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Marine resource flows to terrestrial arthropod predators on a temperate island: the role of subsidies between systems of similar productivity

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Abstract Marine-terrestrial resource flows can subsidies recipient consumers at various trophic levels. Theory suggests that the importance of such spatial subsidies depends on the productivity gradient between adjacent systems; however, the empirical data required to test this assumption are scarce. Most studies of marine-terrestrial subsidies have been performed in arid coastal habitats of low productivity surrounded by productive ocean waters. We examined the importance of marine resource inputs for terrestrial consumers on a temperate, productive forest island surrounded by a marine system of similar productivity. The importance of marine resources for the dominant arthropod consumers was estimated using stable isotopes and linear mixing models. We compared isotopic signatures of spiders and ants captured along a gradient from shore to inland to estimate how far marine-derived energy penetrates the island. We evaluated the distribution of ground-dwelling arthropods using pitfall-trap transects extending from the supratidal-forest boundary to the middle of the island. The contribution of marine-derived energy assimilated by arthropod consumers differed both among taxa and location. Marine-derived resources contributed >80% to the assimilated C of intertidal spiders and 5–10% for spiders at the forest edge and further inland. Ants assimilated 20% of their C from marine-derived resources and this proportion was not affected by distance from shore. Spiders, ants, and all arthropods combined exhibited no spatial aggregation towards the shore. Our results indicate that on temperate islands marine-terrestrial subsidies might be predominantly an edge effect, confined to intertidal consumers. Mobile consumers that opportunistically forage in intertidal habitats play an important role in transferring marine-derived energy further inland. This suggests that the importance of the productivity gradient for spatial subsidies can be modified by the mobility traits of the recipient consumers and their degree of specialization on the interface habitat.

Keywords Allochthonous inputs · Connectivity · Functional traits · Resource flux · Stable isotopes

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Introduction

The flow of resources from outside the focal habitat (i.e. allochthonous resources) can change the structure and dynamics of populations, communities, and food webs in recipient habitats through arrays of direct and indirect interactions (Polis et al. 1997; Takimoto et al. 2002; Marczak et al. 2007). Such spatial subsidies have been empirically demonstrated in a range of connected systems (Polis et al. 1997); for example, emerging aquatic insects can support high densities of riparian arthropods, lizards, and birds (Nakano and Murakami 2001; Sabo and Power 2002a; Paetzold et al. 2006), detached reef algae can subsidies consumers in less productive seagrass beds (Wernberg et al. 2006), and sea wrack and guano can fuel island food webs (Anderson and Polis 1998; Stapp and Polis 2003a). Despite growing evidence of the importance of allochthonous inputs for different systems, we know very little about the factors that control the flow of resources between habitats (Witman et al. 2004; Baxter et al. 2005; Marczak and Richardson 2007). Theoretical considerations suggest that the importance of allochthonous inputs is largely dependent on a productivity gradient between adjacent systems (Polis et al. 1997). However, empirical information to test this assumption is very scarce because subsidy research has focused on recipient habitats of low productivity that receive inputs from more productive donor habitats (Marczak and Richardson 2007), such as cobble bars along productive rivers (Sabo and Power 2002b; Paetzold et al. 2005) or desert islands surrounded by highly productive coastal waters (Polis and Hurd 1996). Almost nothing is known about the importance of allochthonous resources in systems where productivity of the recipient habitat is relatively high and not overwhelmed by productivity of the donor habitat.

Spatial subsidies can be important along the coastal ecotone because of its large spatial extent and the high productivity of coastal waters (Polis and Hurd 1996). The coastal ecotone occupies about 8% of the Earth's surface along an estimated 594,000 km of shoreline (Polis and Hurd 1996). Marine-derived resources in the form of beach-cast algal wrack and animal carrion can support high densities of detritivorous arthropods, which in turn can form an important food source for a range of terrestrial consumers including arachnids, lizards, and rodents (Polis and Hurd 1995; Stapp and Polis 2003a; Catenazzi and Donnelly 2007). Most of our knowledge of marine-terrestrial subsidies is derived from very unproductive terrestrial habitats juxtaposed with very productive ocean waters, such as desert islands in the Gulf of California or the hyper-arid Peruvian coastal desert (Polis and Hurd 1996; Catenazzi and Donnelly 2007). To appreciate the role of marine-terrestrial resource flows across the coastal ecotone worldwide, we need to know more about their relative importance in other, less extreme, coastal habitats, particularly in those where terrestrial primary productivity is relatively high and similar to that found in surrounding marine ecosystems.

In this study, we examined the importance of marine-derived resources for terrestrial arthropod consumers (spiders and ants) on a small, temperate, hardwood forested island (Horse Island) surrounded by productive waters (Long Island Sound, USA). Terrestrial net primary productivity in forests of southern New England is estimated to be 800–1,200 g C m^{-2} $year^{-1}$ (Aber and Federer 1992; Ollinger et al. 1998); and marine net primary productivity for Long Island Sound is estimated to be 400–1,000 g C m^{-2} $year^{-1}$ (Riley 1956; Goebel et al. 2006). The observation that terrestrial productivity is similar or even likely higher than marine productivity makes Horse Island an ideal system to explore the role of the productivity gradient in controlling spatial subsidies. We selected a small island (~0.04 km^2) for detailed investigations because any process involving resource flows between marine and terrestrial systems should be most pronounced on small islands as a result of their higher perimeter to area ratio (Polis and Hurd 1996).

Specifically, we addressed the question to what degree do major guilds of the most abundant terrestrial arthropod predators/scavengers (cursorial and web spiders and ants) derive energy from marine inputs in the form of stranded shore wrack; and how far do marine resource inputs penetrate the island? Stable isotopes were used to estimate the importance of marine-derived resources to the diet of spiders and ants captured along a gradient from shore to inland. Additionally, we examined whether arthropod consumers are more abundant near shore than in inland areas. This study provides the first empirical assessments of the importance of marine resource inputs in a system where primary productivity in the recipient habitat is relatively high and similar to that of the donor habitat.

Materials and methods

Study site

Fieldwork was conducted on Horse Island (41°14.7′N, 72°45.5′W) during summers in 2003–2004. Horse Island is the largest (area, 0.04 km^2; perimeter, ~1,000 m) and one of the outermost islands of the Thimble Island chain in the Long Island Sound, Connecticut, USA (Goldstein 1975). The island rises to ~15 m above sea level and has a large, rocky intertidal zone that slopes up to the vegetation line. Most of the island is covered with dense oak–hickory forest with woody shrubs and vines such as poison ivy. Forests of similar stand composition at Harvard Forest, Massachusetts, are estimated to have annual net primary productivity of 650–700 g C m^{-2} $year^{-1}$ (Turner et al. 2005), but the longer growing seasons of coastal southern Connecticut produced annual net primary productivity of >1,000 g C m^{-2} $year^{-1}$ (Aber and Federer 1992; Ollinger et al. 1998). Long Island Sound is characterized by relatively high algal primary productivity. Annual net primary productivity increases from 400 g C m^{-2} $year^{-1}$ in eastern Long Island Sound to around 1,000 g C m^{-2} $year^{-1}$ in western Long Island Sound (Riley 1956; Goebel et al. 2006). Net primary productivity in the waters immediately surrounding Horse Island is estimated to be around 400 g C m^{-2} $year^{-1}$ (Goebel et al. 2006).

Stranding of shore drift represents the main conduit of marine resource inputs, while transfer via guano is insignificant because of the absence of nesting seabird colonies on the island (personal observation). Major sources of shore drift are the dense beds of benthic macroalgae (*Fucus* spp.)

in the rocky intertidal, and reed beds and tidal marshes along the Connecticut coast and estuaries. Estimated plant productivity of tidal marshes in Long Island is more than 93,000 Mg plant material year^{-1} which is potentially available as a source of plant detritus (Niering and Warren 1980). Standing stock of shore wrack above mean tide line in July/August 2003 was 254.53 kg dry weight, based on two surveys of the total area of wrack in combination with dry weight estimates of a number of sub-samples ($n = 56$) taken randomly at different locations along the supratidal. Marine detritus consisted mainly of macroalgae (*Fucus* spp.) and grasses (*Phragmites* spp.), but also included larger marine invertebrates, such as crabs and jellyfish, mussels, and marine birds.

Stable isotopes

We used natural abundance of C and N stable isotopes to estimate the role of marine subsidies for dominant generalist terrestrial consumers (cursorial spiders, web spiders, and ants). Stable isotopes have been successfully applied to track the flow of marine resources to terrestrial food webs because of the generally large differences in the C stable isotope ratio (δ^{13}C) and N stable isotope ratio (δ^{15}N) of marine and terrestrial primary producers and their consumers (Anderson and Polis 1998; Stapp and Polis 2003a; Catenazzi and Donnelly 2007).

Organisms for isotope analysis were collected in July–October 2003, and in July/August 2004. Superficial leaf litter and marine-derived detritus including algae (*Fucus)* and reeds (*Phragmites*) were collected from different sites around the island. We sampled herbivorous insects (Lepidoptera larvae and Auchenorrhyncha) and detritivorous terrestrial (Collembola, Acari, and *Oniscus spp.*) and intertidal arthropods (Amphipoda, Diptera) to indicate the isotopic signature of the potential food sources for the terrestrial arthropod consumers. Intertidal arthropods were collected from accumulations of the stranded marine detritus. Web spiders, cursorial spiders, and ants were collected in the upper intertidal to supratidal habitat and in the forest at different distances (0–5 and 10–40 m, maximum distance from the intertidal to the middle of the island ~40 m) from the supratidal boundary. Samples were frozen shortly after sampling and later dried at 60°C for 48 h. Dried samples were ground into a fine powder prior to analyses. For all samples we analysed a homogenized composite sample of five to ten individuals, except for spiders which were analysed individually. We needed to combine smaller organisms (potential prey) into composite samples in order to derive enough biomass for analysis. Further, composite samples also provide a robust measure of the prey because they integrate individual based variation in isotopic signatures. For the spiders, however, we were interested in the individual variation in the importance of marine-derived prey.

We used a single isotope (δ^{13}C), two-source linear mixing model as reported in Phillips (2001), to estimate the proportion of marine-derived prey in the diet of terrestrial arthropod predators. The model incorporates isotopic variance of the food sources and the consumers. We assumed a trophic fractionation of 0.4‰ for δ^{13}C (Post 2002). We used a two-source mixing model because a dual isotope (δ^{13}C and δ^{15}N) three-source mixing model (marine detritivores, terrestrial detritivores, and terrestrial herbivores), assuming a trophic fractionation of 3.4‰ for δ^{15}N (Post 2002), resulted in negative values for the herbivorous prey as a result of its depleted δ^{15}N values (Fig. 1). This indicates that herbivores did not contribute substantially to the diet of the arthropod consumers. Consequently, we used terrestrial and marine detritivores as isotopic baselines of the endmembers. The use of δ^{13}C of the terrestrial detritivores as terrestrial endmember resulted in a more conservative estimate (i.e. potentially a small underestimation) of the proportion of marine-derived prey in the consumers because δ^{13}C of detritivores (-26.1 ± 0.2‰) was slightly enriched (i.e. more similar to the δ^{13}C signature of the marine-derived prey: -14.7 ± 0.3‰) in comparison to the herbivores (-28.8 ± 0.6‰). For instance, in the hypothetical case that the terrestrial prey component of a consumer with an intermediate $\delta^{13}\text{C} = -22$‰ would have consisted of 50% herbivores and 50% detritivores, instead of 100%

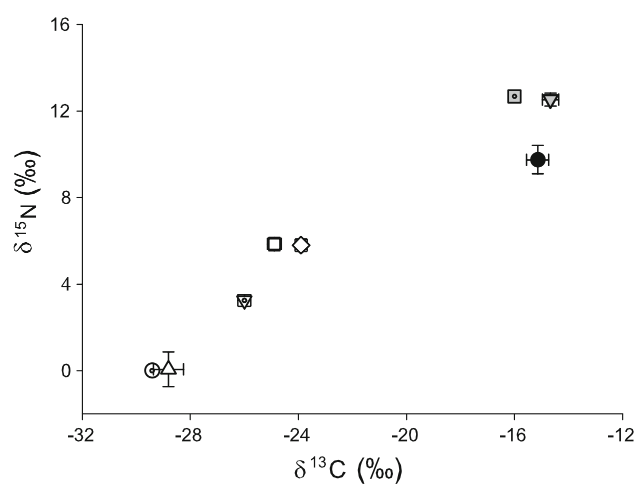

Fig. 1 Natural δ^{13}C and δ^{15}N values (mean ± SE) of marine plant detritus ($n = 6$), terrestrial plants ($n = 4$), intertidal ($n = 8$) and terrestrial detritivores ($n = 10$), intertidal ($n = 17$) and terrestrial spiders ($n = 46$), terrestrial herbivores ($n = 6$) and ants ($n = 10$). Each replicate for spiders represents a single individual and for all other arthropod groups composite samples of five to ten individuals. *Black symbols* Marine origin, *grey symbols* intertidal origin, *white symbols* terrestrial origin, *circles* plant material, *inverted triangles* detritivores, *triangle* herbivores, *squares* spiders, *diamond* ants

detritivores as assumed in the mixing model, we would underestimate the proportion of marine-derived energy by ~7% (36% instead of 43%). However, as indicated by the δ^{15}N signature, such a high proportion of herbivorous prey was unlikely. Stable isotope samples were pooled across 2003 and 2004 because there was no significant difference in δ^{13}C between years for the main food sources (intertidal detritivores, $t = 0.46$, $df = 7$, $P = 0.66$; terrestrial detritivores, $t = 0.94$, $df = 11$, $P = 0.37$). We did not correct for lipid content (Post et al. 2007a) because the C:N ratio for all organisms was consistently low (4.29 ± 0.09) and there were no significant differences in the C:N ratios among the food sources ($F_{2,16} = 2.15$, $P = 0.12$) and the different consumer groups ($F_{2,40} = 1.94$, $P = 0.16$). Further, the signal-to-noise ratio was high because of the large difference in δ^{13}C of the endmembers (11.4‰). Results are reported in the δ notation expressed relative to Vienna Pee Dee Belemnite and air, respectively.

Lateral distribution of ground-dwelling arthropods

We sampled ground-dwelling arthropods along three transects extending from the supratidal-forest boundary to the middle of the island using pitfall traps. At each transect we placed groups of three pitfall traps at 0, 5, 10, 20, and 40 m (pitfall traps at 20 and 40 m were set at only two of the transects because at one transect the distance from the middle of the island to the supratidal was only 12 m). Pitfall traps consisted of plastic cups (diameter, 9 cm) filled with antifreeze. Traps were deployed over a period of 6 weeks from July to mid-August and were emptied weekly. Arthropods were stored in 70% ethanol for further identification. Spiders were identified to family and all taxa at least to order. Catches in pitfall groups at each location were combined and averaged across the 6 sampling weeks to calculate catch per unit effort (CPUE; average number of individuals caught per day).

Data analyses

To determine whether the proportion of marine-derived C in the different arthropod consumers was affected by distance from shore, we classified the major consumers into three distance classes based on capture location and compared δ^{13}C among distance classes using one-way ANOVAs. We used Tukey tests for all post-hoc pairwise comparisons. We used one-way ANOVAs to determine whether CPUE of ground-dwelling spiders, ants, and all arthropods was higher near shore. CPUE data were square-root transformed to standardize variance and improve normality. Unless indicated otherwise, values presented are mean ± 1 SE. All statistical tests were performed in SPSS 14.0 (SPSS 2005).

Results

Stable isotope signatures of the primary resources, terrestrial leaves, and marine detritus were clearly separated (Fig. 1). Detritivores of marine wrack and terrestrial detritus differed significantly in their δ^{13}C signatures (−14.7 ± 0.3 and −26.1 ± 0.2, respectively; $t = 35.49$, $df = 20$, $P < 0.001$). Isotopic signatures of spiders captured in the supra- and intertidal were similar to that of intertidal detritivores, while isotopic signatures of spiders captured further inland were more similar to that of terrestrial prey. Distance had a significant effect on the δ^{13}C of spiders (ground-dwelling spiders, $F_{2,37} = 323.25$, $P < 0.001$; web spiders, $F_{2,22} = 17.03$, $P < 0.001$), with δ^{13}C values significantly higher for spiders captured in the intertidal than at the forest edge and further inland (Tukey test, $P < 0.001$). This is reflected in the estimates from the mixing model with >80% of marine-derived prey in the diet of intertidal spiders and <5% for ground-dwelling spiders and 10% for web spiders in the forest edge and inland (Fig. 2). The diet of ants consisted of 20% marine-derived prey and their δ^{13}C was not affected by distance from shore (ant δ^{13}C, $F_{2,6} = 0.92$, $P = 0.449$; Fig. 2).

Spiders and ants contributed 15 and 14%, respectively, to the CPUE of all ground-dwelling arthropods and 32 and 38%, respectively, to the CPUE of all ground-dwelling arthropod predators. Lateral distributions of all arthropods, spiders, and ants were not significantly influenced by

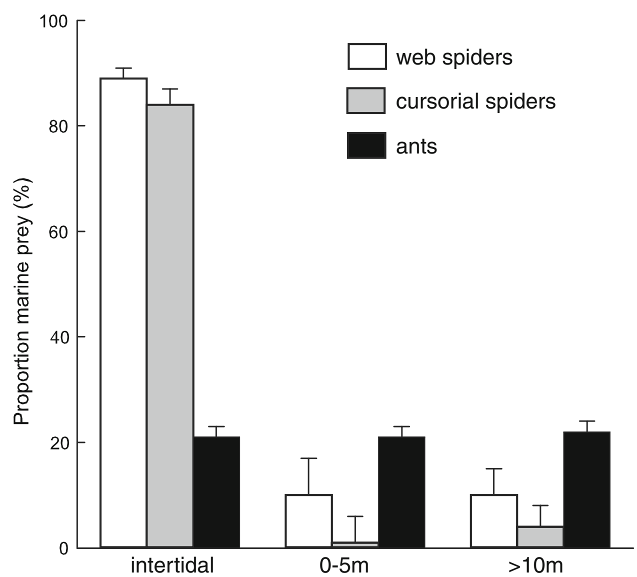

Fig. 2 Proportion of marine-derived energy assimilated by abundant predators/scavengers with distance from the supratidal-forest boundary estimated from a two-source mixing model using δ^{13}C data. For web spiders, $n = 3$, 10, 12 for intertidal, 0–5 m, and >10 m, respectively; for cursorial spiders, $n = 17$, 10, 13 in respective order; and for ants, $n = 3$ for each distance class. Each replicate for spiders represents a single individual and for ants a composite sample of ten individuals

distance (all arthropods, $F_{4,8} = 1.48$, $P = 0.29$; spiders, $F_{4,8} = 0.03$, $P = 0.99$; ants, $F_{4,8} = 1.38$, $P = 0.32$; Fig. 3).

Discussion

The relatively low contribution of marine-derived resources to the diet of arthropod consumers of the forest, together with a lack of consumer aggregation at the forest-supratidal interface, demonstrates that overall marine-derived prey were less important for the terrestrial food web on Horse Island. This suggests that overall marine resource inputs tend to be less important for terrestrial food webs on productive temperate islands compared to desert islands where primary production is low. Based on the proportion of intra- and supratidal habitat, where most of the marine subsidies occurred, we estimated that 24.3% of the island area was substantially influenced by marine resource input. This is in strong contrast to similar-sized desert islands in the Gulf of California (e.g. Coronadito: 0.07 km^2) where densities of arthropods supported by marine inputs were elevated throughout the island (Polis and Hurd 1996) suggesting nearly 100% of the island area was influenced by marine inputs. The overall low contribution of marine-derived resources to the terrestrial arthropod food web of the productive Horse Island is in line with the broad theoretical assumption that the relative importance of spatial subsidies depends on the productivity gradient between the donor and the recipient habitat (Polis et al. 1997). Similarly, Stapp and Polis (2003b) demonstrated that in years of above-average rainfall, when terrestrial productivity of arid oceanic islands

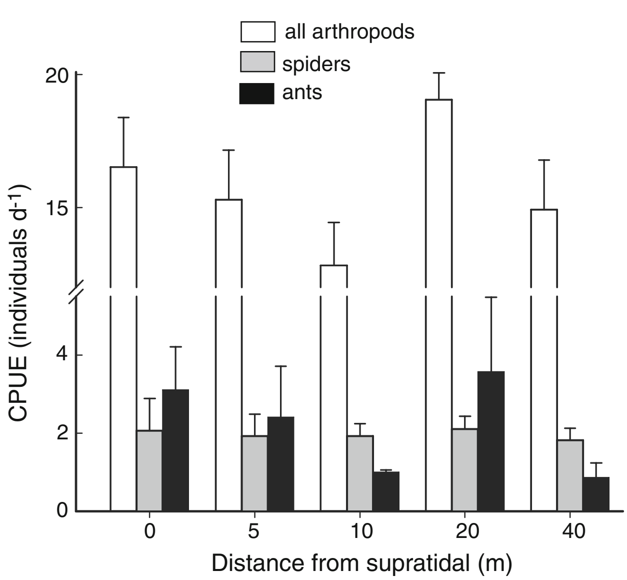

Fig. 3 Pitfall trap catches per unit effort (mean ± SE) for all arthropods combined and for spiders and ants individually

increased, the importance of marine subsidies for omnivorous rodents decreased.

Despite the overall low importance of marine resource inputs for arthropod predators across the entire island, marine-derived prey contributed significantly to the diet of arthropod predators that live or forage in the inter- and supratidal, and to a lesser degree also to the diet of ants further inland. The ground-dwelling spider community in the intertidal was dominated by wolf spiders, many of which are habitat specialists, such as *Pardosa lapidicina* (Morse 1997). These intertidal specialist spiders mainly feed and reproduce in the intertidal and supratidal habitat and move further inland only during autumn/winter for overwintering (Morse 1997). Consequently, the intertidal specialist spiders were only weakly connected to the inland food web. This explains the sharp drop in the proportion of marine resources in cursorial spider diets at the supratidal-forest boundary (Fig. 2). Within the web spiders it appears that some individuals have specialized on feeding in the supratidal habitat, at least during summer. Web spiders tend to remain resident at locations where prey is abundant because of the high cost of web construction and their limited dispersal ability (Wise 1993). However, a low level of diffusion of marine-derived prey in web spider diets (10%) into the forest occurred. This might have resulted from spiders actively relocating their webs between supratidal and forest locations and from movement of flying stages of intertidal detritivores (e.g. shore flies) further inland.

The similar proportion of marine prey (20%) in the diet of ants across the island indicates that ants are important for the transfer of marine-derived prey further inland. Similarly, ants in a braided river flood plain opportunistically feed on stranded riverine-derived organisms which they can effectively transport to their nests further away from the flood-prone river banks (Paetzold et al. 2006). This indicates that mobile consumers that opportunistically exploit marine inputs in intertidal habitats can be important vectors for the transfer of marine resources further inland. Active dispersion of primary consumers of the wrack (e.g. shore flies) into the forest was likely to be limited because many wrack consumers feed during all life stages on marine detritus (Foote 1995). The high physical complexity of the forest edge further reduces the capacity for passive transport by wind of intertidal wrack consumers inland. In contrast, on open desert and rock islands transport of marine-derived resources by wind is likely to be more important (Polis and McCormick 1987). In coastal systems, other mobile organisms in higher trophic levels, such as birds, bats and rodents, that forage in both intertidal and forested habitats might potentially play an important role in linking the intertidal with the forest web (Anderson and Polis 1998; Stapp and Polis 2003a) and deserve further attention in future research.

On temperate islands, the relative importance of marine-derived prey for terrestrial predators might fluctuate seasonally, similarly to the dynamics observed in forested headwater streams where forest birds were mainly subsidized by aquatic inputs in early spring (Nakano and Murakami 2001). Our findings are, however, confined to the summer period when terrestrial arthropod predators tend to be most abundant and active. Future research needs to explore the potential for seasonal asynchrony in the availability of marine inputs and terrestrial prey in temperate coastal systems.

Our results confirm that the productivity gradient may only provide a rough indication of the relative importance of spatial subsidies for recipient systems (Polis et al. 1997; Post et al. 2007b) and the response of individual consumer groups may differ considerably from the overall response. Similarly, a recent meta-analysis of spatial subsidies across a range of systems found that the magnitude of recipient consumer responses to spatial subsidies cannot simply be explained by broad contrasts in productivity among adjacent systems (Marczak et al. 2007). The importance of the productivity gradient for spatial subsidies appears to be modified by a range of other factors including type of the allochthonous input, vector, and the size and physical and biotic characteristics of the donor and recipient habitats (Baxter et al. 2005; Paetzold and Tockner 2005; Marczak et al. 2007; Post et al. 2007b). Our results demonstrate the importance of the biotic characteristics of the recipient consumers for spatial subsidies, more specifically the consumer's mobility traits and degree of specialization on the boundary habitat.

In conclusion, our study provides first empirical evidence that marine resource inputs are less important for recipient terrestrial consumers on productive temperate islands and are mainly confined to intertidal specialist consumers and mobile consumers that opportunistically forage in intertidal habitats. More empirical information is needed to understand the importance of spatial subsidies for relatively productive recipient habitats in order to fully appreciate the ubiquity of spatial subsidy dynamics.

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