

Assessing early recruitment dynamics and its demographic consequences among tropical reef fishes: Accommodating variation in recruitment seasonality and longevity

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Abstract When settlement of pelagic juveniles of reef fishes is highly and predictably seasonal, annual, end-of-season surveys of surviving recruits (which are commonly used on the Great Barrier Reef) are useful for assessing recruitment dynamics and their demographic effects. However, when settlement is continuous or weakly seasonal, with patterns that vary both between species and within species among years, regular, sometimes year-round, recruitment surveys at intervals linked to short-term settlement dynamics are needed to quantify fluctuations in recruitment strength. Monthly recruitment surveys may be appropriate in the tropical northwest Atlantic, where settlement is often both lunar periodic, and broadly and variably seasonal. Use of a variety of recruit-census methods impedes comparisons of recruitment patterns and their demographic effects, because recruit densities and recruit:adult ratios cannot be directly compared when recruits (because they have widely varying post-settlement ages) have experienced very different levels of early post-settlement mortality. Examining the relationship between changes in adult populations and annual, end-of-season recruitment may be satisfactory for long-lived species with strong settlement seasonality and maturation times of approximately 1 year. However, it is inappropriate for short-lived, rapidly maturing species, particularly those that have broad and variable settlement seasons and whose populations fluctuate substantially throughout the year in response to short-term fluctuations in recruitment. Comparisons of demographic effects of recruitment among species with different longevity require the use of non-arbitrary time scales, such as the time to maturity and the adult half-life.

Key words: coral reefs, fish, Great Barrier Reef, longevity, recruitment, seasonality, tropical northwest Atlantic.

INTRODUCTION

The extent to which there is significant regional variation in the processes that organize assemblages of coral-reef fishes is a subject of long-standing interest to reef-fish biologists (e.g. Bohnsack & Talbot 1980; Gladfelter *et al.* 1980; Ogden & Ebersole 1981; Alevizon *et al.* 1985; Thresher 1991; Meekan *et al.* 1995). Juvenile recruitment patterns are thought to often have strong effects on the abundances and distributions of adult reef fishes, and on the structure of their assemblages (e.g. Victor 1986; Doherty & Williams 1988; Williams *et al.* 1994; review by Caley *et al.* 1996). Consequently it is important to establish how recruitment dynamics and its demographic consequences varies among species in different regions in the tropics. This paper considers how variation in recruitment seasonality affects how recruitment

dynamics can be measured and compared in the two regions in which there has been most research activity to date: the tropical northwest Atlantic (TWA) and the Great Barrier Reef (GBR). It also considers how wide variation in the longevity of reef fishes affects the usefulness of annual censuses of recruits and adults in assessments of demographic effects of recruitment.

ASSESSING VARIATION IN RECRUITMENT STRENGTH: EFFECTS OF RECRUITMENT SEASONALITY

Great Barrier Reef

Only three published studies exist of recruitment seasonality of GBR fishes that were based on year-round (or nearly so) monitoring of early recruitment. Russell *et al.* (1977) tracked recruitment of 54 species of a range of families fairly continuously throughout a

2.5 year period. Williams and Sale (1981) monitored recruitment by approximately 20 species from various families intermittently during 1 year. Fowler *et al.* (1992) assessed recruitment by one chaetodontid over 2 years, although with more intensive coverage of summer than winter. These three studies, which were all done at the same site on the southern GBR, found that recruitment by many species occurs primarily in the Austral spring and summer (October–March), with a sharp peak of activity in January/February. However, their data also indicate that recruitment by approximately one-third to a half of those species do not conform closely to that seasonal pattern, and have either broader seasonality, recruitment throughout the year or suggestions of autumn/winter peaks of activity. The strong summer peak in activity by many species at this site has led to recruitment strength generally being measured by yearly censuses made at the end of summer on the GBR (e.g. Eckert 1984; Sale *et al.* 1984; Doherty & Williams 1988; Doherty 1991; Fowler *et al.*

1992). Estimates of annual recruitment derived by this method have been used to assess demographic effects of recruitment variation (e.g. Doherty & Fowler 1994). Williams *et al.* (1994) compared estimates of recruitment derived from end-of-summer censuses and more frequent (six week intervals) censusing during the preceding 4 months, for 23 species (almost all from two families) over two summers at a site on the northern GBR. They concluded that the end-of-summer censuses did accurately measure relative cumulative recruitment and possibly relative cumulative settlement.

Tropical northwest Atlantic

In the TWA many reef fishes spawn throughout much or all of the year (Munro 1983; Hunt von Herbing & Hunte 1991; Robertson 1991), and the recruitment of some species occurs year-round, or at least through most of the year (Victor 1986; Shulman & Ogden 1987;

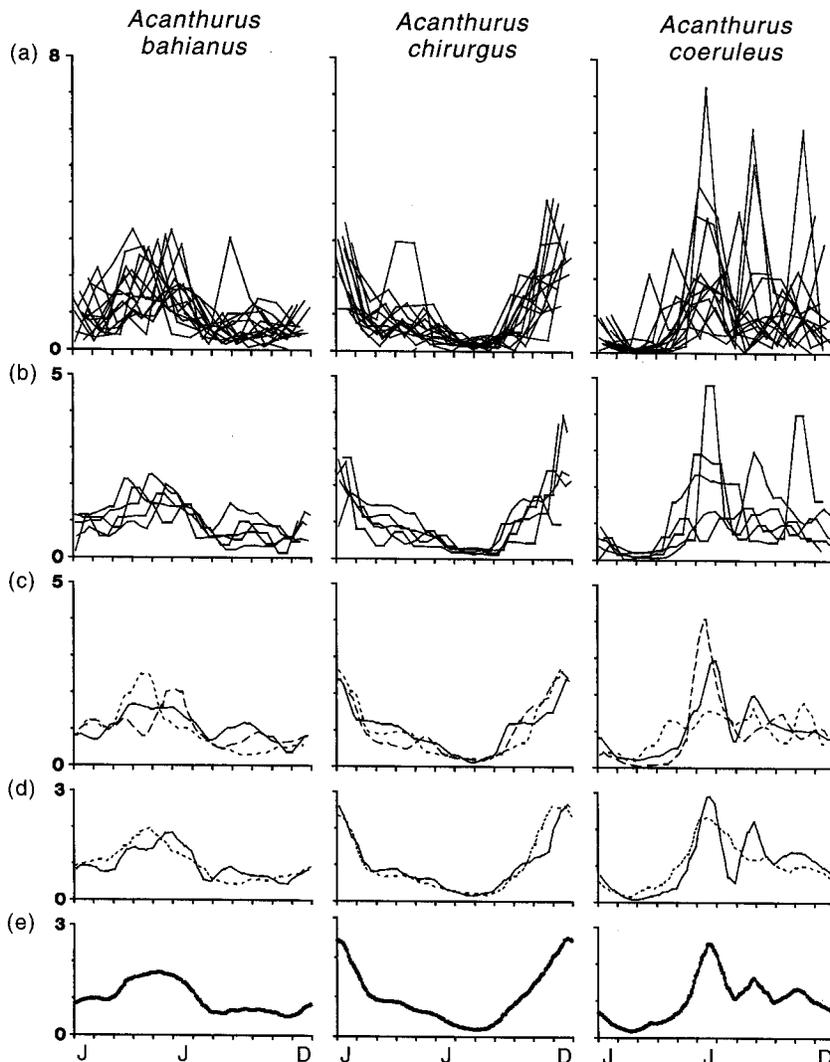


Fig. 1. Interannual variation in the seasonality of recruitment of three surgeonfishes at San Blas, Caribbean Panama. (a) Recruitment pattern for each of 16 years (1980–95). (b), (c) and (d) Average seasonal patterns for periods of 3 years, 5 years and 7 years respectively (periods were chosen randomly without replacement from the entire 16 years). (e) Average seasonal pattern over all 16 years. Censuses of recruits each month were made just before a full moon, because settlement of those species at that site is lunar cyclic and maximal around a new moon (Robertson 1992). To accommodate effects of variation in habitat type and the area of the fixed census plots ($n = 14$ plots scattered across $\sim 5 \text{ km}^2$), each raw datum (i.e. the number of recruits censused in any month) from a plot was scaled relative to the mean of the entire time series of data from that plot. As the measure of a month's recruitment we used the mean of the scaled values for that month from the entire set of plots. On the y axis, 1 = the long-term average recruitment level and 2 is double that level. To derive a smoothed average seasonal pattern, such as those shown here and in Fig. 2, we calculated the mean of all monthly recruitment values for census days occurring within (\pm) 15 days of each sequential day of the year, then repeated that procedure.

Robertson 1990; McGehee 1995). There are, however, some TWA species (Shenker *et al.* 1993, and references therein) in which spawning and recruitment is as highly and predictably seasonal as it is for many GBR species.

Multi-year, monthly monitoring of recruitment of 50 species of reef fishes in Caribbean Panama, the most tropical part of the TWA (D. R. Robertson unpubl. data), shows that it occurs throughout the year, with a great diversity of seasonal patterns among different species. Examples of these patterns include: (i) species that recruit year-round (e.g. Robertson 1990; Figs 1, 2); (ii) a continuum of degrees of seasonality among different species, ranging from virtually aseasonal to distinctly but broadly uni- and bimodal patterns (Figs 1, 2); (iii) seasonal peaks of recruitment of ecologically similar members of the same genus occurring at different times of the year and sometimes at opposite extremes of the range of environmental conditions (Robertson 1990; Fig. 1); and (iv) equally importantly, considerable interannual variation in recruitment seasonality within individual species (Fig. 1; and see Shulman & Ogden 1987). Such variability is sufficiently high that, in order to define the underlying seasonal pattern, between 3 and 7 years of monthly monitoring may be required (Fig. 1).

Substantial geographical variation in recruitment seasonality seems likely to occur throughout the TWA.

(1) There is evidence of distinct intraspecific geographical variation in spawning seasonality within the TWA (Robertson 1991; Carter & Perrine 1994), with a tendency towards lower seasonality in the more tropical parts of that region in some species, and spawning

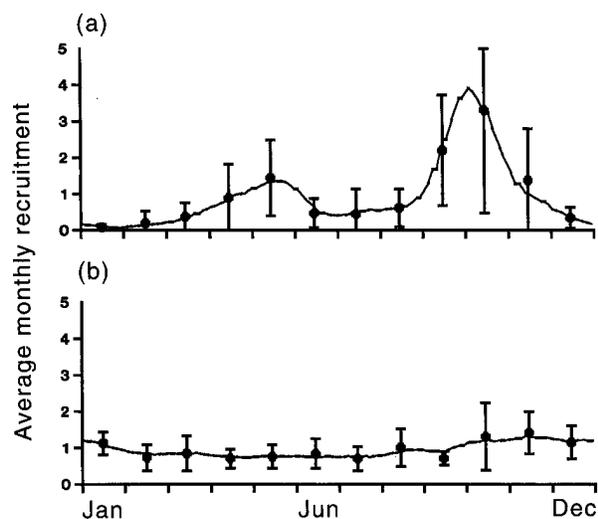


Fig. 2. Average seasonal patterns of early recruitment by two gobies at San Blas, Caribbean Panama: (a) *Coryphopterus personatus* (9 years) and (b) *Gobiosoma illecebrosus* (10 years). Points represent mean level (with 95% CI) for each calendar month. The line indicates the average seasonal pattern (calculated as in Fig. 1).

peaks at different times of the year at different locations in others. Unfortunately, it may not be possible to readily predict local recruitment seasonality from the local spawning seasonality, because spawning seasonality may vary among habitats at the same location (Robertson 1990), sometimes greatly (Clifton 1995). Also, recruitment seasonality may (Hunt von Herbing & Hunte 1991) or may not (Robertson 1990, 1991) mirror average spawning seasonality at the same location.

(2) Species differ in the extent to which their recruitment seasonality varies in different parts of the TWA; for example, while four *Stegastes* species have fairly strong late-summer peaks of recruitment in the northwest Caribbean (Booth & Beretta 1994; McGehee 1995) they have weaker seasonality in the southwest Caribbean, and their recruitment peaks earlier in the year (6 months earlier in one case) at the latter site (Robertson 1990). On the other hand, recruitment by the labrid *Thalassoma bifasciatum* appears to follow essentially the same seasonal pattern in the northeast, southeast and southwest Caribbean, with a broad peak in summer and fall (Victor 1986; Hunt von Herbing & Hunte 1991; Tupper & Hunte 1994; Caselle & Warner 1996; D. R. Robertson unpubl. data).

(3) Further complicating the picture, the same species may have different recruitment seasonalities on different sides of the same island during the same year (Booth & Beretta 1994; Caselle & Warner 1996).

To date only three multi-year data sets derived from year-round monitoring of recruitment at TWA sites other than Panama have been published (one species of haemulid for 2.2 years at St Croix: Shulman & Ogden 1987; four congeneric damselfishes for 3 years at Puerto Rico: McGehee 1995; one labrid for 2 years at Barbados; Hunt von Hunte 1991; Tupper & Hunte 1994). In addition, Luckhurst and Luckhurst (1977) monitored recruitment by 16 reef fishes for 1 year at Curacao (southern Caribbean) and Tupper and Hunt (1994) did so for two species for 1 year in Barbados (southeast Caribbean). These few studies do not indicate any general (i.e. assemblage-level) geographical pattern of variation in recruitment seasonality within the TWA. While differences between the recruitment patterns of *Stegastes* damselfishes at Panama and Puerto Rico suggest stronger summer peaks of recruitment at higher latitudes, recruitment by reef fishes in a range of families (although possibly not damselfishes) occurs in winter in the Bahamas, which is at a higher latitude than Puerto Rico (see Thorrold *et al.* 1994a). Also, recruitment by a haemulid in St Croix (adjacent to Puerto Rico) occurs at significant levels during almost all of the year (Shulman & Ogden 1987), and recruitment seasonality of the labrid *T. bifasciatum* does not seem to vary across the same parts of the Caribbean (see previous discussion).

An important consequence of the combination of (i) interannual variation and geographical variation in recruitment seasonality within the same species, and (ii) interspecific diversity in seasonal patterns of recruitment at the same site, is that a reasonably accurate picture of both the average seasonal pattern of recruitment by a species at any TWA site, and the level of variability in that pattern probably cannot be obtained without at least several years of year-round monitoring. For example, as can be seen in Fig. 3, tracking of *C. personatus* recruitment in Caribbean Panama in 1992 alone would have led to the conclusion that it is highly seasonal ($\approx 90\%$ of the year's recruitment occurred in one month). However, recruitment dynamics of this species during 1993 and 1994 differed greatly from the 1992 pattern, as well as from each other (Fig. 3; and see Shulman & Ogden 1987). The asymmetrically bimodal average seasonal pattern (Fig. 2) of recruitment of this species at that site only became evident after some 5 years of year-round monitoring. Clearly, planning for new studies of the long-term dynamics of recruitment and its demographic consequences in the TWA must accommodate the distinct possibility of year-round, interannually varying activity, unless it has been shown to be otherwise for all target species at the chosen study site.

Fundamental differences in the recruitment seasonality of many of the fishes examined to date have determined the methods that have been used to measure variation in recruitment strength on the GBR and TWA. Williams *et al.* (1994) concluded that end-of-summer censuses do provide reasonable estimates of annual settlement strength of species in which a few, discrete pulses of settlement occur during one short period of the year. However, they also recognized that such surveys are much less likely to provide good indi-

cations of relative recruitment strength of species that have many settlement pulses per year, or when early mortality among recruits is high and variable (cf. Shulman & Ogden 1987). A cohort of recruits counted in end-of-summer censuses on the GBR contains a mixture of individuals that settled from as little as a couple of weeks to as much as 6 months prior to the census. Also, most members of the cohort are likely to have experienced post-settlement mortality (which can be high in some species: Meekan 1988; Sale & Ferrell 1988; Booth & Beretta 1994) for several months before being censused. The post-settlement age structure of such recruit cohorts may also vary considerably among species and between years within the same species, depending on the degree of variation in the timing of a seasonal peak of settlement between species and between years (e.g. see Williams 1983). If there is much variation, annual surveys made at a fixed date could well under- or over-value the potential contribution of a year's recruit cohort to the adult population, depending how recently most recruits arrived before the survey. Patterns of change in the relative abundances of different species, which have been used to assess whether interactions affect community structure (e.g. Sale & Steele 1989) are likely to be influenced not only by relative sizes of their recruit cohorts but also by variation in the age structures of those cohorts (Robertson 1998).

Annual recruit censuses are appropriate for some GBR species, although for what proportion is far from clear. More data sets based on multi-year, year-round monitoring of recruitment by species from a range of taxa at various latitudes within the GBR are needed to clarify this situation. Annual surveys are probably also appropriate for at least a few TWA species at particular locations (e.g. see Shenker *et al.* 1993). However,

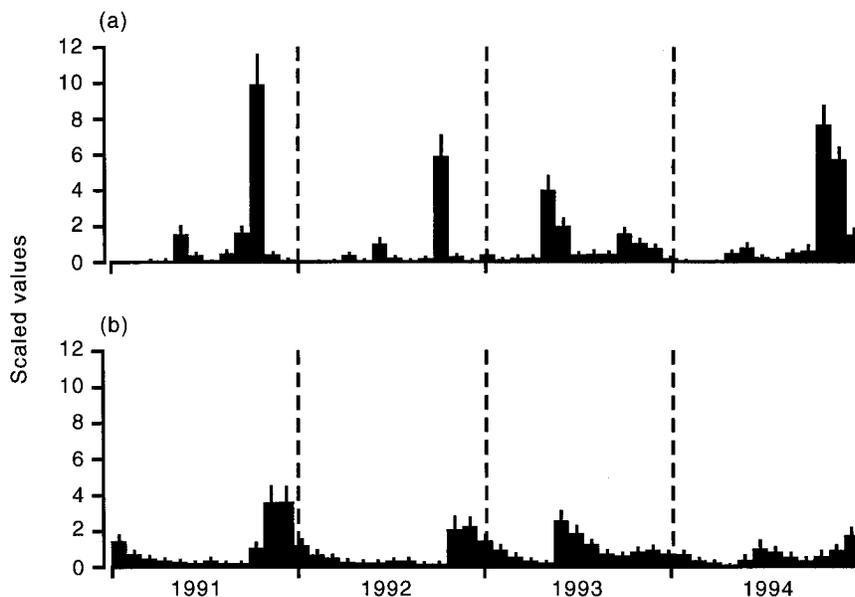


Fig. 3. Intermensual fluctuations in (a) early recruitment and (b) adult population size by the Caribbean goby, *Coryphopterus personatus*, at San Blas, Caribbean Panama. Methods for calculating recruitment levels and adult abundances are described in Fig. 1. Adults and recruits were censused concurrently in 17 plots and entire patch reefs scattered across approximately $\sim 3 \text{ km}^2$.

given what we know about the degree of variation in recruitment seasonality in the TWA, annual or even semi-annual recruitment surveys seem unlikely to be appropriate for assemblage-level studies in that region. What is the best alternative to annual censuses? Settlement evidently is lunar cyclic in many TWA species (Victor 1986; Robertson 1992; Sponaugle & Cowen 1994, 1996; Thorrold *et al.* 1994b; Caselle & Warner 1996), although certainly not all species at all sites (Hunt von Herbing & Hunte 1991; Robertson 1992; Thorrold *et al.* 1994b; Booth & Beretta 1994). Given the logistical costs of multi-year daily monitoring of settlement itself, the best option, from both biological and logistical perspectives, for assessing long-term variation in recruitment intensity in species that have anything other than very short, predictable recruitment seasons may be monthly (lunar) censuses that are made during the part of the lunar cycle when settlement by target species is minimal. However, even among species with strong unimodal lunar settlement cycles there is intermensual variation in the timing of settler influxes (e.g. see Victor 1986; Robertson *et al.* 1988; Robertson 1992). Because mortality of new recruits sometimes is high immediately after settlement (e.g. Victor 1986; Shulman & Ogden 1987; Booth & Beretta 1994; Carr & Hixon 1995; McGehee 1995) variation in the timing as well as the intensity of influxes could well affect the subsequent relative size of the month's recruit cohort. Estimations of relative levels of settlement by any method other than actual monitoring of settlement invariably are subject to some degree of distortion due to effects of early mortality. Recruitment monitoring that aims to make inferences about settlement dynamics and effects of early mortality should census recruits as soon as possible after settlement, and monthly censuses should offer significantly better characterization of settlement patterns than end-of-season censuses.

Recruits are censused at very different post-settlement ages under monthly and annual sampling regimes currently in use (<2 weeks in monthly censuses of many TWA species *vs* an average of 2–3 months and a range of <1–6 months with annual, end-of-season censuses on the GBR). The fact that under those two census regimes recruits have been subject to early mortality for very different periods means that it is impossible to directly compare two primary characteristics of recruitment strength using those different techniques: (i) spatial intensity (recruits/unit area/unit time) and (ii) intensity relative to the size of the resident population (recruits/adult/unit time). Comparisons of spatial intensity are relevant to questions about effects of: population density on competition; mortality and growth rates after settlement; and the intensity of supply of pelagic larvae. Comparisons of the rate of recruitment relative to adult abundance are essential to answer questions about juvenile demography and the

patterning of early mortality and its effects on adult abundance. If the most realistic option for the great majority of TWA species is monthly censuses, then our ability to compare recruitment dynamics and its demographic consequences in those two regions will depend on the addition of monthly censuses to annual recruitment censuses currently in use on the GBR.

TIME SCALES FOR ASSESSING DEMOGRAPHIC EFFECTS OF RECRUITMENT FLUCTUATIONS: EFFECTS OF VARIATION IN ADULT LONGEVITY

One important aspect of assessing demographic effects of recruitment variation among reef fishes that has not received consideration previously is the question of an appropriate (i.e. demographically relevant) time scale on which to do so. For species whose adults live several or more years and take about a year to mature, and in which recruitment is highly and predictably seasonal, each year's cohort of recruits enters the adult population at about the same time. In this case, within-season fluctuations in settlement are unlikely to have significant effects on adult population dynamics. The use of annual, end-of-season censuses of recruits to assess recruitment and annual adult censuses to assess its demographic effects is intuitively appropriate for such species (e.g. see Doherty & Fowler 1994). Many GBR species that have been the primary focus of demographic studies are relatively long-lived (e.g. Aldenhoven 1986; Doherty & Fowler 1994; Choat & Axe 1996; Hart & Russ 1996; Newman *et al.* 1996), although some are much shorter-lived (e.g. Eckert 1987; and see Robertson 1991). In contrast, many TWA species recruit through much of the year, particularly in the southwest Caribbean, and some, perhaps many, are quite short-lived, with maturation times well under a year and average adult longevity of less than 1 year (e.g. Hunte & Cote 1989; Warner & Hughes 1988; Forrester 1995; and see following discussion). In short-lived species that mature rapidly and have extended recruitment seasons, fluctuating recruitment over the course of the year is likely to have strong, transient effects on adult abundance. An extreme example is the goby *Coryphopterus personatus*, which, in Caribbean Panama, has an adult half-life of approximately 1–2 months and takes about 1 month to mature. There, its adult population fluctuates greatly and continuously throughout the year in response to erratic influxes of recruits (Fig. 3). In this species, intermensual variation in recruitment strength is an order of magnitude greater than interannual variation (annual recruitment = cumulative monthly recruitment for the year; mean levels of deviation from the median are 380% and 37%, respectively; $n = 8$ years, $t = -4.75$, $P < 0.001$). The structure of the time series of fluctuations in the abundance of adults of this species

measured by yearly censuses would clearly vary greatly depending on which month was chosen for that census (see Fig. 3), and change in adult abundance from one annual census to the next would bear no relationship to the abundance of recruits in the first census. The demographically appropriate time scale for describing population phenomena and assessing demographic effects of recruitment of that species is approximately 1 month, because that is the scale on which the adult population responds to recruit influxes and on which those influxes have their strongest effect on adult abundance.

In the case of *C. personatus*, which must be at the lower end of the spectrum of longevities of reef fishes, it is easy to see that the year is an arbitrary and biologically meaningless time scale on which to examine the effect of recruitment variation on population dynamics. However, this problem of a biologically appropriate time scale on which to examine recruitment and population dynamics extends to somewhat longer-lived species. Any species that matures in several months, has an average adult longevity under a year, and recruits erratically during the course of a year (e.g. the TWA labrid *Thalassoma bifasciatum*; see Warner & Hughes 1988) is likely to show significant subannual fluctuations in the abundances of adults, which annual population censuses would fail to capture. Determination of the relationship between annual fluctuations in adult population size and the previous year's recruitment in such a species would require knowledge of the timing and relative size of each recruit influx during that period and of age-specific mortality schedules. Similar information on mortality schedules would also be needed to integrate information from annual recruit censuses into assessments of the demographic effects of recruitment variation in species that take longer than a year to mature.

Coryphopterus personatus is distributed throughout the TWA (Robins *et al.* 1986). A species as short-lived as this may face a distinct risk of extinction due to occasional widespread recruitment failures if it relied on highly seasonal reproduction and recruitment. *Coryphopterus personatus* seems likely either to have broad spawning/recruitment seasonality throughout its range, or to combine any geographical increases in seasonality of spawning/recruitment with increased longevity. Increased longevity might occur at higher latitudes, where increased environmental seasonality is likely to limit reproductive seasonality. Increased attention needs to be focused on intra- and interspecific geographical variations in longevity among reef fishes, to establish their extent, latitudinal and taxonomic patterning, and relations to seasonal patterns of reproduction.

While the problem of an appropriate temporal scale on which to assess effects of recruitment is most obvious for rapidly maturing, short-lived species, it also extends to perennial species that mature slowly, are

long-lived and whose adult populations 'store' (Warner & Chesson 1985) a number of years recruitment. One year's recruitment has very different effects on the sizes of the adult populations of two species that have average adult longevities of 3 years and 15 years, and times to maturity of 1 year and 3 years, respectively. Using annual recruitment when comparing demographic effects of recruitment dynamics between these two species is analogous to using intermensual recruitment variation to compare effects of recruitment dynamics in a perennial species and one with an average life expectancy of well under a year.

The ability to assess relationships between recruitment and abundance of reef fishes with widely varying longevities will depend on the use of some standard method of measuring recruitment that takes into account the capacity of populations to be influenced by fluctuations in recruitment on monthly, seasonal and annual time scales. Average adult longevity, and the time to maturity, can provide demographically appropriate time scales for such assessments. Both single-species and assemblage-level studies need to take into account the diversity of demographic characteristics and temporal patterns of settlement when deciding on the temporal regimes they use to measure recruitment and adult population dynamics, and in the inferences they make about demographic effects of recruitment and the processes that structure assemblages. Annual recruit/adult censuses can provide useful demographic information for some species, but their general use in studies of mechanisms that structure assemblages is likely to depend on the integration of detailed information on the recruitment dynamics and demography of each member of the assemblage into those analyses.

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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.
- Alevizon W., Richardson W., Pitts P. & Servis C. (1985) Coral zonation and patterns of community structure of Bahamian reef fishes. *Bull. Mar. Sci.* **36**, 304–18.
- Bohnsack J. A. & Talbot F. H. (1980) Species packing by reef fishes on Australian and Caribbean reefs: an experimental approach. *Bull. Mar. Sci.* **30**, 710–23.

- Booth D. J. & Beretta G. A. (1994) Seasonal recruitment, habitat associations and survival of pomacentrid reef fish in the US Virgin Islands. *Coral Reefs* **13**, 81–9.
- Caley M. J., Carr M. H., Hixon M. A., Hughes T. P., Jones G. P. & Menge B. A. (1996) Recruitment and the local dynamics of open marine populations. *Ann. Rev. Ecol. Syst.* **27**, 477–500.
- Carr M. H. & Hixon M. H. (1995) Predation effects on early post-settlement survivorship of coral-reef fishes. *Mar. Ecol. Prog. Ser.* **124**, 31–42.
- Carter J. & Perrine D. (1994) A spawning aggregation of dog snapper, *Lutjanus jocu* (Pisces: Lutjanidae) in Belize, Central America. *Bull. Mar. Sci.* **55**, 228–34.
- Caselle J. E. & Warner R. R. (1996) Variability in recruitment of coral reef fishes: the importance of habitat at two spatial scales. *Ecology* **77**, 2488–504.
- Choat J. H. & Axe L. (1996) Growth and longevity in acanthurid fishes; an analysis of otolith increments. *Mar. Ecol. Prog. Ser.* **134**, 15–36.
- Clifton K. E. (1995) Asynchronous food availability on neighboring Caribbean coral reefs determines seasonal patterns of growth and reproduction for the herbivorous parrotfish *Scarus iserti*. *Mar. Ecol. Prog. Ser.* **116**, 39–46.
- Doherty P. J. (1991) Spatial and temporal patterns of recruitment. In: *The Ecology of Coral Reef Fishes* (ed. P. F. Sale) pp. 261–93. Academic Press, New York.
- Doherty P. J. & Fowler A. J. (1994) Demographic consequences of variable recruitment to coral reef fish populations: a congeneric comparison of two damselfishes. *Bull. Mar. Sci.* **54**, 297–313.
- Doherty P. J. & Williams D. McB. (1988) The replenishment of coral reef fish populations. *Oceanogr. Mar. Biol. Ann. Rev.* **26**, 487–551.
- Eckert G. J. (1984) Annual and spatial variation in recruitment of labroid fishes among seven reefs in the Capricorn/Bunker group, Great Barrier Reef. *Mar. Biol.* **78**, 123–7.
- 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.
- Forrester G. E. (1995) Strong density-dependent survival and recruitment regulate the abundance of a coral reef fish. *Oecologia* **103**, 275–82.
- Fowler A. J., Doherty P. J. & Williams D. McB. (1992) Multiscale analysis of recruitment of a coral reef fish on the Great Barrier Reef. *Mar. Ecol. Prog. Ser.* **82**, 131–41.
- Gladfelter W. B., Ogden J. C. & Gladfelter E. H. (1980) Similarity and diversity among coral reef fish communities: a comparison between tropical western Atlantic (Virgin Islands) and tropical central Pacific (Marshall Islands) patch reefs. *Ecology* **61**, 1156–68.
- Hart A. M. & Russ G. R. (1996) Response of herbivorous fishes to crown-of-thorns starfish *Acanthaster planci* outbreaks. III. Age, growth, mortality and maturity indices of *Acanthurus nigrofasciatus*. *Mar. Ecol. Prog. Ser.* **136**, 25–35.
- Hunt von Herbing I. & Hunte W. (1991) Spawning and recruitment of the bluehead wrasse *Thalassoma bifasciatum* in Barbados, West Indies. *Mar. Ecol. Prog. Ser.* **72**, 49–58.
- Hunte W. & Cote I. M. (1989) Recruitment in the redlip blenny *Ophioblennius atlanticus*: is space limiting? *Coral Reefs* **8**, 45–50.
- Luckhurst B. E. & Luckhurst K. (1977) Recruitment patterns of coral reef fishes on the fringing reefs of Curacao, Netherlands Antilles. *Can. J. Zool.* **55**, 681–9.
- McGehee M. A. (1995) Juvenile settlement, survivorship and *in situ* growth rates of four species of Caribbean damselfishes in the genus *Stegastes*. *Env. Biol. Fish.* **44**, 393–401.
- Meekan M. G. (1988) Patterns of settlement and mortality of juvenile reef fishes at Lizard Island, northern Great Barrier Reef. *Proc. 6th Int. Coral Reef Symp.* **2**, 779–84.
- 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**, 151–61.
- Munro J. L. (1983) Caribbean coral reef fishery resources. *ICLARM Stud. Rev.* **7**, 1–276.
- Newman S. J., Williams D. McB. & Russ G. R. (1996) Variability in the population structure of *Lutjanus adetti* (Castelnau, 1873) and *L. quinquelineatus* (Bloch, 1790) among reefs in the central Great Barrier Reef, Australia. *Fish. Bull.* **94**, 313–29.
- Ogden J. C. & Ebersole J. P. (1981) Scale and community structure of coral reef fishes: a long-term study of a large artificial reef. *Mar. Ecol. Prog. Ser.* **4**, 97–103.
- Robertson D. R. (1990) Differences in the seasonalities of spawning and recruitment of some small neotropical reef fishes. *J. Exp. Mar. Biol. Ecol.* **144**, 49–62.
- Robertson D. R. (1991) The role of adult biology in the timing of spawning of tropical reef fishes. In: *The Ecology of Coral Reef Fishes* (ed. P. F. Sale) pp. 356–82. Academic Press, New York.
- Robertson D. R. (1992) Patterns of lunar settlement and early recruitment in Caribbean reef fishes in Panama. *Mar. Biol.* **114**, 527–37.
- Robertson D. R. (1998) Implications of body size for interspecific interactions and assemblage organization among coral-reef fishes. *Aust. J. Ecol.* **23**, 252–7.
- Robertson D. R., Green D. G. & Victor B. C. (1988) Temporal coupling of reproduction and recruitment of larvae of a Caribbean reef fish. *Ecology* **69**, 370–81.
- Robins C. R., Ray G. C. & Douglass J. (1986) *A Field Guide To Atlantic Coast Fishes of North America*. Houghton Mifflin, Boston.
- Russell B. C., Anderson G. R. V. & Talbot F. H. (1977) Seasonality and recruitment of coral reef fishes. *Aust. J. Mar. Freshwat. Res.* **28**, 521–8.
- Sale P. F., Doherty P. J., Eckert G. J., Douglas W. A. & Ferrell D. J. (1984) Large scale spatial and temporal variation in recruitment and fish populations on coral reefs. *Oecologia* **64**, 191–8.
- Sale P. F. & Ferrell D. J. (1988) Early survivorship of juvenile coral reef fishes. *Coral Reefs* **7**, 117–24.
- Sale P. F. & Steele W. J. (1989) Temporal variability in patterns of association among fish species on coral patch reefs. *Mar. Ecol. Prog. Ser.* **28**, 165–74.
- Shenker J. M., Maddox E. D., Wishinski E., Pearl A., Thorrold S. R. & Smith N. (1993) Onshore transport of settlement-stage Nassau grouper *Epinephelus striatus* and other fishes in Exuma Sound, Bahamas. *Mar. Ecol. Prog. Ser.* **98**, 31–43.
- Shulman M. J. & Ogden J. C. (1987) What controls tropical reef fish populations: recruitment or benthic mortality? An example of the Caribbean reef fish *Haemulon flavolineatum*. *Mar. Ecol. Prog. Ser.* **39**, 232–40.
- Sponaugle S. & Cowen R. K. (1994) Larval durations and recruitment patterns of two Caribbean gobies (Gobiidae); contrasting early life histories in demersal spawners. *Mar. Biol.* **120**, 133–43.
- Sponaugle S. & Cowen R. K. (1996) Larval supply and patterns of recruitment for two Caribbean reef fishes, *Stegastes partitus* and *Acanthurus bahianus*. *Mar. Freshwat. Res.* **47**, 433–47.

- Thorrold S. R., Shenker J. M., Wishinski E., Mojica R. & Maddox E. D. (1994a) Larval supply of shorefishes to nursery habitats around Lee Stocking Island, Bahamas. I. Small-scale distribution patterns. *Mar. Biol.* **118**, 555–66.
- Thorrold S. R., Shenker J. M., Maddox E. D., Mojica R. & Wishinski E. (1994b) Larval supply of shorefishes to nursery habitats around Lee Stocking Island, Bahamas. II. Lunar and oceanographic influences. *Mar. Biol.* **118**, 567–78.
- Thresher R. E. (1991) Geographic variability in the ecology of coral reef fishes: evidence, evolution, and possible implications. In: *The Ecology of Coral Reef Fishes* (ed. P. F. Sale) pp. 401–36. Academic Press, New York.
- Tupper M. E. & Hunte W. (1994) Recruitment dynamics of coral reef fishes in Barbados. *Mar. Ecol. Prog. Ser.* **108**, 225–35.
- Victor B. C. (1986) Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. *Ecol. Monogr.* **56**, 145–60.
- Warner R. R. & Chesson P. L. (1985) Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. *Am. Nat.* **125**, 769–87.
- Warner R. R. & Hughes T. P. (1988) The population dynamics of reef fishes. *Proc. 6th Int. Coral Reef Symp.* **1**, 149–55.
- Williams D. McB. (1983) Daily, monthly and yearly variability in recruitment of a guild of coral reef fishes. *Mar. Ecol. Prog. Ser.* **10**, 231–7.
- Williams D. McB., English S. & Milcich M. J. (1994) Annual recruitment surveys of coral reef fishes are good indicators of patterns of settlement. *Bull. Mar. Sci.* **54**, 314–31.
- Williams D. McB. & Sale P. F. (1981) Spatial and temporal patterns of recruitment of juvenile coral reef fishes to coral habitats within 'One-Tree Lagoon', Great Barrier Reef. *Mar. Biol.* **65**, 245–53.