Estuarine, Coastal and Shelf Science 125 (2013) 43–56

Contents lists available at SciVerse ScienceDirect

Estuarine, Coastal and Shelf Science

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

An innovative statistical approach to constructing a readily comprehensible food web for a demersal fish community

Ben French [a], K. Robert Clarke [a,b], Margaret E. Platell [a,c], Ian C. Potter [a,*]

[a] Centre for Fish and Fisheries Research, Murdoch University, South Street, Murdoch 6150, Australia
[b] Plymouth Marine Laboratory, Prospect Place, West Hoe, Plymouth PL1 3DH, UK
[c] School of Environmental and Life Sciences, University of Newcastle, Brush Rd, Ourimbah, 2258 NSW, Australia

ARTICLE INFO

Article history:
Received 29 November 2012
Accepted 16 March 2013
Available online 2 April 2013

Keywords:
gut contents
predator guilds
prey guilds
multivariate analyses
Australia

ABSTRACT

Many food webs are so complex that it is difficult to distinguish the relationships between predators and their prey. We have therefore developed an approach that produces a food web which clearly demonstrates the strengths of the relationships between the predator guilds of demersal fish and their prey guilds in a coastal ecosystem. Subjecting volumetric dietary data for 35 abundant predators along the lower western Australia coast to cluster analysis and the SIMPROF routine separated the various species × length class combinations into 14 discrete predator guilds. Following nMDS ordination, the sequence of points for these predator guilds represented a 'trophic' hierarchy. This demonstrated that, with increasing body size, several species progressed upwards through this hierarchy, reflecting a marked change in diet, whereas others remained within the same guild. A novel use of cluster analysis and SIMPROF then identified each group of prey that was ingested in a common pattern across the full suite of predator guilds. This produced 12 discrete groups of taxa (prey guilds) that each typically comprised similar ecological/functional prey, which were then also aligned in a hierarchy. The hierarchical arrangements of the predator and prey guilds were plotted against each other to show the percentage contribution of each prey guild to the diet of each predator guild. The resultant shade plot demonstrates quantitatively how food resources are spread among the fish species and revealed that two prey guilds, one containing cephalopods and teleosts and the other small benthic/epibenthic crustaceans and polychaetes, were consumed by all predator guilds.

1. Introduction

There has been an increasing and worldwide recognition of the need to adopt an ecosystem-based approach to fisheries management (EBFM) in order that ecosystems, and thus the fisheries they support, are sustained in a healthy state (Ecosystems Principles Advisory Panel, 1996; Bergen Declaration, 2002; Essington and Punt, 2011; Espinoza-Tenorio et al., 2012). Such an approach involves considering the ecosystem as a whole, rather than just the target species, and thus represents a holistic approach that emphasises the importance of understanding the reciprocal interactions of humans and marine resources (Pikitch et al., 2004; Curtin and Prezello, 2010; Dickey-Collas et al., 2010; Espinoza-Tenorio et al., 2012). In its report to the United States Congress, the Ecosystems Principles Advisory Panel (1996) recommended that a Fisheries Ecosystem Plan (FEP) should be developed and that this should involve a series of actions. One of the eight suggested actions included the proposal that a conceptual model of the food web in an ecosystem should be constructed, based on data for the predator and prey of each targeted species over time. This would then permit the anticipated effects of the allowed harvest on predator–prey dynamics to be addressed.

The production of a sound food web requires a thorough understanding of the trophic interrelationships of the main fished and unfished species in that ecosystem. Such webs are traditionally constructed using the trophic interactions between the various predators and their prey and is typically based on analyses of gut contents and/or stable isotope ratios (Ecosystems Principles Advisory Panel, 1996; de Ruiter et al., 2005; Field and Francis, 2006; Moloney et al., 2011). When developed from gut content data, they are often represented by complex 'spider-web' or 'birds-nest' diagrams (e.g. Hori et al., 1993; Link, 2002). Consequently,

* Corresponding author.
E-mail address: I.Potter@murdoch.edu.au (I.C. Potter).

0272-7714/$ – see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.ecss.2013.03.014

they are often so complex that they "conceal more than they reveal" and, as a result, fundamental patterns may be obscured by the high level of detail (Raffaelli, 2000). The need to reduce the complexity of the representation of the interactions between predators and their prey led many workers to combine predator species into either functional groups (Raffaelli, 2000) or trophic guilds that comprise species with similar prey (Root, 1967; Bulman et al., 2001; Reum and Essington, 2008) and thereby reduce the number of entities within the food web. This thereby facilitates a clearer understanding of the main aspects of the structure and function of ecosystems (Fulton et al., 2007) and the potential for inter-specific competition (Pianka, 1980). Scientists have also attempted to reduce the complexity of food webs by decreasing the number of prey entities through, for example, combining them into functional categories (e.g. Reum and Essington, 2008). The above efforts to reduce complexity involve a degree of subjectivity regarding the level and extent to which the predator and/or prey species are grouped, which has often varied among studies and thus hindered comparisons between studies.

The dietary compositions of many fish species change as those species increase in body size (Werner and Gilliam, 1984; Blaber and Bulman, 1987; Platell et al., 1998a, 2010; Shepherd and Clarkson, 2001; Cocheret de la Morinière et al., 2003; French et al., 2012) and also sometimes change with time of year (Jaworski and Ragnarsson, 2006; Lek et al., 2011; Schückel et al., 2011). It is thus necessary to consider whether the details of the food web are influenced by the body sizes of the various species and/or are related to season, recognising that although a number of species may undergo size-related and/or seasonal changes, they may not all follow the same trends and body size may thereby not exert an overall significant influence on the structure of the food web. In a study of the guild structure of fishes in Puget Sound (USA), based on the diets of 21 species, the individuals were separated into large and small fish, when data were available for both size groups, and according to the season of sampling, i.e. autumn, summer and winter (Reum and Essington, 2008). That dietary study had the great advantage of identifying statistically the various groups of predators that consume similar prey, through using the permutation-based SIMPROF test (Clarke et al., 2008), which does not assume any *a priori* hypotheses as to which predators form a guild. In the context of time of year, that study found no evidence that the structure of the overall food web changed with season, which is consistent with the conclusions drawn from comparable detailed studies of fish communities on the upper shelf of south-eastern Australia and the mid-slope of southern Tasmania (Bulman et al., 2001, 2002).

The initial aim of this study was to produce a food web that illustrates the relationships between the abundant demersal fish species and their prey on the lower west coast of Australia, through employing the detailed quantitative dietary data that were derived from analyses of the gut contents of those species in samples covering a wide size range of each species and each season (Table 1). It soon became apparent that, as in numerous other studies, traditional approaches would yield a complex food web that was not readily comprehensible and thus of immediate value to managers and ecologists. We thus used an innovative multivariate approach, which involved the use of SIMPROF, to identify statistically the various predator and prey guilds and thereby reduce, to a manageable level, the number of groups required for constructing the food web. This approach, which is still based on sound quantitative data and a series of objective statistical hypothesis tests, enabled us to produce a food web in the form of a readily interpretable 'shade plot' that reveals the magnitude of the trophic relationships between the fish predators and their prey.

Table 1
The 35 demersal fish species whose diets were used to explore the trophic relationships between fish species and their prey on the lower west coast of Australia, together with the relevant publications or data sources.

Families	Species	Publications
Elasmobranchs		
Heterodontidae	*Heterodontus portusjacksoni*	Sommerville et al. (2011)
Myliobatidae	*Myliobatis australis*	Sommerville et al. (2011)
Rhinobatidae	*Aptychotrema vincentiana*	Sommerville et al. (2011)
Squatinidae	*Squatina australis*	Sommerville et al. (2011)
Urolophidae	*Trygonoptera mucosa*	Platell et al. (1998a)
	Trygonoptera personata	Platell et al. (1998a)
	Urolophus lobatus	Platell et al. (1998a)
	Urolophus paucimaculatus	Platell et al. (1998a)
Teleosts		
Atherinidae	*Atherinomorus ogilbyi*	Hourston et al. (2004)
Carangidae	*Pseudocaranx georgianus*	French et al. (2012)
	Pseudocaranx wrighti	Platell et al. (1997)
Clupeidae	*Spratelloides robustus*	Schafer et al. (2002)
Gerreidae	*Parequula melbournensis*	Platell et al. (1997)
Glaucosomatidae	*Glaucosoma hebraicum*	Platell et al. (2010)
Labridae	*Bodianus frenchii*	Platell et al. (2010)
Leptoscopidae	*Lesueurina platycephala*	Hourston et al. (2004)
Mullidae	*Upeneichthys lineatus*	Platell et al. (1998b)
	Upeneichthys stotti	Platell et al. (1998b)
Pempherididae	*Parapriacanthus elongatus*	Platell and Potter (1999)
	Pempheris klunzingeri	Platell and Potter (1999)
Platycephalidae	*Platycephalus longispinis*	Platell and Potter (1998)
Pleuronectidae	*Ammotretis elongatus*	Hourston et al. (2004)
	Pseudorhombus jenynsii	Schafer et al. (2002)
Scorpaenidae	*Maxillicosta scabriceps*	Platell and Potter (1998)
Serranidae	*Epinephelides armatus*	Platell et al. (2010)
Sillaginidae	*Sillaginodes punctata*	Hyndes et al. (1997) and Platell (unpublished data)
	Sillago burrus	Hyndes et al. (1997)
	Sillago robusta	Hyndes et al. (1997)
	Sillago schomburgkii	Hourston et al. (2004)
	Sillago vittata	Hyndes et al. (1997)
	Sillago bassensis	Hyndes et al. (1997)
Sparidae	*Pagrus auratus*	French et al. (2012)
	Rhabdosargus sarba	Ang (unpublished data)
Triglidae	*Lepidotrigla modesta*	Platell and Potter (1999)
	Lepidotrigla papilio	Platell and Potter (1999)

2. Materials and methods

2.1. Sampling of fish and treatment of gut samples

The 35 demersal fish species, whose dietary data were used in the current study (Table 1), were collected from coastal marine waters along the lower west coast of Australia between Lancelin at ca 33°00 S and Cape Naturaliste at ca 33°30 S and in which these species are abundant. Each species was sampled by one or more of the following methods: otter trawling, rod and line fishing, long lining, gill netting, seine netting and spear fishing. The fish were placed on ice immediately after capture and the whole fish, or the carcass and gut contents when the fish had been filleted, were transported to the laboratory where they were frozen. The total length (TL) of each fish was measured to the nearest 1 mm and, when the gut contained food, it was removed and placed in 70% ethanol, except in the case of the larger guts which were first fixed in 10% formalin.

The dietary items in the guts of each fish were examined under a dissecting microscope and identified to the highest taxonomic separation possible. A total of 468 different taxa were identified in the gut contents of the 35 fish species. The percentage volumetric contribution of each dietary taxon to the total volume of the stomach and/or intestinal contents (%V) was estimated visually (Hynes, 1950; Hyslop, 1980). Unidentifiable material was not included in the analyses.