moëze-Oléron, Ligue pour la Protection des Oiseaux, Plaisance, 17180 Saint-Froult, France

ARTICLE INFO

Article history:
Received 2 January 2013
Received in revised form 16 February 2014
Accepted 24 February 2014
Available online 6 March 2014

Keywords:
Trophic Level
$\delta^{15}N$
$\delta^{13}C$
Isotopic Niches
Mudflat Ecosystem
Scolopacidae
Charadriidae

ABSTRACT

In ecological systems, it is necessary to describe the trophic niches of species and their segregation or overlap to understand the distribution of species in the community. In oceanic systems, the community structure of top predators such as seabird communities has been well documented with many studies in several biogeographical areas. But for coastal habitats, very few investigations on the trophic structure have been carried out in avian communities. In this study, the trophic resource partitioning was investigated on eight of the most abundant species of a shorebird community on the central Atlantic coast of France. Our work comprised a comprehensive sample of birds with different ecomorphogical patterns and data on their main prey to encompass potential sources of overlap and segregation in this community. We examined the stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic composition of blood to investigate the trophic structure (1) on a temporal scale by comparing migration and wintering periods; (2) on a spatial scale through inter-site comparisons; and (3) on the community level within groups of phylogenetically related species. Diets appeared different in several cases between periods, between sites and between juveniles and adults for the same sites. A clear trophic partitioning was established with four functional groups of predators in winter inside the community. The Grey Plover, the Bar-tailed Godwit, the Curlew and a majority of the dunlins were worm-eaters mainly feeding on *Nereis diversicolor* or *Nephtys hombergii*. Two species were predominantly deposit-suspensivorous mollusc-eaters, including the Red Knot and the Black-tailed Godwit feeding mainly on *Macoma balthica*. The Oystercatcher fed mainly on suspensivorous molluscs like *Cerastodrema edule* and two species including the Redshank and some dunlins adopted opportunistic behaviours feeding on mudflat and/or in marshes.

1. Introduction

Predator–prey relationships and their dynamics in space and time are among the fundamental basis of the structure of animal communities and their evolution (Paine, 1980). Numerous theoretical models have attempted to define different aspects of food webs and their implications in the stability, complexity, connectivity and equilibrium of communities' parameters (Fussmann and Heber, 2002). In order to understand the distribution of species in the community (e.g. Myers and Worm, 2003) it is necessary to describe the trophic niches of species and their segregation or overlap, as well as parameters including species richness, relative abundance and spatial or temporal variations. Previous studies have emphasized that the overlap in the diets of different organisms with possible intra- and interspecific competition for food influences the variation in composition of species in communities (Aguilera and Navarrete, 2011; Forero et al., 2004; Werner and Gilliam, 1984). Progress in this domain is however restricted as it is difficult to deliver empirical evidence supporting theoretical developments in community ecology, especially for marine systems.

In marine systems, the structure of seabird communities established from specific trophic niches' comparison has been well documented from birds caught during their breeding season (e.g. Bearhop et al., 2006; Cherel et al., 2008; Forero et al., 2004; Jaeger et al., 2010; Kojadinovic et al., 2008; Phillips et al., 2011). But for shorebird communities very few investigations on the trophic interactions between predators on intertidal mudflat have been carried out. Most shorebird species are predators specialized on intertidal mudflat habitats during the non-breeding period (Colwell, 2010; van de Kam et al., 2004). On the Western European coastline, birds arrive in late summer-early

☆ Given her role as Guest Editor/Editor-in-Chief, Christine Dupuy had no involvement in the peer-review of this article and has no access to information regarding its peer-review. Full responsibility for the editorial process for this article was delegated to Carl Van Colen.

* Corresponding author at: UMR 7266 LIENSs, CNRS-University of La Rochelle, 2 rue Olympe de Gouges, 17000 La Rochelle, France. Tel.: +33 5 45 46 82 92; fax: +33 5 45 46 82 64.

E-mail address: pbocher@univ-lr.fr (P. Bocher).

http://dx.doi.org/10.1016/j.seares.2014.02.011
1385-1101/

autumn from their breeding sites in Northern Europe or Arctic latitudes, and part of them stay during the entire winter period on coastal wetlands (Delany et al., 2009). Other populations use the same sites only as stopovers coming back from breeding sites in autumn or on route from wintering area from Africa in spring (Delany et al., 2009; van de Kam et al., 2004). A dozen of species are common on the coast of Western Europe and forage exclusively or regularly on intertidal mudflat according to tidal rhythms (van de Kam et al., 2004). Shorebirds commonly aggregate in dense, mixed-species flocks feeding on the same areas (Burger et al., 1979; Metcalfe, 1989). They feed on benthic prey from macrofauna communities (Meire et al., 1994; Yates et al., 1993; Zwarts and Wanink, 1993) and smaller species may also ingest biofilm and microfauna (Kuwae et al., 2012). The mechanisms by which species of shorebirds are segregated should involve the combination of diet, feeding area, feeding methods and behaviour (Baker and Baker, 1973). Moreover, differences in bill morphologies and sizes inside the community of shorebirds are adapted for feeding on a subset of potential prey and should avoid competition. The functional relationships between bill morphology and diet should lead to specialization on a limited array of prey species (Nebel and Thompson, 2011; Nebel et al., 2005). Species should differ in selection of prey of different sizes, with larger-bodied species feeding on larger prey of wider size range and small-bodied species feeding on smaller prey with less variability in their selection.

Different methods such as stomach content or faeces analysis have previously been used to describe the diet and consequently contribute to define the trophic niche (Colwell, 2010). But these methods, while they can give high degree of precision on prey type and size, are nevertheless time consuming and thus cannot be applied to a high number of individuals. An alternative and complementary approach to these methods is the measurement of naturally occurring stable isotopes in consumers and their prey (Layman et al., 2012). The principle underlying this approach is that stable isotope deviations of nitrogen and carbon in consumers reflect those of their prey as they are enriched in a predictable manner. Conventionally expressed as $\delta^{15}N$ (‰), the deviation of ^{15}N to ^{14}N generally exhibits a stepwise enrichment from 2 to 5‰ relative to dietary nitrogen (Kelly, 2000). This discrepancy of $\delta^{15}N$ is caused by a selective retention of the heavy isotope and excretion of the light one. It provides a tool for comparing the relative trophic level of various consumers living in the same environment. The deviation of ^{13}C to ^{12}C (denoted as $\delta^{13}C$) is also enriched with respect to dietary carbon, but to a much lesser degree than $\delta^{15}N$, on the order of 1‰ (De Niro and Epstein, 1978). Stable isotope deviations also have the advantage of offering information on a larger time scale according to the isotopic turnover rates of the considered tissue, $\delta^{15}N$ and $\delta^{13}C$ measurements of multiple tissues providing dietary information on several days to several weeks (Hobson and Clark, 1992).

In this study, the trophic resource partitioning in a shorebird community was investigated on the central Atlantic coast of France. On the same sites, previous diet investigations on Red Knot *Calidris canutus* (Quaintenne et al., 2010) and Black-tailed Godwit *Limosa limosa* (Robin et al., 2013) revealed a high degree of specialization on a low number of prey species. However, the number of species foraging at the same time on a same mudflat could be high, and relationships among them are unknown and poorly studied for shorebirds. Our work comprised a comprehensive sample of shorebirds and their main prey to encompass the potential sources of overlap and segregation in the community. Our overall objective was to describe the trophic structure of a complex assemblage of shorebirds at different scales and determine the degree of ecological overlap/segregation among species. More specifically, we investigated the trophic structure at multiple scales: (1) temporal in comparing migration and wintering; (2) spatial by inter-site comparison; and (3) among individuals and species within the same temporal and spatial conditions.

2. Materials and methods

2.1. Study sites and periods

The Pertuis Charentais, on the French Atlantic coast, are shallow coastal embayments formed by the islands of Oléron and Ré (Fig. 1). Protected by these offshore islands, the coastline is constituted of a series of muddy estuaries and bays followed by dyked-up polders and marshes reclaimed from the saltmarshes. The local wintering shorebird populations were studied at three sites (Fig. 1): on Ré Island (46°13′N; 01°30′W) with c. 23,000 individuals for 20 species counted in mid-January 2010; in Yves Bay (46°02′N; 01°03′W) with c. 10,000 individuals for 14 species; and on the main study sites of the Marennes-Oléron Bay, (45°53′N; 1°05′W) with c. 67,000 individuals for 18 species (Caillot and Elder, 2000–2010; Mahéo, 2011). The study was carried out only during the non-breeding period and precisely during the post-breeding migration designated as the autumn stage (July to September) and the winter stage (October to March). Very few shorebirds breed in France and almost all the individuals in the Pertuis Charentais come from northern Europe, Siberia, Greenland or Arctic Canada after their breeding stage (Delany et al., 2009). During autumn individuals migrating toward the African coast or southern Europe can mix with local wintering residents. The pre-breeding migration occurs in April and May for most of the species but some individuals of some species can stay locally during the stopover in March when coming from Africa or Iberia (Delaporte Pers.Com.). The birds were sampled in three different sites, distant from each other by only a few tens of kilometres but comprising distinct mudflat habitat characteristics. The sites of Moëze and Yves are bare mudflats with soft sediment in Moëze and a gradient of sandy to muddy sediment in Yves Bay (Bocher et al., 2007). In Ré island, on the intertidal area of the bay where most of the shorebirds forage, the mudflat is covered with a seagrass bed of *Zostera noltii*.

2.2. Capture and sampling

Shorebirds were caught in mist-nets on high tide roosts during non-moonlit nights from February 2007 to November 2009. However, 68% of the individuals sampled were caught at the roost in the Moëze marshes in the Marennes-Oléron Bay (Table 1). At the two other sites, the capture effort was concentrated between September and November 2007 or 2008. The number of individuals sampled per species, per site and per season depended on catching success and field facilities for sampling blood on birds in safe conditions. In this study, we retained only species most successfully caught and listed among the ten most common species in the Pertuis Charentais. These species were, from the smallest (c. 45 g) to the largest (c. 750 g): Dunlin *Calidris alpina*, Redshank *Tringa totanus*, Red Knot *C. canutus*, Grey Plover *Pluvialis squatarola*, Bar-tailed Godwit *Limosa lapponica*, Black-tailed Godwit *L. limosa*, Eurasian Oystercatcher *Haematopus ostralegus* and Eurasian Curlew *Numenius arquata* (Table 1). Feathers and whole blood were sampled from randomly selected birds, after which the birds were immediately released (Table 1). Juveniles (JUV) considered as the individuals between their birth and the second moult in autumn were distinguished from adults (AD) using isotopic signatures in wing feathers (Atkinson et al., 2005; Bocher et al., 2012). It was however not possible to sex all individuals according to biometric or plumage characteristics. The most common and abundant benthic invertebrate species and the microphytobenthos of adjacent tidal mudflat of Moëze marshes (main catch site) were collected on two stations at high and medium intertidal levels in February 2008. Terrestrial invertebrates were collected in Moëze marshes in March 2008. All the species were considered as potential prey for birds (van de Kam et al., 2004) and their isotopic signatures were established to provide values of food sources.