

Implications of body size for interspecific interactions and assemblage organization among coral-reef fishes

D. ROSS ROBERTSON

Smithsonian Tropical Research Institute (Balboa, Panama) Unit 0948, APO AA 34002–0948, USA

Abstract Population size-structure is often ignored in assemblage-level studies of reef fishes, which usually rely on static and dynamic patterns of relative total abundance to infer what mechanisms organize those assemblages. However, body size has substantial effects on processes that affect competitive relationships between species: (i) small, recently recruited fish, which usually(?) suffer high mortality, can dominate total abundance and strongly influence the dynamics of the relative total abundances of different species, while having little effect on interspecific biomass relations; (ii) numeric abundance and biomass of a species can vary independently, due to habitat variation in population size-structure resulting from variation in mortality and growth, as well as habitat selection; and (iii) population size-structure affects the potential for and outcome of interspecific competition due to (a) ontogenetic change in types of resources used, (b) levels of resource needs being dependent on individual and species biomass rather than numbers, (c) advantages due to large size in behavioural contests, (d) variation in population size-structure being linked to habitat preference, which affects expression of competitive dominance, and (e) size dependency in the development of interspecific resource-sharing relationships. Assemblage-level analyses that ignore such size effects may fail to detect important effects of interspecific interactions.

Key words: assemblage structure, biomass, competition, coral reefs, fish, numeric abundance, population size-structure.

INTRODUCTION

Studies of reef-fish population biology fall into two groups with respect to how they examine local populations. Single-species studies recognize that detailed examination of population structure is essential, and consider how various factors that influence juvenile growth and survival subsequently affect adult numbers (see Jones 1991 for review). On the other hand, assemblage-level studies often simply ignore population age/size structure and use total abundance as their unit of comparison (e.g. Russ 1984; Findley & Findley 1985; Bouchon-Navaro 1986; Galzin 1987; Williams 1991; Roberts *et al.* 1992; Sale *et al.* 1994; Meekan *et al.* 1995; Waltho & Kolasa 1996). Although invariably nothing is said about why total abundance is used in assemblage studies, there probably are two main reasons. First, it is convenient. Visual censuses are the easiest means of estimating abundance, and the person assessing total abundance only needs to know how to identify fishes accurately and make reliable counts. Second, analyses using total abundance are relatively simple. Species can be combined into broad trophic

groups, and relations between their numeric abundances can be inspected for evidence of associations or interactions within and between such groups. Total abundances also are used to examine relations between abundances of fishes and resources, and allow the calculation of species diversity indices that are used to characterize assemblages. An assemblage-level analysis that involved detailing the ecological significance of population structure would be a more complicated effort, to both collect and analyse the data.

The aim of this paper is to reinforce the recognition by single-species studies of the importance of population size-structure, by pointing out reasons why it needs to be taken into account when assessing processes that determine abundances and distributions of groups of species, particularly when attempting to make inferences about the effects of interactions among ecologically similar species, and effects of the distribution and abundance of resources.

SIZE, MORTALITY RATES AND PATTERNS OF CHANGE IN RELATIVE ABUNDANCE

Mortality rates of juvenile reef fishes may typically be higher than those of conspecific adults (e.g. Eckert

1987; Warner & Hughes 1988; Hixon 1991; although see Caley 1998). Hence, not only interspecific differences in mortality rates of two species but also the initial abundances of juveniles in their populations will affect the pattern of subsequent change in their relative total abundances. Because recruits often arrive in large numbers, young juveniles may numerically dom-

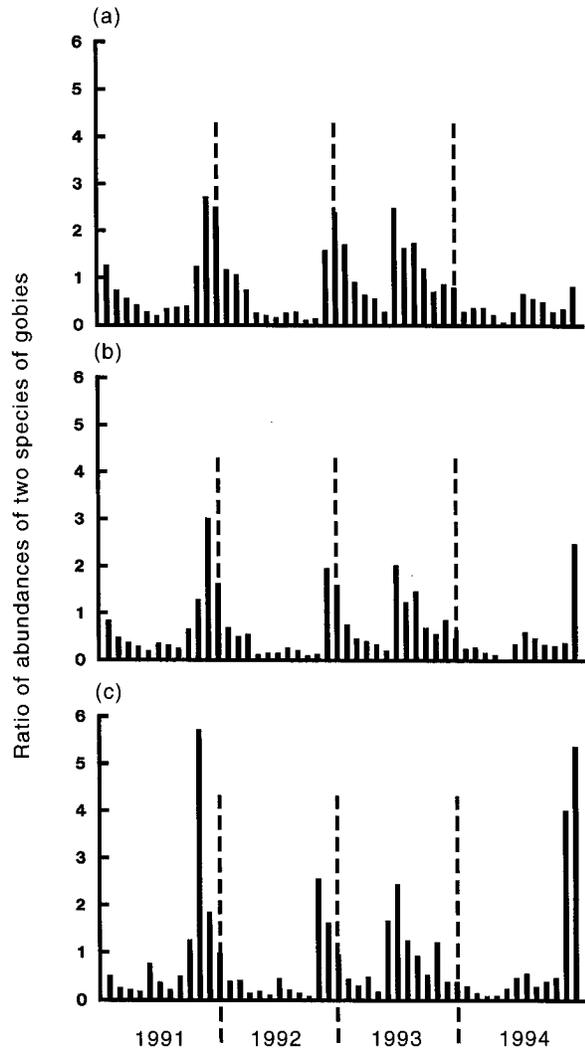


Fig. 1. Intermensual fluctuations in the relative abundances of two Caribbean gobies in San Blas, Panama. Relative abundance = abundance of *Gobiosoma illecebrosus*/abundance of *Coryphopterus personatus*. (a) Adults only; (b) adults + juveniles; and (c) adults + juveniles + recruits. These two species belong to different trophic groups and their populations are highly unlikely to interact. This figure shows how relative abundances can fluctuate rapidly, and in changing patterns depending on whether recruits of the month [which arrive intermittently throughout the year (Robertson & Kaufmann 1998)] and older juveniles are included in the populations. The relative abundances of adults of the two species fluctuate rapidly due to rapid maturation and low longevity.

inate a population shortly after a recruit influx, but do so for only a short time due to high juvenile mortality rates (e.g. Shulman & Ogden 1987). When recruitment occurs intermittently during an extended season, pulses of recruitment may also lead to substantial, frequent, short-term fluctuations in relative total abundances of different species. In the tropical northwest Atlantic, recruitment by many reef fishes occurs throughout all or most of the year, and there are high levels of both interspecific diversity and intraspecific, interannual variability in recruitment seasonality (Robertson & Kaufmann 1998). As a result, the relative abundances of different species can fluctuate considerably over the course of the year, to differing degrees and on somewhat different temporal patterns, depending on which age classes are incorporated in the 'population' (e.g. Fig. 1). The temporary, high abundance of a subset of a population that contributes very little to species biomass, and may have relatively weak interactions with older components of the same or different species (see below: Relative size and the strength of competitive interactions), could confound attempts to detect effects of interspecific interactions among older fishes on abundance.

HABITAT VARIATION IN POPULATION SIZE-STRUCTURE

Habitat variation in the size structures of adult populations has been examined for a few reef fishes (Ralston 1976; Robertson & Lassig 1980; Waldner & Robertson 1980; Fowler 1990; Hart & Russ 1996). While in some cases such spatial variation must result from habitat selection and redistributions of fish as they grow (e.g. Robertson 1988), in others it arises through variation in both adult longevity and growth (Ralston 1976; Fowler 1990; Aldenhoven 1986; Hart & Russ 1996). One consequence of intraspecific spatial variation in demographic characteristics is that the relative total abundances of pairs of species are likely to be governed by quite different processes in different habitats or sites, differences that may be undetectable using simple comparisons of relative total abundance.

In a habitat occupied by a single member of an ecological guild, that species' population often contains a high proportion of large adults (at least in territorial damselfishes; Robertson & Lassig 1980; Waldner & Robertson 1980). Such 'exclusive-use' habitats probably represent 'preferred' habitat because adults living in them probably achieve the highest fecundity and longevity. Because the structure of dominance relations between two species may vary in different habitats (Ebersole 1985), with the ecologically dominant species asserting its dominance only in the habitat it prefers (Robertson 1995), habitat preference could have important effects on the outcome of interspecific interactions by reinforcing size effects on dominance ability.

RELATIVE SIZE AND THE STRENGTH OF COMPETITIVE INTERACTIONS

Major ontogenetic changes in the types of resources used commonly occur among reef fishes (e.g. diet: Emery 1973; Bellwood 1988; Harmelin-Vivien 1989; microhabitat and habitat use: Clarke 1977; Shulman & Ogden 1987; Robertson 1988; Harmelin-Vivien 1989; Williams 1991; Lirman 1994; Green 1996). In fact juveniles may have such specialized and different habitat requirements from adults that an entire local population may disappear in response to the loss of juvenile habitat due to disturbance that has no apparent effect on adult habitat (e.g. Williams 1986). Such ontogenetic variation in resource use is likely to affect the strength of interactions between size classes of both the same (Harmelin-Vivien 1989) and different species.

Examinations of the effects of both intra- and interspecific interactions on demography of reef fishes generally focus on adult-juvenile and juvenile-juvenile relations (see Jones 1991 for review). However, interactions among adults are at least as important. To an adult fish, an adult of another closely related, ecologically similar species probably constitutes a greater competitive threat than does a small juvenile of the latter species, because adults of those species are more likely to require the most similar types of resources and to have the largest needs. Consequently competitive interactions are likely to be most intense between individuals of similar size (cf. Ebersole 1977; Harrington 1993), and those among adults are likely to be more intense than those between adults and juveniles. The onset of density-dependent limitation of growth as fish approach maturity (Jones 1991; Pitcher 1992) reflects such size dependency in the intensity of competition. Much effort has been devoted to assessing the extent to which patterns of growth and mortality of recently recruited reef fishes modify the relationship between larval supply and subsequent abundance (see review in Jones 1991). Attention also needs to be given to the extent to which processes affecting 'recruitment' of subadults into the adult population modify the effects of earlier events (cf. Harmelin-Vivien 1989; Jones 1991). Variation in such subadult 'recruitment' has the potential to affect the abundance of adults and the biomass of a species at least as strongly as does the demography and growth of young juveniles.

RELATIVE SIZE AND THE OUTCOME OF COMPETITIVE INTERACTIONS

Body size is an important determinant of behavioural dominance between individuals not only of the same species but also of different, closely related species of reef fishes (Robertson 1995). Consequently, the relative size structures of populations of two such species are likely to affect the extent to which a dominant

species controls resources. For example, in its primary habitat in Caribbean Panama, the large, uncommon territorial damselfish *Stegastes diencaeus* is competitively dominant over two much more abundant congeners, *Stegastes dorsopunicans* and *Stegastes planifrons*, at least in part because adults of the latter two tend to be smaller in that habitat than in other habitats (Robertson 1995).

Small to moderate differences in the body sizes of different species may affect the outcome of competitive interactions between their populations by determining which individuals of which species have exclusive access to behaviourally contested resources. However, large differences in body size may actually reduce the effectiveness of interspecific behavioural interactions and lead to heterospecifics cohabiting and sharing space and food resources they defend against conspecifics and other species. In some cases it appears that adults of large species cannot effectively exclude those of much smaller species because the latter exploit refuges the former cannot access (e.g. Robertson & Polunin 1981). Conversely, adults of a large species may be able to behaviourally dominate and prevent adults of smaller species excluding them (Robertson 1984; Roberts 1985). While a preliminary experiment indicated a negative effect of one species on the growth of another in one such cohabitation relationship (Robertson 1984), the consequences of such resource sharing for the abundance, population size-structure, biomass, demography and reproduction of cohabitant species have not yet been examined in any depth. Determination of those consequences will help reveal the fundamental nature of such cohabitational relationships; that is, are they competitive (with one or both species losing to some extent), neutral (with neither gaining nor losing) or somehow mutually beneficial? Such size-dependent interspecific cohabitation has been documented among territorial, benthic-feeding herbivores from several families (cf. Robertson & Polunin 1981; Robertson 1984; Roberts 1985). Whether similar relationships occur among other taxa, and whether their occurrence is related to the type of resources used and the mode of access to them, remains to be determined.

INDIVIDUAL SIZE, SPECIES BIOMASS AND RESOURCE NEEDS

While resource use must increase with body size and, intuitively, use of feeding space should be related to resource abundance, studies of space use by territorial reef fishes have not found any simple relationship between territory size and resource density (Ebersole 1980; Hixon 1980; Tricas 1989). At present there are no data on how quantitative requirements for food and space change during the life history of any coral-reef

fish. Apart from juveniles of large species tending to have faster growth (and therefore higher resource needs) than juveniles of smaller near-relatives (Buesa 1987; Legrende & Albaret 1991), there is almost no information on how size dependency in resource requirements varies among potentially interacting reef fishes. Relationships between numerical abundances and assessments of the relative impact of interactions between species may be difficult to interpret without such data.

Examinations of the relationship between resource abundance and the abundance of members of a consumer guild have been made for only one group of reef fishes, the corallivorous chaetodontids. Studies of that family have found only weak relationships between live coral cover (i.e. resource biomass) and total abundances of fish (e.g. Fowler 1990; Roberts *et al.* 1992; and references therein). However, the ratio of biomass to total abundance of a consumer taxon can vary several-fold among habitats (cf. Bellwood & Alcalá 1988) and, because they are much larger than juveniles, adult fish are likely to account for most of the consumption by a population even when they are in a numerical minority. Re-examination of fish-coral abundance relationships among chaetodontids, using biomass of fishes as well as corals (or better still an index of consumption/production), is needed to test conclusions about putative patterns indicated by numeric abundances of fishes. Such reassessments should also incorporate more refined characterizations of resources, as different chaetodontids eat different corals (e.g. Cox 1994).

The extent of interspecific competition between two species must be related to the overall intensity of resource use by the population of each. Because a certain amount of resources could support different numbers of individuals depending on their sizes, relations between the density and size of adults of different species, or the biomass of those classes within their populations that have overlapping resource requirements, are likely to provide much better indications of the importance of resource limitation and competition than relations between total abundance. For example, in response to the experimental removal of the territorial Caribbean damselfish *Stegastes planifrons*, both total and adult populations of a common congener, *Stegastes partitus*, increased sharply (Robertson 1996). However, the response of another, less abundant congener, *Stegastes variabilis*, was less clear cut: while its adult population doubled after the removal of *S. planifrons*, its total population showed only a statistically non-significant increase. Juveniles of *S. variabilis* may have been little affected by competitive interactions with *S. planifrons* because their individual and combined resource requirements were minor compared to those of conspecific adults: juveniles of *S. variabilis* were relatively uncommon compared with conspecific adults

and may have a somewhat different diet (Emery 1973). In this case testing for effects of interspecific competition using only change in total abundance would have failed to detect a substantial effect of competition, namely an effect on biomass. If the relative biomass of two species determines the nature and intensity of an interaction between them it could be difficult to find evidence of such an interaction from a simple analysis of total abundances, if population size-structure varies spatially.

CONCLUSIONS

The benthic populations of most species of reef fishes include individuals with widely varying body weights, with 1–3 orders of magnitude of variation in weight being common within species. Also, there is likely to be considerable habitat variation in the relationship between numbers and biomass across a broad range of species. Variation in body size of reef fishes is linked to variation in mortality rates, and the types, symmetry and intensity of interspecific competitive interactions. The importance of body size to ecological relationships among members of ecological guilds is widely recognized in other ecosystems (Ebenmann & Persson 1988), and some methods have been developed for dealing with population size-structure when assessing the potential for interactions (e.g. Wissinger 1992). However, population size-structure has received little attention in studies of mechanisms that structure reef-fish assemblages, and biomass relations among reef fishes have been considered primarily in analyses of trophic-level structure and fisheries management assessments (Bellwood & Alcalá 1988; Williams 1991; Jennings *et al.* 1996; and references therein). Given that biomass and body-size relations are likely to be crucial for interactions within guilds, analyses of spatial distributions and population dynamics of members of ecological guilds that rely on total abundance may well fail to detect major interspecific interactions. While total abundance may allow an initial description of an assemblage, its use for assessing mechanisms of assemblage organization should be justified and the assumptions involved in that use should be explicitly stated and defended.

ACKNOWLEDGEMENTS

I thank K. Clifton for comments on a draft of this paper, and the Kuna General Congress and the Departamento de Recursos Marinos of the Republica de Panama for allowing fieldwork in San Blas. This research was supported by the Smithsonian Tropical Research Institute's Marine Environmental Sciences Program, and general research funds from STRI.

REFERENCES

- Aldenhoven J. M. (1986) Local variation in mortality rates and life-expectancy estimates of the coral reef fish *Centropyge bicolor* (Pisces: Pomacanthidae). *Mar. Biol.* **92**, 237–44.
- Bellwood D. R. (1988) Ontogenetic changes in the diet of early post-settlement *Scarus* species (Pisces: Scaridae). *J. Fish Biol.* **33**, 213–19.
- Bellwood D. R. & Alcalá A. C. (1988) The effect of minimum length specification on visual estimates of density and biomass of coral reef fishes. *Coral Reefs* **7**, 23–7.
- Bouchon-Navarro Y. (1986) Partitioning of food and space by chaetodontid fishes on coral reefs. *J. Exp. Mar. Biol. Ecol.* **103**, 21–40.
- Buesa R. J. (1987) Growth rate of tropical demersal fish. *Mar. Ecol. Prog. Ser.* **36**, 191–9.
- Caley M. J. (1998) Age-specific mortality rates in reef fishes: Evidence and implications. *Aust. J. Ecol.* **23**, 241–5.
- Clarke R. D. (1977) Habitat distributions and species diversity of chaetodontid and pomacentrid fishes near Bimini, Bahamas. *Mar. Biol.* **40**, 277–89.
- Cox E. F. (1994) Resource use by corallivorous butterflyfishes (Family Chaetodontidae) in Hawaii. *Bull. Mar. Sci.* **54**, 535–45.
- Ebenmann B. & Person L. (1988) *Size-structured Populations, Ecology and Evolution*. Springer-Verlag, Berlin.
- Ebersole J. P. (1977) The adaptive significance of interspecific territoriality in the reef fish *Eupomacentrus leucostictus*. *Ecology* **58**, 914–20.
- Ebersole J. P. (1980) Food density and territory size: An alternative model and a test on the reef fish *Eupomacentrus leucostictus*. *Am. Nat.* **115**, 492–509.
- Ebersole J. P. (1985) Niche separation of two damselfish species by aggression and differential microhabitat utilization. *Ecology* **66**, 14–20.
- Eckert G. J. (1987) Estimates of adult and juvenile mortality for labrid fishes at One Tree Reef, Great Barrier Reef. *Mar. Biol.* **95**, 167–71.
- Emery A. R. (1973) Comparative ecology and functional osteology of fourteen species of damselfish (Pisces: Pomacentridae) at Alligator Reef, Florida Keys. *Bull. Mar. Sci.* **23**, 649–770.
- Findley J. T. & Findley M. T. (1985) A search for pattern in butterfly fish communities. *Am. Nat.* **126**, 800–16.
- Fowler A. J. (1990) Spatial and temporal patterns of distribution and abundance of chaetodontid fishes on the Great Barrier Reef. *Mar. Ecol. Prog. Ser.* **64**, 39–53.
- Galzin R. (1987) Structure of fish communities of French Polynesian coral reefs. II. Temporal scales. *Mar. Ecol. Prog. Ser.* **41**, 137–45.
- Green A. L. (1996) Spatial, temporal and ontogenetic patterns of habitat use by coral reef fishes (Family Labridae). *Mar. Ecol. Prog. Ser.* **133**, 1–11.
- Harmelin-Vivien M. L. (1989) Implications of feeding specializations on the recruitment processes and community structure of butterflyfishes. *Env. Biol. Fish.* **25**, 101–10.
- Harrington M. E. (1993) Aggression in damselfish: adult–juvenile interactions. *Copeia* **1993**, 67–74.
- Hart A. M. & Russ G. R. (1996) Responses of herbivorous fishes to crown-of-thorns starfish *Acanthaster planci* outbreaks. III. Age, growth, mortality and maturity indices of *Acanthurus nigrofuscus*. *Mar. Ecol. Prog. Ser.* **135**, 25–35.
- Hixon M. (1980) Food production and competitor density as the determinants of feeding territory size. *Am. Nat.* **115**, 510–30.
- Hixon M. (1991) Predation as a process structuring coral reef fish communities. In: *The Ecology of Fishes on Coral Reefs* (ed. P. F. Sale) pp. 475–508. Academic Press, New York.
- Jennings S., Boullé D. P. & Polunin N. V. C. (1996) Habitat correlates of the distribution and biomass of Seychelles reef fishes. *Env. Biol. Fish.* **46**, 15–25.
- Jones G. P. (1991) Postrecruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. In: *The Ecology of Fishes on Coral Reefs* (ed. P. F. Sale) pp. 294–328. Academic Press, New York.
- Legrende M. & Albaret J. J. (1991) Maximum observed length as an indicator of growth rate in tropical fishes. *Aquaculture* **94**, 327–41.
- Lirman D. (1994) Ontogenetic shifts in habitat preferences in the three-spot damselfish, *Stegastes planifrons* (Cuvier), in Roatan Island, Honduras. *J. Exp. Mar. Biol. Ecol.* **180**, 71–81.
- Meekan M. G., Steven A. D. L. & Fortin M. J. (1995) Spatial patterns in the distribution of damselfishes on a fringing coral reef. *Coral Reefs* **14**, 151–62.
- Pitcher R. C. (1992) Growth of juvenile coral reef damselfish: spatial and temporal variability, and the effect of population density. *Aust. J. Mar. Freshwat. Res.* **43**, 1129–49.
- Ralston S. (1976) Anomalous growth and reproductive patterns in populations of *Chaetodon miliaris* (Pisces, Chaetodontidae) from Kaneohe Bay, Oahu, Hawaiian islands. *Pac. Sci.* **30**, 385–403.
- Roberts C. M. (1985) Resource sharing in territorial herbivorous reef fishes. *Proc. 5th Int. Coral Reef Symp.* **4**, 17–22.
- Roberts C. M., Dawson-Shepherd A. R. & Ormond R. F. G. (1992) Large-scale variation in assemblage structure of Red Sea butterflyfishes and angelfishes. *J. Biogeog.* **19**, 239–50.
- Robertson D. R. (1984) Cohabitation of competing territorial damselfishes on a Caribbean coral reef. *Ecology* **65**, 1121–35.
- Robertson D. R. (1988) Settlement and population dynamics of *Abudefduf saxatilis* on patch reefs in Caribbean Panama. *Proc. 6th Int. Coral Reef Symp.* **2**, 839–43.
- Robertson D. R. (1995) Competitive ability and the potential for lotteries among territorial reef fishes. *Oecologia* **103**, 180–90.
- Robertson D. R. (1996) Interspecific competition controls abundance and habitat use by territorial Caribbean damselfishes. *Ecology* **77**, 885–99.
- Robertson D. R. & Kaufmann K. W. (1998) Assessing early-recruitment dynamics and its demographic consequences among tropical reef fishes: Accommodating variation in recruitment seasonality and longevity. *Aust. J. Ecol.* **23**, 226–33.
- Robertson D. R. & Lassing B. L. (1980) Spatial distributions and coexistence of a group of territorial damselfishes from the Great Barrier Reef. *Bull. Mar. Sci.* **30**, 187–203.
- Robertson D. R. & Polunin N. V. C. (1981) Coexistence: symbiotic sharing of feeding territories and algal food by some coral reef fishes from the western Indian Ocean. *Mar. Biol.* **62**, 185–95.
- Russ G. (1984) Distribution and abundance of herbivorous grazing fishes in the Central Great Barrier Reef. I. Levels of variability across the entire continental shelf. *Mar. Ecol. Prog. Ser.* **20**, 23–34.
- Sale P. F., Guy J. A. & Steel W. A. (1994) Ecological structure of assemblages of coral reef fishes on isolated patch reefs. *Oecologia* **98**, 83–99.

- Shulman M. J. & Ogden J. C. (1987) What controls tropical reef fish populations: recruitment or benthic mortality? An example in the Caribbean reef fish *Haemulon flavolineatum*. *Mar. Ecol. Prog. Ser.* **39**, 233–42.
- Tricas T. C. (1989) Determinants of feeding territory size in the corallivorous butterflyfish, *Chaetodon multicinctus*. *Anim. Behav.* **37**, 830–41.
- Waldner R. E. & Robertson D. R. (1980) Patterns of habitat partitioning by eight species of territorial Caribbean damselfishes (Pisces: Pomacentridae) *Bull. Mar. Sci.* **30**, 171–86.
- Waltho N. D. & Kolasa J. (1996) Stochastic determinants of assemblage patterns in coral reef fishes: a quantification by means of two models. *Env. Biol. Fish.* **47**, 255–67.
- Warner R. R. & Hughes T. P. (1988) The population dynamics of coral reef fishes. *Proc. 6th Int. Coral Reef Symp.* **1**, 149–55.
- Williams D. McB. (1986) Temporal variation in the structure of reef slope fish communities (central Great Barrier Reef): short-term effects of *Acanthaster planci*. *Mar. Ecol. Prog. Ser.* **28**, 157–64.
- Williams D. McB. (1991) Patterns and processes in the distributions of coral reef fishes. In: *The Ecology of Fishes on Coral Reefs* (ed. P. F. Sale) pp. 437–74. Academic Press, New York.
- Wissinger S. A. (1992) Niche overlap and the potential for competition and intraguild predation between size-structured populations. *Ecology* **73**, 1431–44.