

Assessing the effects of large mobile predators on ecosystem connectivity

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Abstract. Large predators are often highly mobile and can traverse and use multiple habitats. We know surprisingly little about how predator mobility determines important processes of ecosystem connectivity. Here we used a variety of data sources drawn from Palmyra Atoll, a remote tropical marine ecosystem where large predators remain in high abundance, to investigate how these animals foster connectivity. Our results indicate that three of Palmyra's most abundant large predators (e.g., two reef sharks and one snapper) use resources from different habitats creating important linkages across ecosystems. Observations of cross-system foraging such as this have important implications for the understanding of ecosystem functioning, the management of large-predator populations, and the design of conservation measures intended to protect whole ecosystems. In the face of widespread declines of large, mobile predators, it is important that resource managers, policy makers, and ecologists work to understand how these predators create connectivity and to determine the impact that their depletions may be having on the integrity of these linkages.

Key words: connectivity; isotope; management; marine; Palmyra Atoll; predator; reserve.

INTRODUCTION

Large predators have been shown to have formative direct and indirect effects on ecosystems as diverse as boreal forests, African savannas, and tropical coral reefs (Heithaus et al. 2008, Terborgh and Estes 2010, Estes et al. 2011). The vulnerability and desirability of large predators as harvest targets has led to their removal or depletion in many ecosystems (Myers and Worm 2005, Ray et al. 2005, Robbins et al. 2006). Being secretive and comparatively rare, it is difficult to describe the effects that large predators have on the ecology of the ecosystems in which they remain. We must directly confront these challenges, however, in order to understand and respond to their declines.

With a larger body size comes a propensity for big predators to undergo longer distance movements (Harestad and Bunnell 1979). This increased mobility brings large predators into contact with multiple habitats and ecosystems. These cross-system movements have the potential to create networks of linkages within and across ecosystems. While the importance of linkage networks and connectivity is broadly recognized to be important in ecology and management, most studies of ecosystem connectivity have focused on connections made via nutrient transfers or propagule dispersal (Polis et al. 1997, Lundberg and Moberg 2003).

In this study we examined the nature and significance of the cross-system linkages that are built by large predators in a remote tropical marine ecosystem situated in the central Pacific. The site for this research, Palmyra Atoll, hosts one of the highest recorded abundances of large reef predators (Stevenson et al. 2007, Sandin et al. 2008). While Palmyra certainly has not been immune to exposure to globally acting anthropogenic disturbances, its relatively undisturbed nature confers a unique opportunity to study patterns of large-predator-mediat-

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ed connectivity and contemplate the implications of these connections.

At Palmyra, we quantitatively investigated the reliance of three abundant large predators on different marine habitats and considered the impact that their mobile foraging has on ecosystem connectivity. To do this we coupled data from visual surveys of the abundance of predators and prey with large-predator foraging data interpreted using stable isotopes and Bayesian mixing models. Our results demonstrate that (1) large predators often utilize resources from different habitats, and thus, couple ecosystems together; and (2) these intersystem dependencies are sometimes cryptic and cannot be readily discerned without multiple information sources; and (3) recognizing this source of connectivity provides insight useful for interpreting the architecture and functioning of these systems. To ecologists, these results deepen our comprehension of the role of connectivity in community and food-web dynamics, contribute to our evolving understanding of the importance of large predators in ecosystems, and help refine the way we delineate communities and ecosystems. For resource managers and policy makers these outcomes call attention to the importance of large mobile predators in ecosystems and the need to think beyond traditional spatial boundaries when managing these predators and the ecosystems which they inhabit.

METHODS

This research was conducted at Palmyra Atoll (5°52' N, 162°04' W), an isolated atoll in the Northern Line Islands that is protected as a U.S. National Wildlife Refuge. We divided the atoll's coastal marine sector into three commonly recognized habitats: "lagoons," or protected seawater bodies in the interior of the atoll; "forereefs," or the sharply sloping reefs seaward of the reef crest; and the "pelagic" zone, or open ocean area that surrounds the atoll (Fig. 1).

We used replicated SCUBA belt transect surveys to inventory fish assemblages in one of these Palmyra habitats: the forereef. A complete fish survey consisted of four belt transects matched to fish size class (see details in Appendix A). Surveys were replicated seven times at each of nine forereef sites. Fish biomass was estimated from survey data using length-mass conversion factors obtained from FishBase (*available online*)⁷ or other published literature.

Ecosystem connections built by large predators can be visualized using a variety of methods (e.g., electronic tagging, chemical tracking). Here we used stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) so as to be able to directly describe possible energetic connections between predators and different habitats. Isotopes are useful for this application because the signature of a predator reflects the isotopic environment in which it feeds. Fish survey

data guided our selection of the three most abundant focal large predators for use in these isotope analyses: *Carcharhinus amblyrhynchos* (grey reef shark; $n = 53$ individuals), *C. melanopterus* (blacktip reef shark; $n = 9$), and *Lutjanus bohar* (two-spot red snapper; $n = 30$). Focal large predators can be encountered in lagoon, forereef, and pelagic habitats and were assumed to obtain their prey from these three sources. All focal predators were sampled on the forereef, the interface between these habitats. End member values for the three source habitats were defined using the mean isotope values of predatory fish that resided exclusively in each habitat (for lagoon, *Lutjanus fulvus* (blacktail snapper); forereef, *Epinephelidae* (grouper); pelagic, *Thunnus albacores* (yellowfin tuna); Fig. 1; Appendix B). Isotopic values of these source predators concurred well with the isotopic signatures of primary producers sampled in these same habitats (Appendix B). Both focal and source predators were captured using handlines, sampled non-lethally (biopsy of dorsal white muscle removed), and released. We used a fully Bayesian isotope mixing model to quantify the probable contribution of forereef-, pelagic-, and lagoon-derived food items to the diet of focal large predators and visualize the cross-system connections they may create (Moore and Semmens 2008, Ward et al. 2010). The construction of this model acknowledges the fact that there is uncertainty in our estimates of the means and variances of source signatures and accounts for this uncertainty by incorporating into the model the underlying probability distribution of source statistics. We also included the use of a residual error term to account for the possibility of additional unquantified error in source parameters (Jackson et al. 2009, Semmens et al. 2009, Parnell et al. 2010). See further details on model implementation in Appendix A and the Supplement.

RESULTS

Fish surveys indicate that the mean biomass of large predatory fish (>75 cm maximum total length; TL) on Palmyra's forereefs is very high: 0.5 metric tonnes/ha. These large predators comprise ~28.6% of the total forereef fish biomass (Appendix C). The three focal large predators we selected for isotopic analyses, *C. amblyrhynchos*, *C. melanopterus*, and *L. bohar*, were by far the most common constituents of this large-predator guild. Taken together, these three species make up an important proportion (~25%) of the total forereef fish biomass and a dominant portion (~85%) of the biomass of large predatory fish (Appendix C). The $\delta^{13}\text{C}$ values for forereef, pelagic, and lagoon source end members showed strong discrimination (Fig. 2). Forereef and lagoon $\delta^{13}\text{C}$ were more positive than pelagic $\delta^{13}\text{C}$ values, matching documented $\delta^{13}\text{C}$ gradients at Palmyra and elsewhere (France 1995, Young et al. 2010). $\delta^{15}\text{N}$ values for end member consumers showed less separation, although differences between end members were statistically significant. Forereef source predators had

⁷ www.fishbase.org

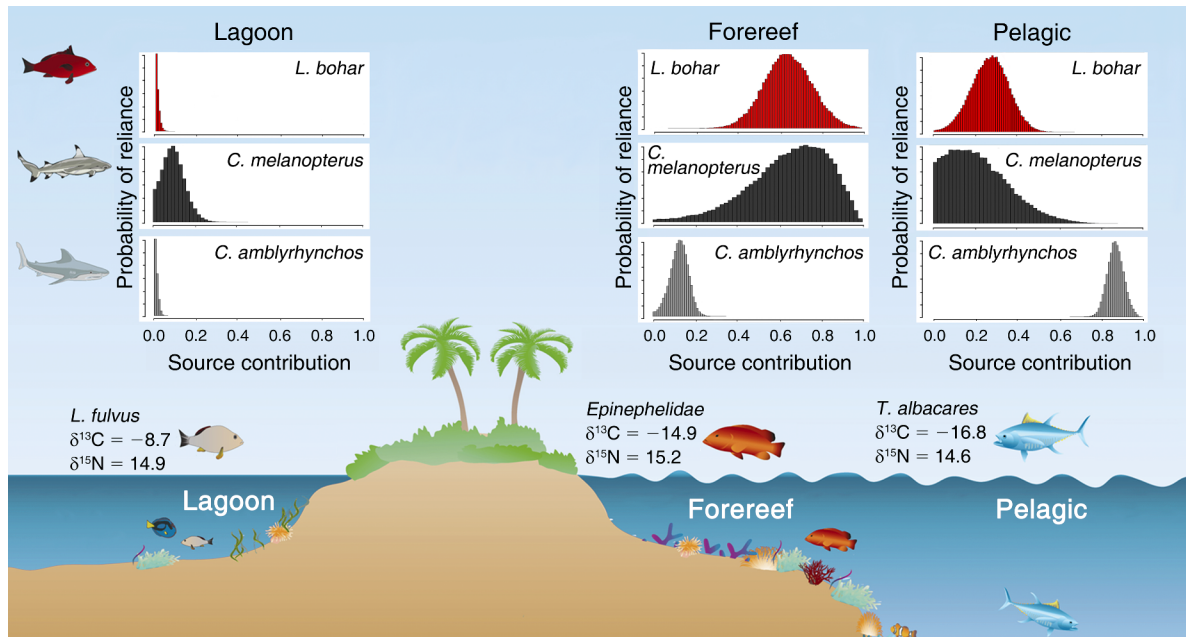


FIG. 1. The marine ecosystem of Palmyra Atoll was divided into lagoon, forereef, and pelagic habitats. Each sector is biologically and isotopically distinct, although the sectors interact physically with one another. Bayesian isotope mixing models were used to determine if three focal predators (*Carcharhinus amblyrhynchos*, grey reef shark, shown with gray bars; *Carcharhinus melanopterus*, blacktip reef shark, shown by black bars; and *Lutjanus bohar*, two-spot red snapper, shown with red bars), abundant on the forereef, were reliant on resources in lagoon, forereef, or pelagic habitats. End member values used to characterize the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of each of these three potential prey source habitats were defined using mean values from predators confined to each source (lagoon, *Lutjanus fulvus*, blacktail snapper; forereef, *Epinephelidae*, grouper; pelagic, *Thunnus albacares*, yellowfin tuna). Posterior probability distributions indicate model predictions of a focal predator's reliance on a given source. Higher values indicate source contributions that are more likely. Scales of the y-axes vary between histograms to facilitate data visualization.

slightly elevated $\delta^{15}\text{N}$, possibly indicative of increased food chain length in these diverse habitats.

Results from Bayesian mixing models indicate that all three focal fish predators sampled on the forereef take some proportion of their prey from habitats other than the forereef (Fig. 1; Appendix D). The importance of external food sources was most pronounced for the shark *C. amblyrhynchos*. Median values of the posterior distribution generated by the mixing model (indicative of the most probable contribution of source prey) for *C. amblyrhynchos* suggest that they derived ~86% of their biomass from pelagic resources. *L. bohar* were also reliant on pelagic prey (29%), although the majority of their biomass appeared to come from forereef sources (69%). *L. bohar* and *C. amblyrhynchos* took only a negligible amount of their energy from Palmyra's lagoons. Model outputs generated for *C. melanopterus* indicate that they are heavily reliant on forereefs (67%), but also derive some of their biomass from pelagic (22%) and lagoon sources (11%). These utilization predictions do not appear to be much affected by the fractionation values we used to parameterize our models (Appendix D) or by the size of the focal large predators that we sampled (Appendix E). Plots of residual error for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for each focal predator are reported in Appendix F.

DISCUSSION

Observations made in relatively undisturbed settings like Palmyra provide rare and valuable insight into the role that large predators assume in communities and ecosystems and shed light on the ecological functions that may be disrupted when they are removed. Our work on large reef predators at Palmyra demonstrates that large predators can and often do utilize resources from different habitats. This observation suggests that these predators may play an important role in shaping patterns of ecosystem connectivity by energetically coupling resource pools in different habitats. If the patterns we detected for the species of predators we studied at Palmyra hold in other contexts, and we believe they do, then we will need to invest more effort generally in interpreting the function and structure of communities within habitats in light of the effects of predator-mediated connectivity. We will also need to endeavor to source information on these linkages to managers seeking to effectively protect both large-predator populations and ecosystem integrity.

Bayesian mixing model interpretations of our isotope data indicate that large predators are often heavily reliant on one habitat for their energy intake, but also connect and are themselves energetically linked in

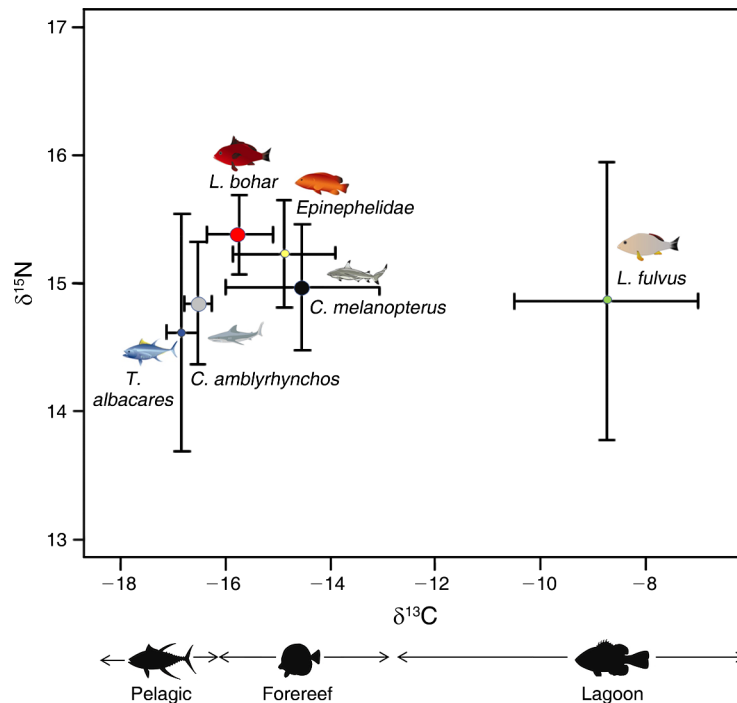


FIG. 2. Values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of focal predators *Carcharhinus amblyrhynchos* (grey reef shark, grey circle), *Carcharhinus melanopterus* (blacktip reef shark, black circle), and *Lutjanus bohar* (two-spot red snapper, red circle) plotted alongside end member values of lagoon (*Lutjanus fulvus*, blacktail snapper, green circle), forereef (*Epinephelidae*, grouper, yellow circle), and pelagic source habitats (*Thunnus albacares*, yellowfin tuna, blue circle). Focal predators are shown with large circles. All values are means \pm standard deviation. Values for lagoon source (*L. fulvus*) were adjusted one trophic step to account for trophic fractionation; all other values were plotted uncorrected.

nonobvious ways to other systems. For example, the blacktip reef sharks, *C. melanopterus*, that we sampled on Palmyra's forereefs mostly feed in this habitat, but also draw resources from pelagic and lagoon habitats (Fig. 1; Appendix D). Predicting the impact that the loss of access to any of these forage bases would have on a large predator, such as *C. melanopterus*, is difficult. Assembling these types of first descriptions of patterns of predator's energetic reliance on different habitats, however, will help us to search in a directed fashion for any deleterious effects that habitat dispossession may have on the ecology of predator populations and to consider how changing habitat access may alter the overall influence of these predators on ecosystems.

An equally interesting finding that emerged from these "you are what you eat" isotope analyses is that some of the large predators we studied were, in a sense, not "where they ate": Certain large-predator taxa were extremely common on the forereef, even though this habitat contributed very little to their overall energy intake. The grey reef shark, *C. amblyrhynchos*, provides the most extreme example. Grey reefs were the most abundant shark (by biomass; Appendix C) counted in forereef fish surveys, but they take the vast majority of their prey from sources external to the forereef (Figs. 1 and 3). This result has important implications for protecting large predators and their ecosystems. Man-

agers cannot simply assume that the places where large predators are commonly observed are, energetically speaking, the most important habitats to them. This finding also has implications for ecologists endeavoring to compare the relative importance of different large predators in an ecosystem. The disconnect we observed between the abundance of predators in a habitat and their direct consumptive effects on that system suggests that, in some communities, simply counting and comparing numbers of predators may be an insufficient strategy for ranking their ecological importance. At Palmyra, for instance, blacktip reef sharks were found to feed more from forereefs than the numerically dominant grey reef sharks, raising the possibility that, while less abundant, blacktips may in fact be stronger direct interactors in forereef habitats (Fig. 1). Assessing the overall ecological influence of a predator, however, is not a simple matter of quantifying rates of direct consumption. Even small amounts of predation by large-bodied consumers can have major impacts on affected communities and the indirect effects of their physical presence in a habitat can still have dramatic behavioral effects on community function (Polis et al. 1997, Schmitz et al. 1997).

Our observations that certain large predators in Palmyra's marine ecosystem use resources from different habitats may have important implications for the way



FIG. 3. Stable-isotope mixing models indicate that grey “reef” sharks (*Carcharhinus amblyrhynchos*) at Palmyra Atoll obtain large fractions of their energy from off-reef prey. Model outputs are consistent with field observations at Palmyra of grey reef sharks feeding in pelagic habitats on aggregations of Clupeid fishes. Photo credit: K. Pollock.

that we generally view the influence of large predators on ecosystem functioning. Theory developed elsewhere predicts that connections built by large predators can play an important role in controlling the stability of entire ecosystems (McCann et al. 2005, Rooney et al. 2006). While we do not engage these questions in this study, our results provide empirical support that such connections exist and, in fact, may be quite common in less disturbed settings where large mobile predators remain abundant. This observation raises the possibility that ongoing declines in large-predator abundance may be reshaping the connectivity, integrity, and stability of ecosystems.

Our results provide also an opportunity to critically examine the ways that we operationally define communities and interpret the ecological effects of large predators. Data from the visual surveys that we conducted on the atoll’s forereefs generate the impression that the superabundant large predators in this system are having major impacts on reef communities and that unusual endogenous processes must be at play to support their exceptionally large biomass (Appendix C). Other researchers interpreting these top-heavy community patterns on Palmyra’s reefs have described the trophic architecture of this system as an “inverted trophic pyramid” because the biomass of observed predators outnumbers the biomass of prey (Stevenson et al. 2007, Sandin et al. 2008). Methods used in these surveys have been shown to overestimate predator abundance (Ward-Paige et al. 2010, McCauley et al. 2012), helping in part to explain this unusual trophic architecture. The stable-isotope data we report herein provides another valuable means for making sense of these putative structural inversions. Mixing model outputs suggest that a considerable proportion of the large-predator biomass observed on Palmyra’s forereefs is actually being sustained by prey generated outside of the forereef. Taking this into account and reconsidering the porosity of forereef community boundaries can help considerably to develop portraits of reef community

structure and dynamics at Palmyra that are more thermodynamically and ecologically parsimonious.

Stable isotopes provide a uniquely insightful tool for visualizing these types of cryptic but important patterns of predator-mediated connectivity. Interpretations built using isotopes, however, depend on a number of key assumptions. One major assumption that we make is that the source predators that we use as end members in our mixing model (comprised of single species, or small numbers of species) accurately reflect the general isotopic signature of the habitats in which they reside. While the source predators we selected almost certainly do not perfectly represent the full isotopic geometry of these habitats, the general concordance between the isotopic values of these source predators and lower trophic level organisms (Appendix B) suggests that they do serve as suitably accurate isotopic proxies for each habitat. As such, we believe they are wholly suitable for use in the construction of these insightful first approximations of how large predators utilize and connect resource pools endemic to different habitats at Palmyra. While stable isotopes provide solid evidence that these connections exist, they offer no information on the spatial or temporal scale at which these linkages are being constructed. The habitat interfaces that we consider at Palmyra are very intimate. As such, predators may only need to travel very short distances to collect prey from adjacent habitats and these excursions may be very short in duration or highly periodic. The future use of tools such as tracking, electronic monitoring of foraging behavior, and advanced predator survey methods will help resolve the mechanics and dynamics of these connections.

The topology of these predator initiated cross-system connections is clearly complex. Each of the three focal large-predator species that we studied linked communities together in a different fashion. Furthermore, the isotopic variability inherent to certain of these predator species (e.g., $\delta^{13}\text{C}$ of *C. melanopterus*; Fig. 2) suggests that individual animals may be making connections in

unique ways. The complexity of this connectivity becomes further compounded when we consider the fact that sampling focal predators in other habitats (i.e., besides the forereef) would almost certainly reveal new and different patterns of ecosystem connectivity. For example, isotope sampling of *C. melanopterus* populations in Palmyra's lagoons indicated that the shark population in this habitat relies principally on lagoons and may only marginally utilize resources from other habitats (Papastamatiou et al. 2010): a pattern quite different than what we observed for forereef *C. melanopterus*. Coming to understand how large predators holistically link together the communities in an ecosystem will require making sense of these diverse intersections of connectivity.

Numerous examples from other systems demonstrate dynamics similar to those observed at Palmyra. The interplay between wolves, their ungulate prey, and plant assemblages (sensu Ripple and Larsen 2000) is likely influenced by the movements of both wolves and elk to and from the areas in which they are protected. The proposed influence of Pacific-wide whaling operations on the behavior of killer whales and the collapse of sea otters and coastal marine ecosystems (Estes et al. 1998, Springer et al. 2003) provides an additional analogue. Many other such cases undoubtedly await discovery in both terrestrial and marine settings.

Taken in sum, our observations from Palmyra provide substantial evidence that large predators can rely upon and connect different habitats in critically important ways. Based on these ecological observations we wish to submit two general recommendations for environmental managers and conservationists. First, given the importance of large predators in creating connectivity, we need to redouble our efforts to protect large-predator populations. Overfishing and overhunting has disproportionately affected large predators (Myers and Worm 2005, Terborgh and Estes 2010). Their declines are very likely impacting the cross-ecosystem linkages that they construct. The potential role that these large predator created linkages may play in controlling whole ecosystem stability provide a strong incentive for conserving these taxa. Second, we need to be more ambitious with the spatial scale at which we approach environmental management so as to protect the integrity of these large-predator connections. These linkages are being built at spatial scales larger than many of the habitat-centric management programs we currently have in place. The connectivity maintained by large predators can be most effectively protected via the implementation of large reserves that include multiple different habitats and effectively encompass the activity spaces of entire populations of large mobile predators (e.g., Papahānaumokuākea Marine National Monument, Phoenix Islands Protected Area). In regions where the establishment of large reserves is simply untenable we may still be able to provide some measure of protection for large predators and the connectivity they

foster through the establishment of networks of marine reserves that are constructed using information about the spatial and energetic requirements of large predators. But such networks must be married to large-scale zoning regulations that effectively manage predator populations when they range outside or between these reserves.

The overall rapidity by which large predators are declining globally necessitates that diverse coalitions of scientists and environmental leaders be organized to better understand the role that large predators play in fostering cross-system connections on land and in the oceans, to prepare actions that can help curb large-predator depletions, and establish protocols for responding to the effects that these declines may be having on ecosystem connectivity.

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SUPPLEMENTAL MATERIAL

Appendix A

Additional description of methods used in fish surveys, stable-isotope sampling, and stable-isotope mixing models (*Ecological Archives* A022-091-A1).

Appendix B

Description of the stable-isotope values of lower trophic level organisms and resident predatory fish collected from lagoon, forereef, and pelagic habitats (*Ecological Archives* A022-091-A2).

Appendix C

Biomass of fish recorded in SCUBA surveys of the forereef habitat (*Ecological Archives* A022-091-A3).

Appendix D

Predictions of the reliance of focal predators on source habitats derived using Bayesian isotope mixing models parameterized with different fractionation values (*Ecological Archives* A022-091-A4).

Appendix E

Relationship between the total length of focal predators and their stable-isotope values (*Ecological Archives* A022-091-A5).

Appendix F

Plots of residual error incorporated into the stable-isotope mixing model (*Ecological Archives* A022-091-A6).

Supplement

JAGS code used in the stable-isotope mixing model (*Ecological Archives* A022-091-S1).