Fishery reserve effects on sparid recruitment along French Mediterranean coasts

Hazel Arceo, Adrien Cheminée, Pascaline Bodilis, Luisa Mangialajo, Patrice Francour

University of Nice-Sophia Antipolis, EA 4228 ECOMERS, Faculty of Sciences, Parc Valrose, BP 71 06108 Nice, France Corresponding author: <u>arceo@unice.fr</u>

Abstract. Many studies have reported increasing trends in fish abundance and biomass inside marine reserves. This "reserve effect" may lead to increased fecundity and production inside the reserve, enhancing recruitment in surrounding areas. However, the increase in piscivorous and other large carnivorous fish species (i.e. predators) could also translate to higher predation inside the reserve, thus reducing recruitment. In this study, juvenile *Diplodus sargus* (Sparidae) were surveyed in their nursery habitats in Saint-Raphäel, French Mediterranean to determine the effects of protection on density and mortality. Visual census was undertaken weekly during the recruitment season (June to August 2011) in 12 nursery coves situated across two zones: inside the *Cantonnement de Pêche du Cap Roux* (Cap Roux Fishery Reserve) and outside (control) the reserve. There were no significant differences in juvenile peak density between zones although it was slightly higher outside than inside the reserve. Instantaneous mortality rate was significantly higher in the reserve than outside (1-way ANOVA, p = 0.024). Mortality seems to be density-independent. This study shows indications that recruitment of the rocky reef fish, *D. sargus*, is lower inside the reserve compared to nearby fished areas and that this pattern could be attributed to predation. However, further research is warranted to obtain more unequivocal conclusions.

Key words: Recruitment, Mortality, Fishery reserve, Sparidae, Mediterranean.

Introduction

Various studies have documented the positive effects of protection on fish assemblages, especially commercially-exploited species. Higher fish abundance and biomass have been observed inside marine reserves than in unprotected areas (e.g. Polunin and Roberts 1993; Claudet et al. 2008; Molloy et al. 2009). Marine reserves have been promoted as a management strategy to improve and sustain adjacent fisheries (e.g. Roberts and Polunin 1991; Seytre and Francour 2008) possibly either through the net emigration of adults and juveniles across boundaries (i.e. spillover) and/or the export of pelagic eggs and larvae which is enhanced by the increased production and fecundity inside the reserve (Rowley 1994; Russ 2002; Garcia-Charton et al. 2008). Despite the growing literature on the biological and ecological effects of protection on fish populations, its effect on recruitment has been infrequently studied (Pelletier et al. 2005).

Recruitment, as used in this study, refers to the number of post-transition juveniles (already adapted to necto-benthic life) and immature adults (already attained adult-like morphology and coloration), as defined by Vigliola and Harmelin-Vivien (2001). It differs from settlement, which is the process of moving from the pelagic zone to the benthic habitat (Sale et al. 1984). The maximum density of settlers ("peak density") best accounts for the settlement event intensity ("settlement rate"), i.e. the number of new individuals joining the benthic habitat for a given nursery area. The number of juveniles remaining at the end of the post-settlement period, (i.e. settlers who survived arbitrary periods of time after settlement and may join adult assemblages), gives a proxy of the recruitment success for a given nursery habitat (Levin 1994a, 1994b; Macpherson 1998). This recruitment success ("recruitment level") can be assessed by monitoring the mortality of juveniles during the post-settlement period in the nursery until their dispersal towards adult habitats (Macpherson et al. 1997).

Protection can have two possible opposing effects recruitment inside marine reserves: (1) on enhancement, due to the protection of preferred habitats and lower disturbance which is especially relevant to settling larvae with distinct habitat preferences (Planes et al. 2000) and to increased abundance of adult conspecifics (Arceo et al. 2007); or (2) reduction, due to higher mortality caused by increased predation (Tupper and Juanes 1999; Webster 2002). The present study focuses on the second hypothesis. Early juvenile survivorship is potentially important in determining recruitment rate variation to older age classes if post-settlement mortality is high (Sale and Ferrel 1988) and if recruitment is low (Fontes et al. 2009). Because of the increase in piscivorous and other large carnivorous fish species (i.e. predators) inside marine reserves as observed in previous studies, juvenile fish mortality could be higher, resulting to lower levels of recruitment. Macpherson et al.

(1997) have previously reported no significant differences in juvenile fish mortality between protected and unprotected areas in the northwestern Mediterranean. However, their study pooled sites across a large geographic scale (i.e. three countries), and may have masked the intrinsic characteristics of the protected areas surveyed.

The objective of this study was to determine the effects of protection on juvenile fish density (settlement intensity) and mortality (proxy of recruitment success) at a local scale. More specifically, abundances of juvenile sea breams, Diplodus sargus (Sparidae), were monitored in their natural nursery habitats in and around a fishery reserve in Saint-Raphäel, French Mediterranean during the 2011 recruitment season. D. sargus was selected as the focal species because of its welldescribed seasonality and habitat requirements during settlement (Garcia-Rubies and Macpherson 1995; Harmelin-Vivien et al. 1995; Macpherson 1998; Vigliola and Harmelin-Vivien 2001; Cheminée et al. 2011). Furthermore, it is a commercially-targeted species for both recreational and professional fisheries. Mortality rate of juvenile D. sargus inside and outside the reserve was then computed. Indicative patterns of mortality are presented, and their implications to marine reserve dynamics are briefly discussed.

Material and Methods

Study Area

The study was conducted in the *Cantonnement de Pêche du Cap Roux* (Cap Roux Fishery Reserve) and adjacent areas in Saint-Raphaël, along the French Mediterranean coast (Fig. 1). The fishery reserve was established in December 2003 through the initiatives of the professional fishers from the *Prud'homie de Pêche* of Saint Raphaël. The reserve is a no-take zone, and covers an area of approximately 450 hectares extending from the coastline up to the 80-meter isobath.

An initial survey was conducted in December 2009 to identify suitable nursery habitats for D. sargus in and adjacent to the Cap Roux Fishery Reserve. This species settles onto very shallow waters (0-1 m), usually within small coves that are rocky on both sides of the beach and with a gently sloping heterogeneous substrate consisting of coarse sand, pebbles and boulders (Harmelin-Vivien et al. 1995). Based on these characteristics, twelve coves (sampling stations) were then selected: four to the north, four inside and four to the south of the reserve (Fig. 1). Care was taken in the cove selection such that they were similar in substrate characteristics and that they were sufficiently separated from neighboring coves to avoid movement of juvenile fish among coves which could bias estimation of mortality rates. Juveniles of D. sargus display high fidelity to their nursery habitat and start to move to deeper waters

only around 6 months after settlement at 50-60 mm lengths (Garcia-Rubies and Macpherson 1995).



Figure 1: Location of the sampling stations (yellow circles indicating the number of coves) inside and adjacent to the Cap Roux Fishery Reserve and its boundaries (red line). (Map source: Google-Earth). Inset map: France.

Field Methods

An initial study done during the recruitment season in 2010 validated the presence of settlers in the selected sampling stations. However, only 2 surveys could be done (June and August) and data were excluded from the analyses. For the main experiment, surveys were done weekly, weather permitting, from 14 June to 17 August 2011. This resulted to seven separate surveys over 10 weeks.

To count the juvenile fish in the sampling stations, the methods described in Cheminée et al. (2011) were followed. The abundance and size of all juvenile D. sargus encountered were estimated using underwater visual census wherein an observer snorkeled very slowly along the shoreline of the entire cove, covering a narrow strip from the shore up to 10 meters seawards (variable depending on the physical characteristic of each cove) with a depth range of 0-2 m. Hence, the whole nursery area is usually covered. The slow swimming avoids disturbing the juveniles and allows for ease in counting and size estimation (Harmelin-Vivien et al. 1985). Total length was estimated using a diagram of fish silhouettes of 5-mm size classes as a guide. The precision of this method is approximately ± 3.5 mm for Diplodus species (Macpherson 1998). Data were recorded on a plastic slate. Surveys were done around the same time of the day (0900 - 1500) and completed for all coves in two days. Other observations, such as water turbidity and weather conditions, were also noted.

Data Analysis

Mean peak density (abundance over the total area surveyed for each cove and standardized to 100 m^2) of juvenile *D. sargus* was obtained and compared between the two zones (reserve and control). Data for the north and south stations were pooled into the control zone since the means were very similar in terms of values; hence, an unbalanced design having 4 replicates for the reserve and 8 replicates for the control was used in the analyses.

To estimate mortality, individual abundance values for each survey were log-transformed (ln x+1) and plotted over time (in days) starting from the time of peak abundance for each cove. The resulting slope of this linear regression corresponds to the instantaneous mortality rate. The use of time-series data has been suggested to be more accurate in estimating mortality rates compared to using only the final and initial density values (see Macpherson et al. 1997).

One-way Analysis of Variance (ANOVA) was then used to test for differences in juvenile density and mortality rate between the two zones. Cochran's test was used to test for homogeneity of variances. The effect size Hedges' g (which takes into account unequal sample sizes) and statistical power were also computed using packages in the R Software (version 2.15.0).

The correlation between peak density and mortality rate was determined using Spearman's Rank Correlation Coefficient.

Results

Settlement of *D. sargus* in the sampling stations occurred in a single pulse with all but two stations showing peak abundances during the second survey (5 to 8 days after the first survey). The sizes of the juvenile fish recorded ranged from >10 mm to 60 mm. The smallest size classes (>10 to 25 mm) were observed during the first 3 surveys, and the dominant size class on the last survey ranged from 40-55 mm.

Mean peak densities (*standard deviation*) in the reserve and control stations were 5.65 (2.11) and 7.83 (3.71) individuals per 100 m², respectively. There were no statistically significant differences between zones [F(1,10) = 1.154, p = 0.308] although peak density was slightly lower in the reserve than in the control (Fig. 2). The effect size for this difference (g = 0.6072), when converted to Cohen's (1988) convention for d, is moderate. Posthoc analysis showed the power of the test to be low



Figure 2: Mean peak density (\pm SE) of juvenile *Diplodus sargus* inside (reserve) and outside (control) the Cap Roux Fishery Reserve.

(0.164). Increasing the power to the recommended 0.80 level to detect the same moderate effect would require a sample size of 38 for each zone.

The highest reduction in abundance of juveniles was mainly observed between the second (observed peak abundance) and third surveys which were 6 to 8 days apart. In 10 out of the 12 sampling stations, at least 50% up to 80% of the newly-settled juveniles (size class of >10 to 15 mm) were lost during this period. There was a statistically significant difference in mean instantaneously mortality rate between zones [F(1,10) = 7.076, p = 0.024], with mortality rate being higher inside the reserve than in the control (Fig. 3). The effect size was high (g = 1.504) and the power was approximately 0.670. A balanced design of 8 replicates per zone would have further increased the power to the recommended 0.80 level.



Figure 3: Mean instantaneous mortality rate (\pm SE) of juvenile *Diplodus sargus* inside (reserve) and outside (control) the Cap Roux Fishery Reserve.

A comparison between mortality rate and peak density indicated no significant pattern (Table 1). The correlation between the two variables showed a non-significant relationship (Spearman R = -0.014, p = 0.965).

Zone	Station	Mortality	Density (Peak / Final)
Reserve	Maubois	-0.05927	5.75 / 0.05
	Nbeach 1	-0.02936	6.74 / 1.63
	Nbeach 2	-0.02905	7.45 / 2.24
	Nbeach 3	-0.04985	2.66 / 0.16
Control	Figuer 1	-0.00831	4.46 / 1.34
(north)	Figuer 2	-0.02745	1.67 / 0.42
	Trayas 2	-0.02046	11.20 / 2.36
	Trayas 3	-0.03687	13.10 / 1.81
Control	Antheor 1	-0.01662	6.41 / 2.43
(south)	Anglais 1	-0.02792	7.98 / 1.21
	Anglais 2	-0.03119	10.28 / 2.38
	Anglais 3	-0.00777	7.57 / 2.86

Table 1: Mean mortality rate (individuals per day) and density (peak and final, in individuals per 100 m^2) of juvenile *D. sargus* across the sampling stations in the two zones.

Discussion

Several factors have been observed to influence the survival of juvenile fish after settlement: abiotic sources of mortality (i.e. disturbance), predation (e.g. encounter rates, vulnerability), competitive interactions with residents (conspecifics, juvenile/adults, predators) and availability of resources such as food or shelter (Shulman 1985; Piko and Szedlmayer 2007; Juanes 2007). In MPAs, predation on juvenile fish can be higher due to an increased number of piscivorous fish usually targeted by fishing (Tupper and Juanes 1999). This increased predation has been observed for juveniles of a commercially important invertebrate, the spiny lobster Palinurus elephas, inside the Medes Islands MPA in the northwestern Mediterranean (Diaz et al. 2005). The higher predator biomass inside MPAs, as has been observed in some Mediterranean MPAs (Francour et al. 2010), could mean more intense predation so that local survivorship could be affected. The present study was able to detect significantly higher mortality patterns of juvenile D. sargus inside the reserve compared to the outside areas (at p<0.05). These results differed with Macpherson et al. (1997) who did not find significant differences in juvenile mortality for the same species between inside and outside MPAs. The potential predators of D. sargus juveniles are mainly small predatory species or small individuals of large species that may not be seriously affected by the reserve effect (Macpherson et al. 1997). However, in the shallow Posidonia oceanica meadows of the Cap Roux Fishery Reserve, Seytre and Francour (2009) highlighted significant differences between the density of Serranidae inside and outside the reserve (Reserve > Outside). In all the 12 sampled coves of the present study, the bottom is covered by dense P. oceanica meadows, ending some meters before the beaches. Seagrass habitats are therefore close to the nursery habitats so that Serranidae could represent potential predators of the sparid juveniles that respond to protection. Continued recruitment surveys will be needed to take into account the natural spatial and temporal variability of recruitment and obtain more conclusive results.

Most species experience the greatest rates of mortality during their early weeks in the coral reef environment (e.g. Victor 1986, Schmitt and Holbrook 1999; Almany and Webster 2006, Holmes and McCormick 2006) although this may widely vary among species (Steele and Forrester 2002). Similar patterns have been observed for temperate species. For example, Planes et al. (1998) report that 24.3% to 99.4% of the initial population of *Diplodus* spp. disappeared within three months after settlement. The results of the present study were consistent with these observations. A reduction of 50-80% of the smallest size class (i.e. recently-settled) occurred approximately one week after settlement.

The lack of correlation between mortality and peak density suggests that mortality of juvenile D. sargus in the study area is not density-dependent. In fact, the reserve zone had slightly lower peak density but higher mortality rate than the outside zones. Previous studies have also reported densityindependent juvenile mortality in some coral reef (e.g. Victor 1986, Jones 1987) and temperate (Levin 1994a) fish species. In opposition to these findings, Macpherson et al. (1997) and Planes et al. (1998) observed strong density-dependent mortality rates for juveniles of *Diplodus* spp. However, when mortality rates of D. sargus were compared in protected and unprotected sites in the northwestern Mediterranean, there were no significant differences among sites (Planes et al. 2000). Whether increased predation on juvenile fish in protected areas, when present, is a major factor influencing natural recruitment patterns cannot be ascertained in the present study. White (2007) has observed a strong relationship between predator abundance and the nature of density-dependent mortality of Thalassoma bifasciatum settlers. He noted that wrasse mortality was inversely density-dependent in sites with few predators and positively densitydependent in sites with higher predator densities. Hixon and Carr (1997) also observed that mortality of juvenile Chromis cyanea is spatially densitydependent in the presence of two suites of predators (transients and residents) but density-independent in the absence of these predators.

The present work is one of few studies specifically designed to test the effects of protection on fish recruitment. It has shown indicative results that recruitment of the rocky reef fish, Diplodus sargus, is lower inside a reserve compared to fished areas and that this pattern could be attributed to predation. This observation suggests that protection may have a more substantial effect on fish recruitment, specifically on post-settlement mortality, as previously observed. Due to the possible variation of recruitment between years and lag time of ecological responses to protection, censuses have to be continued for several years to monitor juvenile densities and mortality and obtain unequivocal results. The geographic scale of the experimental design, i.e. proper controls or outside sampling stations near the MPA being studied, should also be carefully considered because it could influence the sensitivity of the study to detect protection effects on fish recruitment.

Acknowledgement

The authors would like to thank M. Clozza for her valuable assistance during the fieldwork. The main author is being funded by the Erasmus Mundus Mobility with Asia (EMMA) program of the EU-EMCW. The study was funded by the *Agence de l'Eau Rhône Méditerranée*.

Proceedings of the 12th International Coral Reef Symposium, Cairns, Australia, 9-13 July 2012 13E Fisheries: General session

References

- Almany GR, Webster MS (2006) The predation gauntlet: earlypost-settlement mortality in reef fishes. Coral Reefs 25:19-22
- Arceo HO, Aliño PM, Nañola CL (2007) Adult-juvenile reef-fish relationships and their significance to marine protected areas. In Day JC, Senior J, Monk S, Neal W (eds) First Intl Mar Protected Areas Congress, 23-27 October 2005, Conference Proc, Geelong, Victoria, Australia, 1:358-360
- Champely S (2009) pwr: Basic functions for power analysis. R package version 1.1.1. http://CRAN.R-project.org/package= pwr
- Cheminée A, Francour P, Harmelin-Vivien M (2011) Assessment of Diplodus spp. (Sparidae) nursery grounds along the rocky shore of Marseille (France, NW Mediterranean). Sci Mar 75:181-188
- Claudet J, Osenberg CW, Benedetti-Cecchi L, Domenici P, Garcıa-Charton JA, Perez-Ruzafa A, Badalamenti F, Bayle-Sempere J, Brito A, Bulleri F, Culioli J, Dimech M, Falcon JM, Guala I, Milazzo M, Sanchez-Meca J, Somerfield PJ, Stobart B, Vandeperre F, Valle C, Planes S (2008) Marine reserves: size and age do matter. Ecol Letters 11:481-489
- Cohen J (1988) Statistical power analysis for the behavioral sciences. Lawrence Erlbaum Associates, Inc., New Jersey
- Del Re AC (2012). compute.es: Compute Effect Sizes. R package version 0.2.1. http://CRAN.R-project.org/package= compute.es
- Diaz D, Zabala M, Linares C, Hereu B, Abello P (2005) Increased predation of juvenile European spiny lobster (*Palinurus elephas*) in a marine protected area. New Zeal J Mar Fresh 39:447-453
- Fontes J, Caselle JE, Afonso P, Santos RS (2009) Multi-scale recruitment patterns and effects on local population size of a temperate reef fish. J Fish Biol 75:1271-1286
- Francour P, Mangialajo L, Pastor J (2010) Mediterranean marine protected areas and non-indigenous fish spreading. in Galani D, Appelbaum-Galani B (eds.) Fish invasions of the Mediterranean Sea: change and renewal. Pensoft Publishers, Sofia-Moscow, pp 35-56
- Garcia-Charton JA, Perez-Ruzafa A, Marcos C, Claudet J, Badalamenti F, Benedetti-Cecchi L, Falcon JM, Milazzo M, Schembri PJ, Stobart B, Vandeperre F, Brito A, Chemello R, Dimech M, Domenici P, Guala I, LeDireach L, E.Maggi E, Planes S (2008) Effectiveness of European Atlanto-Mediterranean MPAs: do they accomplish the expected effects on populations, communities and ecosystems? J Nature Cons 16:193-221
- García-Rubies A, Macpherson E (1995) Substrate use and temporal pattern of recruitment in juvenile fishes of the Mediterranean littoral. Mar Biol 124:35-42
- Harmelin-Vivien ML, Harmelin JG, Leboulleux V (1995) Microhabitat requirements for settlement of juvenile sparid fishes on Mediterranean rocky shores. Hydrobiologia 300/301:309-320
- Harmelin-Vivien M, Harmelin JG, Chauvet C, Duval C, Galzin R, Lejeune P, Barnabé G, Blanc F, Chevalier R, Duclerc J, Lassère G (1985) Evaluation visuelle des peuplements et populations de poissons: méthodes et problèmes. Rev Ecol (Terre Vie) 40:467–539
- Hixon MA, Carr MH (1997) Synergistic predation, density dependence, and population regulation in marine fish. Science 277:946-949
- Holmes TH, McCormick MI (2006) Location influences sizeselective predation on newly settled reef fish. Mar Ecol Prog Ser 317:203-209
- Jones GP (1987) Competitive interactions among adults and juveniles in coral reef fishes. Ecology 68:1534-1547
- Juanes F (2007) Role of habitat in mediating mortality during the post-settlement transition phase of temperate marine fishes. J Fish Biol 70: 661-677
- Levin P (1994a) Fine scale temporal variation in recruitment of a temperate demersal fish: the importance of settlement versus post-settlement loss. Oecologia 97:124-133
- Levin P (1994b) Small-scale recruitment variation in a temperate fish: the roles of macrophytes and food supply. Environ Biol Fish 40:271-281

- Macpherson E (1998) Ontogenetic shifts in habitat and aggregation in juvenile sparid fishes. J Exptl Mar Biol Ecol 220:127-150
- Macpherson E, Biagi F, Francour P, Garcia-Rubies A, Harmelin J, Harmelin-Vivien ML, Jouvenel JY, Planes S, Vigliola L, Tunesi L (1997) Mortality of juvenile fishes of the genus *Diplodus* in protected and unprotected areas in the western Mediterranean Sea. Mar Ecol Prog Ser 160:135-147
- Molloy PP, McLean IB, Côté IM (2009) Effects of marine reserve age on fish populations: a global meta-analysis. J Appl Ecol 46:743-751
- Pelletier D, Garcia-Charton JA, Ferraris J, David G, Thebaud O, Letourneur Y, Claudet J, Amand M, Kulbicki M, Galzin R (2005) Designing indicators for assessing the effects of marine protected areas on coral reef ecosystems: a multidisciplinary standpoint. Aquat Living Resour 18: 15-33
- Piko, A.A., and Szedlmayer, S.T. (2007) Effects of habitat complexity and predator exclusion on the abundance of juvenile red snapper. J Fish Biol 70:758-769.
- Planes S, Jouvenel JY, Lenfant P (1998) Density dependence in post-recruitment processes of juvenile sparids in the littoral of the Mediterranean Sea. Oikos 83:293-300
- Planes S, Galzin R, Garcia-Rubies A, Goni R, Harmelin JG, Le Direac'h L, Lenfant P, Quetglas A (2000). Effects of marine protected areas on recruitment processes with special reference to Mediterranean littoral ecosystems. Environ Conserv 27: 126-143
- Polunin NVC, Roberts CM (1993) Greater biomass and value of target coral reef fishes in 2 small Caribbean marine reserves. Mar Ecol Prog Ser 100:167-176
- R Development Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-70-0, http://www.R-project.org
- Roberts CM, Polunin NVC (1991) Are marine reserves effective in management of reef fisheries? Rev Fish Biol Fisher 1:65-91
- Rowley RJ (1994) Case studies and reviews marine reserves in fishery management. Aquat Conserv 4: 233-254
- Russ GR (2002) Yet another review of marine reserves as reef fishery management tools. in Sale PF (ed) Coral reef fishes dynamics and diversity in a complex ecosystem. Academic Press, San Diego, California, pp 421–443
- Sale PF, Ferrel DJ (1988) Early survivorship of juvenile coral reef fishes. Coral Reefs 7:117-124
- Sale P, Douglas WA, Doherty PJ (1984) Choice of microhabitats by coral reef fishes at settlement. Coral Reefs 3:91-99
- Schmitt RJ and SJ Holbrook (1999) Mortality of juvenile damselfish: implications for assessing processes that determine abundance. Ecology 80:35-50
- Seytre C, Francour P (2008) Is the Cap Roux marine protected area (Saint Raphaël, Mediterranean Sea) an efficient tool to sustain artisanal fisheries? First indications from visual censuses and trammel net sampling. Aquat Living Res 21:297-305
- Seytre C, Francour P (2009) The Cape Roux marine protected area (Saint-Raphaël, French Mediterranean Sea): changes in fish assemblages within four years of protection. ICES J Mar Sci 66:180-187
- Shulman MJ (1985) Recruitment of coral reef fishes: effects of distribution of predators and shelter. Ecology 66:1056-1066
- Steele MA, Forrester GE (2002) Early postsettlement predation on three reef fishes: effects on spatial patterns of recruitment. Ecology 83:1076-1091
- Tupper, M, Juanes F (1999) Effects of a marine reserve on recruitment of grunts (Pisces: Haemulidae) at Barbados, West Indies. Environ Biol Fish 55:53-63
- Victor BC (1986) Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. Ecol Monogr 56:145-160
- Vigliola L, Harmelin ML (2001) Post-settlement ontogeny in three Mediterranean reef fish species of the genus, Diplodus. Bull Mar Sci 68:271-286
- Webster MS (2002) Role of predator in the early-settlement demography of coral-reef fishes. Oecologia 131: 52-60

Proceedings of the 12th International Coral Reef Symposium, Cairns, Australia, 9-13 July 2012 13E Fisheries: General session

White JW (2007) Spatially correlated recruitment of a marine predator and its prey shapes the large-scale pattern of density-dependent prey mortality