Journal of Marine Systems 146 (2015) 3–16

Contents lists available at ScienceDirect

Journal of Marine Systems

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

Species associations and redundancy in relation to biological hotspots within the northern California Current ecosystem

Douglas C. Reese [a,*], Richard D. Brodeur [b]

[a] Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, OR 97331, USA
[b] Fish Ecology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, Newport, OR 97365, USA

ARTICLE INFO

Article history:
Received 9 September 2014
Received in revised form 13 October 2014
Accepted 22 October 2014
Available online 29 October 2014

Keywords:
Hotspots
Community composition
Species associations
Redundancy
Ecosystem resilience
Nekton
Jellyfish
California Current

ABSTRACT

The dynamic nature of biological hotspots, while well recognized, is not well understood. We hypothesize that the persistence of hotspots in the northern California Current System (CCS), despite seasonal and annual changes in the nekton community species composition, is related to associations among species and their functional redundancy. To address this hypothesis, sampling was conducted during June and August of 2000 and 2002 within two hotspots occurring between Newport, Oregon and Crescent City, California in the coastal CCS. Associations were examined to identify potentially complementary and redundant species. The strongest negative associations were between jellyfish and fish species, with strong positive associations evident among several fish species. Dominant species varied seasonally and annually, although evidence indicated replacement of dominant species by other similar species with respect to functional group and preferred habitat. This finding suggests that the persistence of these biological hotspots is related to species redundancy and is an important attribute contributing to stability within this highly variable system.

1. Introduction

Biological hotspots, known to be ecologically and economically important, are often the focus of conservation efforts (Worm et al., 2003). They are important because of their persistently high species diversity and abundance (Hazen et al., 2013). As a corollary, within these localized areas many species occur in relatively close proximity, foraging for similar prey, seeking to avoid being prey, or are predators. Identifying the ecological basis for associations is important for making predictions about how large-scale changes, such as climate change, will alter distributions and abundances (Millazzo et al., 2013; Nagelkerken and Simpson, 2013; Urban et al., 2013).

Interactions among organisms are known to affect respective local distributions and abundances. Changes in relative abundances of certain species, especially those which are highly mobile, can lead to novel interspecific interactions as species relocate to more tolerable conditions (e.g., Harley et al., 2006; Wilson et al., 2008). Lacking understanding of these community dynamics can lead to less-predictive models used for management (Harley et al., 2006). Temporal changes in community composition can occur over relatively short time spans sometimes, without repeated sampling, making it difficult to identify what is “normal” for a given area. For example, Reese and Brodeur (2006) identified nekton hotspots within the northern California Current System (CCS), noting that species composition varied seasonally and annually. Despite such dynamics, these regions remained as biological hotspots both seasonally and interannually. Such a finding leads to the expectation that different species within functional groups are playing similar roles (i.e., are functionally redundant) since some could be replaced by others without a substantial change at higher levels of biological organization.

The CCS is a dynamic and highly productive eastern boundary current characterized by extensive upwelling (Checkley and Barth, 2009; McGowan et al., 1998). Within the northern portion, changes in species composition and production of all trophic levels are known to occur due to varying environmental conditions (Brodeur et al., 2005; Peterson et al., 2002; Reese et al., 2005). On a seasonal scale, variability is the result of a reversal in wind pattern north of 37° N, blowing equatorward during summer and poleward during winter (Huyer, 2003). The equatorward winds facilitate the coastal upwelling (Barth et al., 2005). Interannual variability is linked strongly to El Niño-Southern Oscillation (Checkley and Barth, 2009; Chelton et al., 1982) and decadal variability coincides with large-scale, decadal regime shifts that alter much of the North Pacific (Chavez et al., 2003; Mantua et al., 1997).

Within the dynamic CCS, Reese and Brodeur (2006), on the basis of species richness, abundance, and/or biomass, identified two persistent biological hotspots in its northern portion. One hotspot, located offshore near the shelf-break, was associated with a retention area near Heceta Bank (about 44° N). The other hotspot was located close to shore near Crescent City, CA (about 42° N) and was upwelling-based.

* Corresponding author.
E-mail address: Doug.Reese@oregonstate.edu (D.C. Reese).

http://dx.doi.org/10.1016/j.jmarsys.2014.10.009
0924-7963/

One mechanism proposed by Reese and Brodeur (2006) for the persistence of these hotspots was the functional redundancy present among species (Naeem, 1996; Walker, 1992). Such a characteristic has deep implications for management with respect to stability, resilience, and resistance to change whether natural or anthropogenic. Frost et al. (1995) examined species compensation and functional complementarity in ecosystem function in a lake system and found that biomass of zooplankton remained at high levels despite the loss of component species from each group. Compensatory increases by other taxa were determined to be responsible for the complementarity of function. A key factor increasing the degree of compensation among associated species in response to environmental change was their functional similarity (Frost et al., 1995). Species redundancy, as reflected in more biologically diverse areas, may therefore preserve ecosystem functioning despite changes in the environment (Naeem, 1996). Likewise, the persistence of the hotspots in the northern CCS despite changing environmental conditions may therefore be related to species complementarity and functional redundancy.

In coastal marine fish assemblages, Micheli and Halpern (2005) found strong positive relationships between fish species and functional diversity, however, some functional groups examined had low species redundancy. For instance, in marine reserves, the authors noted that species recovery resulted in the addition of whole functional groups due to the fact that some functional groups were comprised of only one species. In fact, within no-take marine reserves they identified several functional groups that were not present in fished areas over multiple studies indicating that fishing tends to remove whole functional groups from some systems (Micheli and Halpern, 2005). Although the dataset used in this analysis did not necessarily include species that were found at low abundances thereby precluding potentially important, yet rare species, their work suggests that small changes in species diversity can ultimately result in significant impacts on functional diversity and possibly ecosystem function.

The local distribution and abundance of some species are known to affect the presence of other species due to biological interactions, such as competition and predation (for upper trophic levels: Ainley et al., 2009). Identifying which species are indicators of specific habitats and which species associate with them helps to understand ecosystem structure. Positive associations between species whose dominance fluctuates may facilitate the complementary functioning of species such that if one becomes limited in abundance, another functionally similar species may replace it, thus preserving ecosystem function.

On the other hand, negative associations are also possible. Given the large abundances of large jellyfish encountered in the northern CCS (Suchman and Brodeur, 2005; Suchman et al., 2008) and their high degree of spatial overlap with pelagic fishes (Brodeur et al., 2008, 2014), jellyfish may be significant competitors with some nekton species (Brodeur et al., 2008). For instance, jellyfish and sardines both feed heavily on euphausiid eggs (Miller and Brodeur, 2007; Suchman et al., 2008). Therefore, if there is significant competition between these organisms, and the system becomes dominated by one or the other, this could lead to altered food web dynamics and diversity (Richardson et al., 2009; Ruzicka et al., 2012).

We propose to investigate the hypothesis that the persistence of hotspots in the northern CCS, despite seasonal and annual changes in nekton community structure, is related to species associations and functional redundancy. A primary goal was to identify the strength of species associations. In particular, we were interested in the associations of hotspot indicator species with pelagic jellyfish. Associated, redundant species with similar diets may be competitors and have the potential to alter community structure at highest trophic levels. We took a conservative approach to defining redundancy by adding to the classical definition of the number of species within a functional group, the requirement that redundant species be complementary and overlapping in geographic distributions. Therefore, a compensatory increase in the abundance of one species should be related to a decrease in abundance of another species.

2. Materials and methods

2.1. Study region and sampling design

Sampling was conducted at multiple trawling stations as part of a mesoscale and fine-scale sampling study within the U.S. GLOBEC Northeast Pacific Program (Batchelder et al., 2002). Samples were collected during four cruises to examine seasonal and interannual patterns of community dynamics: during late spring (29 May to 11 June, 2000 and 1 June to 18 June, 2002 (hereafter called June 2000 and June 2002 cruises, respectively) and during late summer (29 July to 12 August, 2000 and 1 August to 17 August, 2002 (hereafter called August 2000 and August 2002 cruises, respectively). All sampling was conducted from chartered fishing vessels and the sampling area extended from Newport, Oregon (latitude 44° 40′ N) to Crescent City, California (41° 54′ N). Sample stations were located along five designated transects 1, 5, 10, 15, 20, 25, and 30 nautical miles from shore although stations were added in areas of particular physical and/or biological interest. All spatial and community analyses were limited to samples collected during daylight to avoid any changes in the day/night community structure within the water column.

Details on sampling methodology are provided in Brodeur et al. (2004). Nekton tows of the surface layer were made with pelagic trawls at each station. Nekton and jellyfish abundances were standardized for differences in effort between tows and based on the volume of water filtered per trawl. For standardization, we only used species richness values acquired from samples in which the volume of water sampled was within two standard deviations of the mean volume of all samples. Additional details on the physical and biological parameters sampled at each station (e.g., temperature, salinity, chlorophyll and surface zooplankton) are provided in Reese et al. (2005).

Differences in total jellyfish densities were evaluated between cruises using a Kruskal-Wallis test (Zar, 1996). A non-parametric test was chosen because our data did not meet assumptions of normality and homoscedasticity. When significant differences were found, Mann-Whitney U tests were performed to compare between the four cruises. The significance levels were adjusted to account for multiple tests being conducted (Shott, 1991). In order to obtain an overall significance level of 0.05, we employed a Bonferroni-adjusted significance level of $0.05/4 = 0.0125$ for each Mann-Whitney U test.

2.2. Spatial analysis

To identify spatial patterns of jellyfish distributions and their spatial relationships to nekton hotspots, geostatistical modeling techniques were employed using ArcGIS v8.3 with the Geostatistical Analyst extension (ESRI, Redlands, CA); see Johnston et al. (2001) and Reese and Brodeur (2006) for further details. Density distributions on each cruise were examined for spatial overlap among the four most common species of large medusae off the coast of Oregon (Suchman and Brodeur, 2005), consisting of three scyphomedusan (*Aurelia labiata*, *Chrysaora fuscescens*, and *Phacellophora camtschatica*) and one hydromedusan (*Aequorea* sp.) species. Data were normalized with a log $(x + 1)$ transformation to prevent violations of normality and homoscedasticity. Both exponential and spherical theoretical models were fit to the empirical semivariograms. These models were then used to estimate the semivariogram values for each distance within the range of observations (Cressie, 1993). We then used kriging to interpolate the expected values of the variables for each cruise. We evaluated model parameters and kriging results using cross-validation. For each variable, numerous exponential and spherical models were evaluated and compared and the best model was selected.