

Effects of a predatory site-attached fish on abundance and body size of early post-settled reef fishes from Gorgona Island, Colombia

C. Mora^{1,2} and F.A. Zapata¹

ABSTRACT

The effects of predation on early post-settlement stages of reef fishes were examined by comparing abundance and body size of fishes settled on standard coral units (SCU) with and without individuals of the small grouper *Serranus psittacinus*. Because of the strong site-attached behavior of this predator, adults of *S. psittacinus* remained associated with SCUs allowing an accurate control of its presence. Three of six analyzed species settled in lower abundance on SCUs with the predator, while the abundance of the remaining three species did not differ between experimental and control SCUs. In some cases the lower settlement in the predator treatment was due to predation by *S. psittacinus*, but in others such pattern can be explained by the avoidance of microhabitats with predators by settling larvae and by the simultaneous effect of *S. psittacinus* and transient predators. The absence of predatory effects on settler abundance of the remaining three species can be explained by anti-predatory traits (e.g. venomous fin spines, body toxins, and cryptic appearance). Because adaptations in morphology and behavior to avoid predation are common among reef fishes, predation as a factor controlling population replenishment, local abundance, and community structure of reef fishes cannot be suggested as a general rule. Conspecific juveniles of *S. psittacinus* had a larger body size in the predator treatment supporting the "bigger is better" hypothesis. However, because most species exhibited low levels of variability in body size, size-dependent predation generally would have little effect on survivorship.

Keywords Reef fishes, Predation, *Serranus psittacinus*, Post-settlement, Abundance, Body size

Introduction

Most marine reef fishes have a complex life cycle that includes a pelagic larval stage and a benthic adult phase. At the end of planktonic life, larvae settle onto reefs and recruit into the benthic population. Thus, most reef fish populations are replenished by the supply of larvae from the plankton (Caley et al. 1996). The importance of this supply in driving population dynamics has been widely recognized (reviewed by Doherty 1991). However, it is not clear whether the major contribution to population dynamics is due to the supply of settlement-stage larvae or to losses shortly after settlement. Recently, it has been considered that the short period after settlement is a critical time for the survival of newly settled fishes (Hixon 1991, Kaufman et al. 1992, Schmitt and Holbrook 1999). In fact, between 30% and 78% of settled individuals can disappear within the first few days after settlement (Doherty and Sale 1985, Victor 1986, Booth 1991). Although these high rates of mortality have been largely attributed to predation, there are few experimental data that demonstrate that this is the case. This is particularly problematic given that other processes are also plausible (e.g. parasitism – Minchella and Scott 1991 and diseases - Schmale 1991).

Progress in the study of predation on reef fishes has been largely inhibited by logistical problems associated with manipulating predators. To date, experimental information of predation on coral reef fishes has been obtained through the use of cages to exclude predators or

by frequent selective removals of predators on reefs (Hixon 1991). However, results based on either cages or predator removals are often biased. It has been found that cages may produce artifacts that cannot be separated from predatory effects. For instance, exclusion of herbivores on caged sites leads to differences in food supply, and therefore, at least two possible factors (differences in food and predation) could explain any difference among treatments (See Doherty and Sale 1985, Steele 1996, Connell 1997 for problems associated with cage experiments). On the other hand, experiments with predator removals have presented problems such as insufficient isolation of experimental reefs (Caley 1993), uncontrolled manipulations (Shpigel and Fishelson 1991) and high variance in predator abundance (Beets 1997). Hence, predation as a process potentially affecting populations and structuring communities of reef fishes has not been fully explored.

One of the most important aspects in the study of predation is how particular traits enhance the survival probability of certain individuals in the same local population. A current paradigm for temperate marine fishes is that predation on early larval stages is often dependent on body size. The most common view is that larger individuals are less vulnerable to predation because they are better able to escape from predators. However, a contrasting view suggests that smaller larvae are inconspicuous to predators and therefore less susceptible to predation (see Litvak and Leggett 1992, Sogard 1997 for reviews). In addition to these contradictory view, rapid development of the muscular and sensory systems during the larval phase limits the extension of these studies to later life-history stage. Also taxonomic differences

¹ Dept. of Biology, Universidad del Valle, Apartado Aéreo 25360, Cali, Colombia

² Present address: Dept. of Biology, University of Windsor, Windsor, ON N9B 3P4 Canada. E-mail: moracarnilo@hotmail.com

between temperate and tropical reef fishes restrict the extrapolation of these views to tropical reef fishes. At the time of settlement body size could effect survival in different ways. For example, smaller fishes can find refuge more easily than larger ones. Larger fish, on the other hand, could escape from predators more easily than smaller ones because of their stronger swimming abilities or, alternatively, because of a predator's inability to prey upon fish beyond a certain body size.

In this study we circumvent the logistical constraints facing previous studies of predation by transplanting adults of a small site attached predator (*Serranus psittacinus*) onto isolated standard coral units. Because of its site-attached behavior, individuals of these species were not able to leave experimental units allowing us to appropriately manipulate predators abundance. The confinement of predator to small areas is not a problem in this study because of the small size of *S.psittacinus* and because it naturally inhabits isolates sall areas. Once we had manipulated the abundance of *S.psittacinus*, our aim was to assess its effects on abundance and body size of newly settled reef fishes.

Material and methods

Study size

This study was done at Gorgona Island (2°58'10"N, 78°11'05"W) on the southern Colombian Pacific coast (see Gylmn et al.1982 for a detailed description of the study area). Gorgona's reefs are among the most developed and diverse in the eastern pacific and contain a representative sample of the reef fish fauna from this region (Zapata and Morales 1997). The experiment was carried out on the eastern coast of Gorgona in a uniform sandy bottom location isolated from natural reefs for at least 1 km and with a depth of 3-4 m at low tide.

Study species

The predatory fish used in this study was the grouper *Serranus psittacinus*. It is small carnivore(11 cm maximum total length), widely distributed in the tropical eastern Pacific (Allen and Robertson 1994), and common on Gorgona's reefs (Zapata and Morales 1997). *S. psittacinus* is a recognized predator that preys upon small fishes and invertebrates (Allen and Robertson 1994). It is also remarkable for its site-attached and territorial behavior (Petersen 1987,1990), it normally lives in close association with the reef bottom, inhabiting coral rubble habitats. When transplanted to an isolated coral colony over sandy bottom, *S.psittcinus* does not stray far from the colony which serves as the only refuge.

Experimental design

In order to reduce possible variation in settlement processes due to variability in habitat characteristic, the experiment was done using "standard coral units" (SCUs; after Sweatman of 1983). SCUs have been broadly used in studies of the biology resident fishes, serve as adequate substrate for the settlement of many species, and are easy

to build and manipulate (Sweatman 1983, Jones 1987, Forrester 1990). A SCU consists of an iron rod driven into the sand which supports 2 or 3 pieces of dead *Pocillopora* sp. Tied together with fishing line to form an irregularly spherical colony of about 0,40 m diameter suspended ~ 0.2 m above the sand. Six SCUs were built and located 20 m a apart form each other and 1000 m away from the nearest reef. On each of three haphazardly selected SCUs we placed an adult of *S. psittacinus* (total leigth 6.3 cm \pm 0.7 cm) collected with manual nets on natural reefs. The other there SCUs remained without a predator and were used as experimental controls. All fishes settled on the SCUs were removed every other day between May 10 and July 10, 1998. To remove the new settlers a 2x2 m piece of nylon net (2 mm mesh) was spread around the base of the holding rod, raised and wrapped around the colony trapping all individuals. The net with the colony was taken to a boat on the surface, where settlers were manually removed, counted, and measured. After removal each colony was returned to it's the iron rod on the bottom. In the case of predator-present-SCUs, the process of removal was quicker and the predator an ther the colony were returned to their location in <5 min. When the *S.psittacinus* adult was placed in it an the corresponding data were not included in the analysis.

During the 60 days of our manipulations a total of 30 replicate experiment were carried out. Data from each SCU were considered as sub-replicates within treatment or control conditions in each replicate observation. A predator-present sub-replicates was considered valid only if the predator was present at the time of sampling. Only replicate experiment with \geq two valid predator-present sub-replicates were considered in the analysis. Only 26 replicate experiments met this condition (i.e. out of 90 [experiments x 3 SCUs] possible predator-present sub replicates, 58 had the predator at the time of sampling). Therefore, four complete replicate experiments were excluded from the analysis

Data analysis

Our aim in this study was to determine the effect of predation on (1) abundance (number of individuals) and (2) body sized (standard length) of newly-settled reef fishes. We used a one-way analysis of variance to compare treatment (predator present) with control (predator absent) SCUs. Tests for normality and homogeneity of variances for each response variable were conducted prior to analysis. Abundance data of Antennariids, *Lutjanus guttatus* and *Halichoeres dispilus* were square root transformed to obtain homoscedasticity and normality. However, data on *L. guttatus* and *H. dispilus* violated normality even after data transformation. Despite this, we performed the ANOVA for these species given that it is robust against non-normality under high replication (n = 26 in our experiment, Johnson 1995).

Results

A total of 24 species belonging to 14 families settled on the SCUs during the study period (Table 1). Of these

species, *Lutjanus guttatus*, *Halichoeres dispilus*, *Scorpaenodes xyris*, *Canthigaster punctatissima*, three combined species of antennariids (*Antennarius sanguineus*, *A. cocineus* and *Antennatus strigatus*), and *Serranus psittacinus* were the most frequent and abundant species. Our analysis focuses on data for these six taxa. The remaining 17 species settled in too low abundance and in sporadic events to warrant statistical analysis and were therefore not considered further.

Table 1 Mean number of individuals and body size (SL) of reef fishes settled on 6 standard coral units (SCUs) every two days between May 10 and June 10, 1998, at Gorgona Island. Sample standard deviations are given in parentheses and the coefficient of variation (CV) in body size is also shown.

Species	N°settlers		
	Mean (SD)	Mean (SD)	CV%
Antennariidae			
Antennariids*	0.40 (0.7)	7.5 (1.2)	16
Scorpaenidae			
<i>Scorpaenodes xyris</i>	1.55 (2.0)	13.2 (1.3)	10
Serranidae			
<i>Serranus psittacinus</i>	0.36 (0.9)	20.7 (9.4)	45
<i>Paranthias colonus</i>	0.10 (0.4)	28.2 (1.7)	6
<i>Alphesites immaculatus</i>	0.01 (0.1)	25.0 (0.0)	0
<i>Cephalopolis panamensis</i>	0.11 (0.4)	23.6 (1.1)	4
Gerreidae			
<i>Eucinostomus gracilis</i>	0.05 (0.5)	17.3 (2.1)	12
Blenniidae			
<i>Plagiotremus azaleus</i>	0.02 (0.1)	30.7 (1.5)	5
Apogonidae			
<i>Apogon dovii</i>	0.18 (0.5)	15.5 (1.7)	11
Lutjanidae			
<i>Lutjanus guttatus</i>	12.35 (15.1)	25.1 (3.6)	14
<i>L. viridis</i>	0.01 (0.1)	28.5 (0.0)	0
Pomacanthidae			
<i>Pomacanthus zonipectus</i>	0.11 (0.4)	16.4 (4.9)	29
Pomacentridae			
<i>Stegastes flavilatus</i>	0.02 (0.1)	14.0 (1.7)	10
<i>Cromis atrilobata</i>	0.01 (0.1)	24.0 (0.0)	0
Cirrhitidae			
<i>Cirrhitichthys oxycephalus</i>	0.23 (0.7)	21.1 (2.5)	12
Labridae			
<i>Halichoeres dispilus</i>	7.45 (7.9)	18.4 (1.1)	6
<i>H. nicholsi</i>	0.01 (0.1)	12.0 (0.0)	0
<i>Thalassoma lucasanum</i>	0.05 (0.3)	11.9 (0.6)	5
Acanthuridae			
<i>Acanthurus xanthopterus</i>	0.01 (0.2)	23.0 (0.0)	0
Balistidae			
<i>Sufflamen verres</i>	0.05 (0.2)	36.7 (16.3)	44
Tetraodontidae			
<i>Canthigaster punctatissima</i>	0.49 (0.9)	18.0 (2.0)	11
<i>Arothron meleagris</i>	0.01 (0.1)	94.0 (0.0)	0

*Antennariids include *Antennarius sanguineus*, *A. cocineus*, and *Antennatus strigatus*.

During the study period, presence of adult *S.psittacinus* had a significant effect on the abundance of settlers in some species. *Lutjanus guttatus*, *Halichoeres dispilus*, and conspecific *S. psittacinus* were significantly

affected by the presence of the predator numbers of settlers of these species were significantly greater on control SCUs than on treatment SCUs (Table 2). The effect of adult *S. psittacinus* was strongest on conspecific settlers, which were 10 times more abundant in the absence of adults. Settlers of *H. dispilus* and *L. guttatus* were only between 33 and 61% more abundant on control compared to treatment SCUs. Settlement of *C. punctatissima*, *S. xyris*, and antennariids did not differ significantly between control and treatment conditions.

Standard length of settlers ranged from 7.5 mm in antennariids to around 31 mm in *Plagiotremus azaleus*. In other species standard length at settlement varied from 12 to 28 mm. These represent the smallest size classes seen on natural reefs at Gorgona, and because the SCUs were isolated from natural reefs, individuals of most species found in them were likely to be newly settled. Although tetraodontiform fishes are known to settle at relatively large sizes, the large mean sizes observed in *Sufflamen verres* and *Arothron meleagris* were due to the presence of a few relatively large individuals of these species in the SCUs. These may have been wandering individuals that had settled previously elsewhere but were attracted to the colonies. Overall, intraspecific variability in body size was rather low; in most species the coefficient of variation in body size was < 10 %, although in many cases this may have been due to small sample sizes. Only *S. psittacinus*, *S. verres*, and *P. zonipectus* presented relatively high coefficients of variation in body size (29 - 45%). Presence of adult *S. psittacinus* significantly affected body size of conspecifics only. Settlers of this species were almost twice as large on treatment than on control SCUs (Table 2). For the remaining 5 species analyzed, size at settlement did not differ significantly between control and treatment (Table 2).

Discussion

The study of predation on coral reef fishes has been considerably inhibited by logistical problems associated with the manipulation of predators in experimental designs (Hixon 1991). In this study, using a territorial predator with a site-attached behavior we were able to manipulate its presence with a success of at least 65 %. Although, some adults were missing at the time of sampling (35% of the times), we attribute these losses to predation by transient predators more than to methodological artifacts. In several cases, transient predators such as moray eels and jacks were observed to approach SCUs and prey upon juveniles, and occasionally upon our treatment adults. In spite of losses due to large predators, the use of a small predator with a site-attached behavior provided enough data to assess the effect of predation on the early post-settlement stages of reef fishes.

Overall, experimental evidence of the effects of predation driving the local abundance of reef fish populations is largely lacking, especially for the short period after settlement when fishes are more susceptible to predation (Kaufman et al. 1992). During this study, the

experimental manipulation of a small site-attached predator significantly reduced the early post-settlement abundance of some species, but not others. The similar abundance on control and treatment SCUs of *Scorpaenodes xyrus*, *Canthigaster punctatissima* and three combined species of Antennariids indicates an absence of predation by *Serranus psittacinus* on these species. This can be explained by the presence in these species of anti-predatory traits such as venomous fin spines, body toxins, and cryptic appearance. In contrast, settlers of *Halichoeres dispilus*, *Lutjanus guttatus*, and *S. psittacinus* were less abundant on treatment than on control SCUs. Because we repeatedly observed adult *S. psittacinus* preying upon settlers of *H. dispilus* we believe that predation was responsible for the pattern observed in this species. However, a lower abundance on treatment than on control SCUs in the remaining species (*L. guttatus* and juvenile *S. psittacinus*) may be explained by the occurrence of more complex mechanisms.

L. guttatus is a species that tends to form peripheral schools. It has been suggested that species with this "peripheral aggregating" behavior generally suffer greater rates of mortality relative to more bottom-attached species (Connell and Gillanders 1997). Although we observed *S. psittacinus* preying upon small settlers of *L. guttatus*, we also observed that *S. psittacinus* did not attack the larger settlers of this species under obvious opportunities for successful predation. Instead, adult *S. psittacinus* were agonistically aggressive against larger *L. guttatus*. As a result of either this agonistic behavior or the risk of predation by *S. psittacinus*, settlers of *L. guttatus* were not able to hide on treatment-SCUs as they did on control-SCUs when threatened (e.g. when either transient predators or divers approached the SCUs). This suggests that *S. psittacinus* may inhibit the ability of *L. guttatus*

settlers to take shelter, therefore increasing the risk of predation by transient predators on treatment SCUs. In support of this idea Hixon and Carr (1997) found that the abundance of the peripheral Caribbean damselfish *Chromis cyanea* was synergistically affected by resident and transient predators in a "sandwich effect" between the attacks of resident piscivorous below and transient piscivorous above. In short, the low settlement of *L. guttatus* on treatment can be explained by at least two factor affecting survival: (1) predation of *S. psittacinus* on small *L. guttatus*, and (2) higher exposure of settlers to predation by transient predators.

Adult *S. psittacinus* also affected the abundance and body size of juvenile conspecifics. Juveniles of *S. psittacinus* were significantly less abundant but larger in the presence of adults than in their absence. This suggests a size-dependent predatory effect of *S. psittacinus* against conspecifics. This was demonstrated by a small experiment in which we released *S. psittacinus* juveniles of different sizes on the reef and observed the behavior of surrounding adult conspecifics. In all cases the smallest juveniles were quickly eaten while the larger ones (to 30 mm SL) were only approached by the adults. These results support the idea that predator-induced mortality in juveniles of *S. psittacinus* is size-dependent, with smaller individuals incurring a higher risk of predation. Other studies have obtained similar results in other reef fish species (Carr and Hixon 1995, Hixon and Carr 1997), and provide additional support for an extension of the "bigger is better" hypothesis (Sogard 1997) from early-life history stages to later stages (e.g. early post-settlers). However, this hypothesis requires sufficiently high levels of variability in body size, which although observed in *S. psittacinus* juveniles, was not observed in many other species in this study.

Table 2 Comparison of mean abundance and body size of newly settled reef fishes on standard coral units with and without adult *Serranus psittacinus* based on n = 26 replicate experiments (see methods). Standard errors are given in parentheses. Significant differences were tested using a one-way ANOVA. Species appear in order of increasing negative effect of *S. psittacinus*.

Species	No. of settlers				SL (mm)			
	Predator		ANOVA		Predator		ANOVA	
	Absent	Present	F	p	Absent	Present	F	p
Antennariids*	0.8 (0.3)	1.0 (0.3)	4.00	0.07	7.6 (1.3)	7.3 (1.0)	3.1	0.08
<i>Scorpaenodes xyrus</i>	1.6 (2.1)	1.3 (2.1)	0.94	0.33	13.1 (1.2)	13.4 (1.5)	1.2	0.28
<i>Canthigaster punctatissima</i>	0.5 (0.9)	0.4 (0.9)	0.03	0.87	18.2 (1.6)	17.6 (2.5)	0.8	0.37
<i>Halichoeres dispilus</i> **	2.4 (1.3)	1.8 (1.0)	4.73	0.03	18.3 (1.1)	18.8 (1.1)	4.0	0.08
<i>Lutjanus guttatus</i> **	2.9 (1.9)	1.8 (1.5)	15.6	0.00	25.0 (3.4)	25.3 (4.2)	0.3	0.56
<i>Serranus psittacinus</i>	0.4 (0.4)	0.04 (0.2)	10.3	0.00	19.2 (8.0)	35.6 (11.5)	10.7	0.00

* Combination of *Antennarius sanguineus*, *A. coccineus*, and *Antennatus strigatus*.

** Data were squared-root transformed.

Although adult *S. psittacinus* can prey upon small conspecifics, such predation may not be necessarily as common under more natural conditions because larvae may select settlement habitats without adults. Habitat selection has been reported in a wide number of species (Hixon 1991, Booth and Wellington 1998), and groupers have been observed to have larval preferences for specific

settlement habitats and a subsequent shift of habitat at a later size. In these species, larvae settle onto low relief substrata in habitats surrounding the reefs and then move to more complex habitats on the reef once the fish have grown larger (Beets and Hixon 1994, Ross and Masser 1995, Light and Jones 1997, Dahlgren and Eggleston 2000). Surrounding habitats might act as temporary

nurseries where fish can grow under a lower risk of predation. Once individuals have reached a certain size nursery habitats may not provide adequate resources while reefs do not impose a higher a risk of mortality any more. These species therefore exhibit a distinct pattern of spatial distribution related with body size. A similar pattern is observed in *S. psittacinus* at Gorgona. Adults of this species are common on reefs while juveniles are more frequent on coral rubble or small rocks on habitats surrounding reefs. It is therefore likely that, as other serranids, *S. psittacinus* exhibits microhabitat selection during settlement and subsequent ontogenetic microhabitat shifts. This is the more likely reason to explain the recruitment of large fishes on SCUs with conspecific adults. With the alternative hypothesis of high predation upon small settlers, it would be very difficult to explain the self-replenishment of this species particularly because *S. psittacinus* is one of the most abundant species in Gorgona's reefs (Zapata and Morales 1997).

Several studies have experimentally demonstrated the importance of predation in regulating juvenile densities of coral reef fishes (Hixon 1991, Caley 1993, Carr and Hixon 1995, Beets 1997, Hixon and Carr 1997). Most of these studies have found lower abundance of prey species on experimental substrates with predators relative to those without, although in some cases the effects of predators may be mediated by microhabitat complexity (e.g. Beukers and Jones 1997). Predation has also been argued to be a major source of density-dependent mortality due to shortages of refuges for prey, and an important post-settlement process altering initial patterns of abundance set by larval supply (Beukers and Jones 1997, Hixon and Carr 1997, Schmitt and Holbrook 1999). Thus predation can be a major force affecting the replenishment, local abundance, and community structure of reef fishes. Nonetheless, our results suggest that this may not apply to all reef fishes. Although, predators can clearly reduce settler abundance in some cases (e.g. *H. dispilus* and *L. guttatus*), anti-predatory adaptations, which are common among reef fishes (Hixon 1991, Booth and Wellington 1998), can effectively reduce the effects of predation. Morphological or chemical anti-predatory traits (such as shown by tetraodontids, scorpaenids and antennariids) appeared to minimize the adverse effects of predation by adult *S. psittacinus*. Additionally, behavioral mechanisms such as larval selection of safe settlement habitats may also reduce predatory effects. In this case predation would act as a factor influencing habitat choice and patterns of distribution more than mortality. On the other hand, it might be argued that anti-predatory adaptations exist because the intensity of predation has been sufficiently high during the evolutionary history of some species to select for these traits in the first place.

Acknowledgments We thank S. Lozano, V. Francisco and C. Muller who assisted with fieldwork. Permits to work at Gorgona Island and logistical support were provided by UAESPNN-Colombian National Parks. Thanks are also extended to P. Sale, D.J. Booth and two anonymous reviewers for comments. This research was

supported by grants from Colciencias to FAZ and from Banco de la Republica Foundation to CM.

References

- Allen G, Robertson DR (1994) Fishes of the tropical eastern Pacific. University of Hawaii Press, Honolulu
- Beets J (1997) Effects of a predatory fish on the recruitment and abundance of Caribbean coral reef fishes. *Mar Ecol Prog Ser* 148:11-21
- Beets J, Hixon MA (1994) Distribution, persistence and growth of groupers (Pisces: Serranidae) on artificial and natural patch reefs in the Virings Islands. *Bull Mar Sci* 2-3:470-483
- Beukers JS, Jones GP (1997) Habitat complexity modifies the impact of piscivores on a coral reef fish population. *Oecologia* 114:50-59
- Booth DJ (1991) The effects of sampling frequency on estimative of recruitment of the domino damselfish *Dascyllus albisella* Gill. *J Exp Mar Biol Ecol* 76:91-106
- Booth DJ, Wellington G (1998) Settlement preferences in coral-reef fishes: effects on patterns of adult and juvenile distributions, individual fitness and population structure. *Aust J Ecol* 23:274-279
- Caley MJ (1993) Predation, recruitment and the dynamics of communities of coral-reef fishes. *Mar Biol* 117:33-43
- Caley MJ, Carr MH, Hixon MA, Hughes TP, Jones GP, Menge BA (1996) Recruitment and the population dynamics of open marine populations. *Annu Rev Ecol Syst* 27:477-500
- Carr MH, Hixon MA (1995) Predation effects on early post-settlement survivorship of coral-reef fishes. *Mar Ecol Prog Ser* 124:31-42
- Connell SD (1997) Exclusion of predatory fish on a coral reef: the anticipation, pre-emption and evaluation of some caging artefacts. *J exp Mar Biol Ecol* 213:181-198
- Connell SD, Gillanders BM (1997) Mortality and abundance of a schooling reef fish. *Proc 8 th Intern Coral Reef Symp Panama*, 1: 1035-1038
- Dahlgren CP, Eggleston DB (2000) Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. *Ecology* 81:2227-2240
- Doherty PJ (1991) Spatial and temporal patterns in recruitment. In: Sale PF (ed) *the ecology of fishes on coral reefs*. Academic Press, San Diego: 261-292
- Doherty PJ, Sale PF (1985) Predation on juvenile coral reef fishes: an exclusion experiment. *Coral reefs* 4:225-234
- Forrester GE (1990) Factors influencing the juvenile demography of a coral reef fish population. *Ecology* 71:1666-1681
- Glynn PW, Von Prahl H, Guhl F (1982) Coral reefs of Gorgona island, Colombia, with special reference to corallivores and their influence on community structure and reef development. *An Inst Inv Mar Punta Betin* 12: 185-214
- Hixon MA (1991) Predation as a process structuring coral reef fish communities. In: Sale PF (ed) *the*

- ecology of fishes on coral reefs. Academic Press, San Diego: 261-292
- Hixon MA, Carr MH (1997) Synergistic predation, density dependence, and population regulation in marine fish. *Science* 277:946-948
- Johnson DH (1995). Statistical sirens: the allure of nonparametrics. *Ecology* 76:1998-2000
- Jones GP (1987) Some interactions between resident and recruits in two coral reef fishes. *J Exp Mar Biol Ecol* 114:169-182
- Kaufman L, Ebersole J, Beets J, McIvor C (1992) A key phase in the recruitment dynamics of coral reef fishes: post-settlement transition. *Env Biol Fish* 34:109-118
- Light PR, Jones GP (1997) Habitat preference in newly settled coral trout (*Plectropomus leopardus*, Serranidae). *Coral Reefs* 16:117-126
- Litvak MK, Leggett WC (1992) Age and size-selective predation on larval fishes: the bigger-is-better hypothesis revisited. *Mar Ecol Prog Ser* 81:13-24
- Minchella DJ, Scott ME (1991) Parasitism: a cryptic determinant of animal community structure. *TREE* 6:250-254
- Petersen CW (1987) The relationships among population density, individual size, mating tactics, and reproductive success in a hermaphroditic fish, *Serranus fasciatus*. *Behaviour* 113:57-80
- Petersen CW (1990) Reproductive behaviour and gender allocation in *Serranus fasciatus*, a hermaphroditic reef fish. *Anim Behav* 35:1601-1614
- Ross SW, Mosser ML (1995) Life history of juvenile gag, *Mycteroperca microlepis*, in North Carolina Stuaries. *Bull Mar Sci* 56:222-237
- Schmale MC (1991) Prevalence and distributions patterns of tumors in bicolor damselfish (*Pomacentrus partitus*) on South Florida reefs. *Mar Biol* 109:203-212
- Schmitt RJ, Holbrook, SJ (1999) Mortality of juvenile damselfish: implications for assessing processes that determine abundance. *Ecology* 80: 35-50
- Shpigel M, Fishelson L (1991) Experimental removal of piscivorous groupers of the genus *Cephalopholis* (Serranidae) from coral habitats in the Gulf of Aqaba (Red Sea). *Env Biol Fish* 31:131-138
- Sogard SM (1997) Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bull Mar Sci* 60:1129-1157
- Steele MA (1996) Effects of predators on reef fishes: separating cage artefacts from effects of predation. *J Exp Mar Biol col* 198:249-267
- Sweatman HPA (1983) Influence of conspecifics on choice of settlement sites by larvae of two pomacentrid fishes (*Dacillus aruanus* and *D. reticulatus*) on coral reefs. *Mar Biol* 75:225-229
- Victor BC (1986) Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. *Ecol Monog* 56:145-160
- Zapata FA, Morales YA (1997) Spatial and temporal patterns of fish diversity in a coral reef at Gorgona island, Colombia. *Proc 8 th Intern Coral Reef Symp Panama*, 1:1029-1034