

# Recruitment variability in sandy beach macroinfauna: much to learn yet

Variabilidad en el reclutamiento de la macroinfauna  
de playas arenosas: aún resta mucho por conocer

OMAR DEFEO

Instituto Nacional de Pesca, Constituyente 1497, 11200 Montevideo, Uruguay\*. E-mail: odefeo@inape.gov.uy  
UNDECIMAR, Facultad de Ciencias, Universidad de la República, Tristán Narvaja 1674, 11200 Montevideo, Uruguay  
Centro de Investigación y de Estudios Avanzados del IPN, A.P.73 Cordemex, 97310 Mérida, Yucatán, México

\* Correspondence address

## ABSTRACT

Knowledge of patterns and processes underlying spatio-temporal variability in recruitment, as well as its relationship with the spawning stock size, is crucial to understand the dynamics of a population through time. In the case of benthic organisms, their complex life cycle often involves a planktonic phase affected by dispersal processes, which are responsible for high variability in recruitment. Exposed, high energy sandy beaches, constitute a distinct and well-defined ecosystem which fall into the category of physically stressed environments. In this sense, it has been largely considered that spatial and temporal recruitment patterns in exposed sandy beach populations should be fully explained by their adaptation to such a dynamic environment, being biotic interdependences mainly limited to low energy beaches. However, little is known about long-term recruitment variability in these populations and, with the exception of two recent examples given in this review, reliable predictions of recruitment from a given level of stock have not been demonstrated. Potential causes are: (1) the inherent difficulties in sampling and experimentally manipulating the generally small or mobile infauna; (2) the horizontal and vertical space partitioning of the habitat, which makes the recognition of biological interdependences very complex; (3) the general lack of long-term data sets directed to estimate such type of relationship; and (4) the absence of information about the scale-dependence of processes and patterns structuring sandy beach populations. In this paper I review existing information about recruitment variability in sandy beach populations. Regulatory mechanisms causing population fluctuations in the long-term and at different spatial scales, and the biotic and abiotic processes responsible for it, are analyzed in comparison with invertebrates of rocky and soft, sheltered shores. It is unclear how the conclusions emanated from intertidal rocky and soft-bottom sheltered habitats apply to exposed beaches. The lack of scientific knowledge emphasizes the need for additional observations on the natural history and long-term dynamics of exposed sandy beach populations. Recent results obtained from long-term studies suggest that the traditional designation of exposed sandy beach populations as physically structured seems incomplete. The definition of the relevant scales of analysis, which will vary according to the research question, and the recognition of a physical-biological coupling in different scales, shows an alternative approach concerning the study of population regulation and dynamics in exposed sandy beaches.

**Key words:** spatial scales, biotic interdependences, long-term.

## RESUMEN

El conocimiento de los patrones y procesos que gobiernan la variabilidad espacio-temporal del reclutamiento, así como su relación con el tamaño del stock desovante que lo genera, es crucial para entender la dinámica de una población en el tiempo. En el caso de organismos bentónicos, su ciclo de vida complejo involucra una fase larval planctónica que es afectada por procesos de dispersión, los cuales ocasionan una alta variabilidad en el reclutamiento. Las playas de arena expuestas constituyen un ecosistema peculiar categorizado como físicamente estresante. En tal sentido, ha sido considerado que la variación espacio-temporal en los patrones de reclutamiento de playas de arena expuestas sería explicada en su casi totalidad por su capacidad de adaptación a ese ambiente dinámico, estando las interdependencias biológicas limitadas principalmente a playas de arena de baja energía. A excepción de dos ejemplos recientes analizados en esta revisión, se sabe poco acerca de la variabilidad en el reclutamiento de estas poblaciones en el largo plazo y no se han cuantificado predicciones confiables del reclutamiento a partir de un nivel dado de stock parental. Posibles razones de esto son: (1) la dificultad de muestreo y experimentación de la generalmente pequeña y móvil fauna; (2) la partición tridimensional del hábitat que dificulta el reconocimiento de interacciones intraespecíficas; (3) la alarmante carencia de estudios de largo plazo que permita estimar tal tipo de relación, y (4) la ausencia de información acerca de estudios a diferentes escalas de espacio sobre los procesos y patrones que estructuran dichas poblaciones. En este trabajo presento una revisión de la información existente sobre la variabilidad en el reclutamiento en poblaciones de playas de arena. Analizo la importancia de algunos mecanismos regulatorios de la abundancia en el largo plazo, las escalas de espacio relevantes y los factores bióticos y abióticos responsables de ellos, a través de un

análisis comparativo con poblaciones de litorales rocosos y de fondos blandos protegidos. Considero que no sería adecuado extrapolar las conclusiones derivadas de hábitats rocosos y de fondos blandos protegidos a playas de arena expuestas. La carencia de conocimiento científico sobre el tópico hace imperiosa la necesidad de lograr observaciones adicionales acerca de la historia natural y dinámica de tales poblaciones. Sin embargo, resultados recientes sobre el tópico, derivados de estudios de largo plazo, sugieren que la designación tradicional de las poblaciones de playas de arena como físicamente controladas es incompleta. La definición de las escalas de análisis relevantes, las cuales variarán con la pregunta en cuestión, así como el reconocimiento de un acoplamiento físico-biológico en las diferentes escalas de espacio y tiempo, parecen indicar una aproximación alternativa al estudio de la regulación y dinámica de poblaciones de playas de arena.

**Palabras clave:** escalas de espacio, interdependencias bióticas, largo plazo.

## INTRODUCTION

The dynamics of a population is determined by the balance between increases in biomass due to recruitment, growth and immigration, and losses due to fishing and natural mortality, and emigration. In this context, knowledge of the relationship between stock size and subsequent recruitment is crucial to understand population variability through time. Recruitment variability includes the role of the probable response to perturbations such as harvesting, and the incidence of environmental stochasticity in its long-term dynamics and at different spatial scales (Orensanz, 1986, Fogarty, 1989).

In benthic invertebrates, recruitment variability can be considered as the main factor affecting stock abundance, with random fluctuations in the physical environment generally outweighing the effects of stock size (Coe, 1956, Hancock, 1973, Connell, 1985, Raimondi, 1990). Their complex life cycle (*sensu* Roughgarden et al., 1988) involves an early planktonic phase in which larvae are affected by dispersal processes on a variety of spatial and temporal scales (Tremblay & Sinclair, 1990, 1992). Subsequent settlement depends on finding available space on adequate substratum, possibly limited by the size of adult population.

In the case of intertidal species living in habitats characterized by high environmental stress (*sensu* Menge & Sutherland, 1987) as exposed sandy beaches, changes in several environmental factors which may act simultaneously in small areas (e.g. a combination of temperature, salinity, humidity and oxygen) introduce another source of variability (Brown & McLachlan, 1990). The observed large fluctuations in abundance of two-phase species (planktonic larvae and benthic adult stage), when compared to otherwise similar one-phase species, have led to their descrip-

tion as resurgent populations (Coe, 1953, 1956, Mikkelson, 1981, Ansell, 1983). In this sense, it has been mentioned that "community and population patterns on exposed sandy beaches are the consequence of individual responses to the swash climate, sand movement and liquefaction on the beach face and are not greatly controlled by biological interactions" (McLachlan, 1988).

Adult-larval and adult-recruit interactions seem to have a greater potential on sheltered shores (Woodin, 1976, 1986, Peterson, 1979, André & Rosenberg, 1991), where there are many species more specialised and less opportunistic than in exposed sandy beaches (McLachlan, 1988). In exposed habitats there is no apparent shortage of food or space, and the extra depth dimension available favors habitat partitioning both horizontally and vertically (Branch, 1984). However, regulatory mechanisms given by interactions between established adults and newly settled recruits have recently been suggested as an alternative way in structuring soft-bottom suspension-feeding populations of exposed sandy beaches (Defeo et al., 1992, Defeo 1993: see below). Hence, a physical and biological coupling might determine survival rates and could have a direct effect on recruitment.

In this paper I review existing information about larval dispersal, settlement, recruitment variability and the stock-recruitment relationship (SRR) in sandy beach populations. Regulatory mechanisms at different spatial scales, and the biotic and abiotic processes responsible for it, are analyzed in comparison with invertebrates of rocky and soft, sheltered shores. Some guidelines for future research are also given.

## LARVAL DISPERSAL

Physical, chemical, and biological factors affecting long range dispersal of early

planktonic stages, may constitute key determinants in explaining recruitment success and variability of coastal invertebrates. Since the early work of Thorson (1950), it has been recognized that pre-settlement processes influence the population dynamics of littoral invertebrates with pelagic larval phase. However, it was not until present that the role of larval recruitment on the population dynamics and community structure of benthic macrofauna is being the centre of active empirical research (Grosberg, 1981, 1982, Roughgarden et al., 1984, Caffey, 1985, Connell, 1985, Gaines & Roughgarden, 1985, Sutherland, 1990, Scheltema, 1986, Menge & Sutherland, 1987, Hughes, 1990, Menge, 1991). The majority of these studies have been focussed on rocky shores, and include mathematical models which deal with the interaction between the adult and larval phases in both space and time (Possingham & Roughgarden, 1990, Pascual & Caswell, 1991).

Dispersal of planktonic larvae is highly variable among benthic species, both in spatial and temporal scales (Mileikovsky, 1971, Mann, 1986; Scheltema, 1986), being conditioned by the length of the planktonic stage as well as the rate and direction of currents along coastlines that transport it (Olson, 1985, Strathmann, 1986, Hill, 1991). In relation to this, seasonal changes in the intensity and direction of coastal winds will determine the magnitude of horizontal transport of larvae (Botsford, 1986a, b, Scheltema, 1986, Roughgarden et al., 1988). As a result, some abiotic variables of a coastal system (e.g. salinity) may fluctuate according to circulation patterns and hence become important agents of larvae mortality. Variability in the short-term tide regime acting as a passive transport agent, may also account for wide fluctuations in larval availability (Levin, 1984, 1986). The amount of suitable habitat and available space to settle are also factors that will determine the amount of larvae that will settle together in one place, hence determining the spatial landscape of the (benthic) adult population (Strathmann, 1974, Palmer & Strathmann, 1981, Connell, 1985).

Studies of larval dispersal of soft bottom macrofauna are less abundant than in their

rocky counterparts, and are referred almost exclusively to sheltered shores (Woodin, 1976, 1986). Little is known about dispersal of meroplanktonic larval phases of exposed sandy beach macrofauna (but see Efford, 1970), and the mechanisms influencing larval distribution are still poorly understood. In a comprehensive review of the genus *Donax*, Ansell (1983) reported the occurrence of a "byssus-pelagic phase" in which the byssus filament is used as a float, allowing resuspension, transport and the selection of substrate by early benthic stages. Brown (1983) suggests that in high energy beaches, habitat choice is critical at the end of larval development, and that it must be made repeatedly as migratory behaviour carries the animals to less favourable or unsuitable habitats. Several sandy-beach species explore the substratum before settling and may even delay metamorphosis until suitable conditions are found, depending on the sedimentology characteristics, including its organic content (Brown, 1983). Other environmental conditions (e.g. salinity gradients) are important in defining suitable areas with greater probability of successful recolonization (Efford, 1970, Defeo et al., 1986).

What is frequently ignored in benthic macrofauna of exposed sandy beaches is how the next generation is recruited to restock the parental population. Up to now, the unique research dealing with the study of the role of currents in the spread of pelagic larvae of such ecosystems is the one of Efford (1970). He attributed the regular occurrence of species with pelagic larvae in certain areas to the existence of mechanisms for repopulation of the parental area despite the dispersal of planktonic phases. Efford suggested four hypothesis to explain dispersal mechanisms and settlement behaviour of sandy beach invertebrates, as exemplified by the sand crab *Emerita analoga*:

- 1) The counter current hypothesis. Larvae would tend to remain near the coastline from which they came, as a result of the presence of coastal current and counter-current running parallel to the shore. The hypothesis implies mixing and therefore no morphological cline.

- 2) The *gyral hypothesis*. A gyral regularly brings larvae back nearshore.
- 3) The *nursery area hypothesis*. Larvae drift for a short time and, after moving offshore, spend the rest of their larval life in nursery areas. Larvae found in the plankton many miles offshore are destined to die or populate new beaches, but not those on their original coastline. Larvae populate beaches adjacent areas from which they came, thus determining morphological differences between populations at the end of the distribution.
- 4) The *rearing current hypothesis*. Species with restricted spawning areas produce planktonic eggs and larvae which are dispersed to another restricted but suitable area for settlement and recruitment.

The point at which physical forces become sufficient to override any active component has not been adequately examined. Moreover, there is not enough knowledge consensus about which mechanism explain better the retention of larvae or spatial variability patterns in settlement of exposed sandy beach populations. Testing Efford's hypotheses is considered a useful aid for analyzing the problem.

#### SETTLEMENT

In this review, *settlement* is defined as the termination of a pelagic larval phase and the assumption of a sessile or nonsessile sedentary life (Scheltema, 1974), and *recruitment* as the number of organisms that have attained a minimum size and have been resident in the benthic population for some time (Keough & Downes, 1982, Connell, 1985).

Settlement variability of intertidal populations has been focussed mainly on hard bottoms, particularly on barnacles (Connell, 1961, 1963, 1985, Denley & Underwood, 1979, Grosberg, 1982, Caffey, 1985, Raimondi, 1990, Possingham & Roughgarden, 1990). Settlement has also been intensively studied in soft-sediment sheltered beaches, lagoons and estuaries (Caddy, 1966, Woodin, 1976, 1986, Peterson, 1977, 1979, 1982, Ertman & Jumars, 1988, André & Rosenberg, 1991). Because of the presence of pre-

settlement (i.e. larval dispersal of planktonic stages) and post-settlement stages, the importance of each stage to the benthic species distribution and abundance in both space and time and the biotic and abiotic factors involved in such processes is often unclear (Underwood & Denley, 1984).

Variability in settlement magnitude of littoral populations has been related to (Raimondi, 1990, and references therein): (1) pre-settlement mortality during dispersal, affected by winds, currents and tide variability; (2) mechanisms affecting delivery from nearshore waters to the substrate (*e.g.* nearshore turbulence); (3) factors affecting larval attachment to the surface, depending on the characteristics of the physical environment; and (4) larval-adult interactions at the time of settlement, which can increase or, in high densities, decrease settlement. Woodin (1986) reviewed study cases in which selective and non-selective settlement of soft bottom populations of sheltered shores were documented. Five patterns of settlement were identified: (1) gregarious settlement; (2) selection of a site due to the presence of a positive cue rather than the presence of conspecifics; (3) no obvious pattern of positive or negative selection; (4) rejection of sites because of the presence of a negative cue; and (5) passive entrainment of larvae. Woodin (1986) stated that some of the cues used by larvae on hard substrata organisms may be different in infaunal systems, and much of the habitat modification through sediment-mediated interactions that is so common in sedimentary systems (see *e.g.* Rhoads & Young, 1970, Rhoads, 1974, Wilson, 1991) has no direct parallel in hard bottoms. Which of the patterns is of greatest importance in determining settlement patterns, has been a source of controversy among workers of soft-bottom communities (Hall, 1983).

Benthic macroinfauna of exposed sandy beaches has highly variable patterns in settlement, both spatially and temporally, among different species and subpopulations of the same species (Coe, 1953, 1956, Efford, 1970, Ansell, 1983, Defeo et al., 1986, 1992), which has led to the concept of resurgent populations. As exposed, dissipative beaches are physically stressed environments, populations and communities are thought to be

regulated mainly by physical factors (McLachlan et al., 1993). Hence, adaptations to abiotic factors are probably the best way of understanding settlement/recruitment variability in such systems (McLachlan, 1983). Organisms often have special behavioural adaptations to settle and live, which includes: motility and ability to burrow rapidly (Ansell, 1983, Brown, 1983), brood protection (Crocker et al., 1975, Wooldridge, 1981), sensitivity to water flow and current direction and a tidal migratory behaviour which involves movement on the beach following the swash zone (McLachlan, 1988). Passive sorting by the "cusp circulation" swash pattern and active selection of suitable areas have been mentioned as the underlying regulating factors in the spatial distribution of settlers, juveniles and adults (McLachlan & Hesp, 1984, Defeo et al., 1986, de Alava, 1989, Donn, 1990, de Alava & Defeo, 1991). These would result in patchy distributions by ages/sizes, with zonation patterns subjected to temporal fluctuations due to predictable (movement and sorting by the swash) or unpredictable (storms) environmental factors (Barnes & Wenner, 1968, Cubit, 1969, Ansell, 1983, McLachlan, 1983, Sastre, 1985, Donn, 1990).

As a result of the above concepts, it has been suggested that such biotic mechanisms are mainly limited to low energy beaches (McLachlan, 1988, 1990). However, alternative explanations of settlement and recruitment regulation resulting from food availability, interactions within age/size classes and a set of compensatory mechanisms (e.g. density-dependent fecundity, growth and survival rates) may also account for the space-time population variability (Crocker & Hatfield, 1980, de Alava & Defeo, 1991, Defeo et al., 1992). In this sense, the lack of scientific knowledge opens a question about the relative contribution of abiotic and biological factors (e.g. larval-adult interactions) in determining settlement patterns.

ADULT-LARVAL AND ADULT-RECRUIT  
INTERACTIONS, WITH SPECIAL REFERENCE TO  
SUSPENSION FEEDING BIVALVES

Adult-larval and adult-recruit interactions are important regulatory mechanisms in dense assemblages of benthic fauna (Wilson,

1991). The majority of the investigations of adult-larval interactions in invertebrates have been done on rocky (Raimondi, 1990) and soft-bottom -sheltered- shores (Peterson, 1979, 1982, Hall, 1983, Black & Peterson, 1988). Detection of intra and interspecific competition in benthic macroinfauna of soft-bottom intertidal areas is comparatively uncommon (Dayton, 1984, Jensen & Kristensen, 1990), primarily because of the inherent difficulties in sampling and experimentally manipulating the generally small or mobile infauna (Dayton & Oliver, 1980, Marelli, 1990), and also because of the three-dimensional structure of the habitat, which makes the detection of biological interdependencies very complex (Peterson, 1979, Branch, 1984, Wilson, 1991).

Many field studies in soft-bottoms, carried out particularly with filter feeding bivalves and designed to test the effects of adults on settling larvae, have yielded variable results (Williams, 1980, Maurer, 1983, André & Rosenberg, 1991). Difficulties in discerning differential mortality of settling larvae with post-settlement dispersal and habitat selection (Woodin, 1986, Holm, 1990), and inadequate sampling design and statistical power of tests used (Ertman & Jumars, 1988) make that the significance of interactions between adults and larvae in structuring soft-bottom communities has been strongly questioned (Black & Peterson, 1988, Ertman & Jumars, 1988, Olafsson, 1989). On the contrary, other studies suggest that adult-larval and adult-recruit interactions in filter feeding organisms may play a major role in explaining growth, mortality and recruitment variability observed in the field (Thorson, 1966, Woodin, 1976, Peterson, 1982, Möller, 1986, Orensanz, 1986, André & Rosenberg, 1991). In such cases, settlement is viewed as an active larval process to select a habitat (Osman et al., 1989), while resident adults have been found to: (1) reduce the settlement rate by either filtering settling larvae out of the water column or seizing available space (Woodin, 1976, 1986, Todd & Doyle, 1981, Crowe et al., 1987, André & Rosenberg, 1991, André et al., 1993); (2) increase settlement through gregarious responses (Crisp, 1984, Raimondi, 1988); or (3) alter settlement by influencing current flow or bottom

boundary layers (Butman, 1987). Concerning point (1), many studies conducted on filter feeders have shown that in cases of lower adult densities, an extensive recruitment occurs; and on the other hand, heavy abundances of adults inhibit settlement when biomass or density are above a threshold (Hancock, 1973, Peterson, 1979, Williams, 1980, Moller, 1986, Orensanz, 1986, Caddy, 1989b, Defeo, 1993).

Food and space have been considered as potential limiting resources in soft-bottom communities (Wilson, 1991, Peterson & Black, 1987, Olafsson, 1988, 1989), with indirect competitive mechanisms (exploitative competition) governing the relationship between adults and recruits (Wilson, 1983, Fréchette & Lefavre, 1990). Sediment-mediated interactions represent another source of variability, as the activity of soft-sediment organisms can drastically modify the physical nature of the habitats (Wilson, 1981, 1984, 1991, Brenchley, 1982). In suspension feeders, the inhalant and exhalant currents produced by siphons provide a source of physical disturbance, because their activity when combined with water movement tends to mobilize and passively accumulate sediment around projecting bivalve siphons, and hence preclude settlement (Peterson, 1979, Ertman & Jumars, 1988).

In sheltered beaches, Hall (1983) found that successful recruitment of the Manila clam *Tapes philippinarum* depends partly on segregating and congregating forces between larvae attempting settlement and the adult population. The former may result in negative interactions between adults and larvae, which in turn generates a regular spacing between individuals as a result of competition for space and food. Density-dependent effects in growth and mortality of the newly settled cohort should be expected.

Though poorly documented, the above mentioned biological interactions had been thought to be unimportant on exposed, high energy beaches (McLachlan, 1988, but see Croker & Hatfield, 1980, Defeo et al., 1992, Defeo, 1993). It was argued that the inability of competitors to crush or undercut in the sediment, the extra depth dimension available, the improbability of starvation and no shortage of resources makes biological

interactions less important than in rocky shores (Branch, 1984, McLachlan, 1988). Nonetheless, it is clear that the presence and degree of biological interactions across the wave exposure gradient requires further study, as its real ecological significance has not been adequately assessed (see McLachlan & Bate, 1983).

SPATIAL PATTERNS OF RECRUITMENT:  
ECOLOGICAL HETEROGENEITY AND THE  
IDENTIFICATION OF THE ADEQUATE  
SCALES OF ANALYSIS

It has been commonly mentioned that the observed regular patterns in physical processes determine the persistence of natural populations (Sinclair, 1987). However, many populations undergo predictable or unpredictable fluctuations associated with spatial and stochastic heterogeneity of the environment. A growing body of evidence suggests that spatial and temporal distribution of marine invertebrates and the surrounding environment are not homogeneous. Benthic habitats can be seen as a mosaic of environmental quality produced by spatio-temporal variability in physical conditions, which, in turn, are responsible for the clumped distribution of macrofauna observed in the field (Crowl & Schnell, 1990, Thrush, 1991, Barry & Dayton, 1991; Günther, 1992).

Any relation between stock size and recruitment in benthic invertebrates is the result of diverse processes decoupled in different spatiotemporal scales (Orensanz, 1986). Recruitment is decoupled from local reproduction by larval dispersal processes of variable intensity, which introduce an important source of variability in the population dynamics of a species (Loosanoff, 1966, Pascual & Caswell, 1991). As a result, benthic populations usually take the form of mega or metapopulations, *i.e.* self-reproducing local aggregations with widely separated, hydrographically defined geographic locations, interconnected by variable degrees of larval dispersal and genetic flow (Orensanz, 1986, Sinclair, 1987, Caddy, 1989a).

It has been mentioned that recruitment to local beaches may be dependent on the local density of the spawning stock (De Villiers, 1975, Defeo et al., 1992, Defeo, 1993).

However, the existence of a common larval pool of several beach populations (*i.e.*, mega or metapopulations) might also contribute to explain recruitment variability through time (Wade, 1968). These studies emphasize the importance of a clear definition of spatial and temporal scales in order to identify sandy beach population patterns and the processes that determine them (see Orensanz et al., 1991 for a clear definition of spatial scales). Space-time scales for biological and physical processes operating on sandy beach populations could not always be the same. For example, stochastic, episodic environmental events, may alter spatial and temporal patterns of abundance (Arntz et al., 1987), whereas regular climatic variations over years to decades might also result in inter-annual changes of distribution and abundance, as observed for other benthic populations (Caddy, 1979, Botsford, 1986a).

As in their rocky counterparts, distribution of the macroinfauna in sandy beaches and other soft-bottom habitats depends on environmental heterogeneity, life history characteristics and biological interactions among community members, all of them operating at different spatial scales (Crowe et al., 1987, Thrush, 1991, Defeo, 1993). For example, while patterns of larval dispersal depend on processes occurring at large spatial scales (*i.e.* tens of kilometers), active larval selection occurs at spatial scales of centimeters. Physical cues, biological interactions and biogenic environmental changes (Brenchley, 1982, see review in Barry & Dayton, 1991) contribute to micro-scale heterogeneity and patchiness.

For sandy beach organisms, the quality of the site affects settlement and hence the distributional pattern of a population (Hall, 1983). The existence of well defined macro (alongshore) and micro (intertidal) environmental gradients conform the general framework of habitat suitability (Bally, 1983a, b, Defeo, 1993, Jaramillo et al., 1994), and produce clear distributional patterns at a variety of spatial scales (*i.e.* geographic patterns and zonation: Bally, 1983b, Jaramillo, 1987a, b). The characteristics of the site chosen for settlement include the magnitude of the adult stock present on the beach, which may constitute an evidence of good conditions for survival (Defeo et al., 1986).

STOCK-RECRUITMENT RELATIONSHIP:  
THEORY AND APPLICATION FOR SANDY  
BEACH POPULATIONS

*Traditional models.* There are two classic approaches which determine the stock-recruitment relationship (SRR). The simplest is the first one of Beverton & Holt (1957), which states that between hatching and recruitment there are two components of mortality, density independent and density dependent:

$$R = \frac{\alpha S}{\beta + S}$$

where  $R$  is recruitment,  $S$  is spawning stock (both expressed in numbers or biomass),  $\alpha$  expresses the density-dependent mortality, and  $\beta$  the density-independent mortality. In this model recruitment is asymptotic to stock.

The second formulation is that of Ricker (1954):

$$R = aSe^{-bS}$$

in which the stock-dependent mortality,  $b$ , is generated by mechanisms such as cannibalism, aggregation of predators and competition for limiting resources.  $a$  is a parameter representing the density-independent mortality. This model is dome-shaped.

Shepherd (1982) introduced a three-parameter recruitment model expressed by the following equation:

$$R = \frac{aS}{1 + (S/k)^b}$$

where  $R$  and  $S$  are defined as above,  $a$  is a positive scaling factor or fecundity constant with no density-dependence,  $b$  is a density-dependent parameter or compensation coefficient and  $k$  is the threshold population size above which density-dependent processes predominate (Cushing, 1988, Saila et al., 1988).

Some knowledge of the possible mechanism underlying the nature of the SRR could be used to decide which theoretical curve is employed (Cobb & Caddy, 1989).

More complex or alternative shapes of models were developed (see Hilborn & Walters, 1992), but the three mentioned above capture most of the biological features underlying population variability through time. That is, the three models consider in a different extent the relative importance of density-dependent, compensatory mechanisms in regulating populations (Cushing, 1988). A compensatory mechanism is a process by which the effect of one factor on a population tends to be counteracted or compensated by a consequential change in another factor (Cooke, 1984: p. 342). On the other hand, the mechanisms underlying the Ricker model are stock-dependent (Hilborn & Walters, 1992) and lead to overcompensation, i.e. the decrease of total recruitment at large spawning stock sizes.

The traditional approach to estimate the parameters of these SRR models has been deterministic. Fogarty (1989) and Fogarty et al. (1991) emphasize the need to develop stochastic models in order to characterize the dynamics of exploited populations. In these models, mortality rates during the planktonic phase may be treated as random variables with no explicit linkage to environmental factors. This is particularly valuable in the case of exposed sandy beach populations with high fecundity, variable periods of planktonic larval phase and high variance in recruitment.

In spite of the important theoretical developments in understanding recruitment dynamics, there is little specific evidence for a direct SRR in invertebrates (Caddy, 1989b, Cobb & Caddy, 1989, Caputi, 1993), although larval-adult interactions can lead to compensatory or overcompensatory mechanisms, and hence to statistical relationships similar to those described by Ricker (1954) (Hancock, 1973, 1979). The type of specific compensatory mechanisms involved depends on the characteristics of the species and type of habitat (Caddy, 1986). The passive filtering of planktonic larvae by established adults or potential competition for food could prevail in soft bottoms. However, the difficulties in detecting density-dependence from field sampling (Solow, 1990), and the lack of observations of specific regulatory mechanisms at appropriate spatial and tem-

poral scales, often frustrate the delineation of a clear SRR.

The combined role of environmental forcing and density-dependence can also account for recruitment variability in invertebrate populations (Botsford, 1986a, 1986b, Caputi, 1993). In this sense, Tang (1985) integrated environmental variables to the stock-recruitment models above described, an approach which has been successfully applied to invertebrates (Penn & Caputi, 1986, Phillips & Brown, 1989, Penn et al., 1989); however, this approach must be treated with caution, as a SRR constructed from catch data would merely reflect spurious correlations derived from the relationship between catch success and environmental variability (Botsford, 1986b, see also Hilborn & Walters, 1992).

Novel approaches. The above mentioned models were developed to outline factors controlling the long-term dynamics of the population, rather than to provide short-term recruitment forecasting. The spatial structure of the population is not considered in these approaches. Recently, Gaines & Roughgarden (1985), Roughgarden & Iwasa (1986), Roughgarden et al. (1985, 1988) and Possingham & Roughgarden (1990) developed detailed models of the coupling between hydrodynamic processes, habitat structure and abundance of larvae and adults, in order to predict the spatial population dynamics of rocky shore organisms with two-phase life cycle. The models thus generated couple processes occurring at different habitats (i.e. planktonic and benthic) with dissimilar time scales (Roughgarden *et al.*, 1988). Pascual & Caswell (1991) extended Roughgarden's deterministic models to benthic populations classified by size, and found that processes freeing space in the system, such as low settlement and high mortality, promote stability, whereas higher growth and settlement rates have a destabilizing effect. The relevance of the cited models, in which recruitment is completely decoupled from local reproduction, depends on the scale of larval dispersal, the mobility of the organisms under study, and the scale selected for observation. In this context, intrinsic characteristics of the life history of sandy beach organisms might be considered in order to apply or construct such kind of models: a

regular mobility with tides and the possibility of vertical and horizontal stratification diminish the probability of space limitation. Moreover, as many of these ecosystems are often characterized by high primary production, food depletion is not expected to be severe (McLachlan, 1980).

An approach to model the spatial component of a SRR in intertidal clams of sheltered beaches, was done by Hall (1983). He integrated the spatial variability of the population subcomponents with respect to the height of the tidal level, also considering three major components which affect the settlement/recruitment process (Hall, 1983: pp. 107-111): congregating (density independent) and segregating (density dependent) forces between stock and recruitment, and a site component which defines the quality of the habitat and its effects on adults and recruits. However, this work is intended to primarily reflect the effects of small-scale spatial distribution of adults and recruits from a snapshot study, rather than to establish a traditional SRR from a long data series.

SRR in exposed sandy beach populations. Studies of the coupling between physical and biological processes at different spatial scales are not found in the "exposed sandy beach literature". However, Defeo (1993, see also Defeo, this volume) and de Alava (1993) recently provided some insights to determine the form and nature of the SRR in two exposed sandy beach populations.

Defeo (1993) showed one of the earliest evidences of the presence of strong intraspecific interactions of a bivalve population inhabiting an exposed sandy beach environment, on the basis of a long-term analysis. The yellow clam *Mesodesma mactroides* of an exposed sandy beach of Uruguay displayed a significant overcompensatory relationship between spawning stock and recruitment density, with two definite trends: 1) larger adult densities originated during a human exclusion experiment (see Defeo, this volume) produced extremely low recruitments; 2) maximum recruitment densities occurred from moderately low and medium sizes of spawning stock. Thus, the SRR was best explained by the Ricker and Shepherd models (see Fig. 1b in Defeo, this volume).

Predicted recruitment by both curves (non-linear fitting) dropped when adult density was above 110-130 ind/m<sup>2</sup>, which means that level of adult density above which overcompensation occurs. Both models have a strong biological meaning: for example, the slope at the origin *a* in the Shepherd model expresses the maximum number of recruits per unit adult density of (mean ± SE) 8 ± 3 recruits/adult, suggesting a strong resilience of the yellow clam population in the presence of low spawning stock densities. The value of *b* was greater than 1, thus indicating intense overcompensation in the yellow clam population. The value of *k* was 132 ± 37 ind/m<sup>2</sup>, which means that density-dependent processes operate mainly above this mean level of adult density (Shepherd, 1982, Cushing, 1988). A potential (non demonstrated) compensatory mechanism of pre-settlement, density-dependent mortality, could be the filtering of larvae out of the water column. Sediment-mediated interactions through the feeding activity may also change adjacent physical properties of the sediment, thus inhibiting settlement. This regulatory mechanism underlying larval survival and recruitment success is consistent with those mentioned as possible causes of overcompensation in stock-recruitment theory (Defeo, 1993).

The results of this long-term research also showed different trends in the population according to the spatial scale considered: whereas at a transect scale, a common distribution pattern of adults and recruits was quantified, at a quadrat scale, high densities of recruits were never coincident with high densities of older clams (see also Defeo, this volume). The recognition of a certain maximum width of the clam bed, and also of the total area covered by the stock, suggested a limitation of available space at an adult density close to 120 ind/m<sup>2</sup>, augmenting the probability of occurrence of compensatory mechanisms. This value was consistent with the results of the SRR.

De Alava (1993), working in the same exposed beach of Uruguay in a long-term study of the sympatric and unharvested wedge clam *Donax hanleyanus*, found that the long-term recruitment variability had no relationship with the magnitude of the

parental stock; recruitment could be explained by a monotonically decreasing exponential function of the density of juveniles + adults of the yellow clam *Mesodesma mactroides* (see Defeo, this volume), i.e. there exists an "interspecific stock-recruitment relationship" (*sensu* Pauly, 1980). The same picture as in the yellow clam example was observed: at a transect scale a common distribution pattern of adults and recruits was quantified, whereas at a quadrat scale high densities of recruits were never coincident with high densities of older wedge or yellow clams (de Alava, 1993). However, the relationship mentioned above was valid only for years 1983 to 1988, whereas for years 1989 and 1990 highest densities of both populations co-occur, as a result of the exclusion of humans in harvesting the yellow clam. This in turn suggests that temporal variations in recruitment could be explained by a technological-side interdependence given by the amount of fishing effort exerted over *Mesodesma mactroides*. In fact, a strong inverse relation between the mean density of recruits for the entire beach and the yellow clam catch or effort was detected for the eight years studied (Defeo & de Alava, 1995). Even though the above, the relatively short time series of the two examples given in this review precluded powerful statements. One-step-ahead forecasts and predictive validation of recruitment strength for subsequent years will be necessary to evaluate with higher degree of confidence the level of certainty attached to the SRR.

Recruitment variability and management of sandy beach stocks. Forecasting the size of year-classes recruiting to an area or a fishery is of fundamental importance in fisheries management. The accuracy and reliability of a robust stock-recruitment relationship (SRR) could enable predictions of year-class sizes to be made with a specified degree of confidence and help to optimize yield for a given level of recruitment (Sissenwine et al., 1988). However, the relatively weak SRR observed is considered one of the major uncertainties in invertebrate fisheries (Caputi, 1993).

In the case of exploited invertebrates of open coasts, management is complex due to the easy access to the resource by the recre-

ational and commercial harvesters (Hall, 1983, Defeo, 1989, Lasiak, 1991). Thus, a major susceptibility to stock depletion related to the sessile or sedentary habit of these species, and the ease with which collectors can remove clumps of individuals, increase the probability of recruitment failure. This fact is often aggravated when the fishery is open-access, unmanaged, or even restricted by an overall catch quota (Defeo, 1987, 1989). Moreover, the possibility of larval immigration from adjacent refuge populations produces "noise" in the search for an overall SRR, limiting the application of traditional population models and providing with more uncertainty in the management process.

As the recruitment pattern is erratic and complicated by the coupling of different spatial scales, short and long-term management decisions become more complex (Hilborn, 1986). In this sense, experimental management strategies with contrasting fishing effort levels, including human exclusion experiments (Cobb & Caddy, 1989, Castilla, 1990, Peterson, 1990, Defeo, 1993, this volume, Defeo et al., 1993) will be needed to provide a broad range of spawning stock sizes, to determine the approximate shape of a SRR, and thus to attenuate uncertainty in the management process. The experimental manipulation of fishing effort and the population through the closure of areas appears to be a major step forward in understanding the dynamics of coastal invertebrate populations (Castilla & Durán, 1985, Oliva & Castilla, 1986, Peterson & Summerson, 1992, Defeo, 1993, this volume), including those inhabiting exposed sandy beaches.

#### SOME BASIC QUESTIONS TO BE ADDRESSED IN THE NEAR FUTURE

The few works dealing with recruitment in exposed sandy beaches have been concentrated on short-term studies and at local spatial scales. However, the recent studies dealing with recruitment variability and its relation with the spawning stock suggest that the designation of exposed sandy beach populations as physically structured is inappropriate, or, at least, incomplete. Defeo (1993), de Alava (1993) and Defeo & de Alava (1995) showed that patterns and processes in

exposed sandy beaches appear to be scale-dependent (*sensu* Wiens, 1990), i.e., population variability in one scale (i.e. larger scale, overcompensation mechanism) may not lead to significant variability on some intermediate scale (i.e. transect scale, positive spatial bivariate of adults and recruits), but it could be reflected at the smallest scale (i.e. quadrat scale, spatial segregation between adults and recruits). Because of the scale dependence, studies in exposed sandy beach macroinfauna should be designed to incorporate a number of hierarchical scales (*sensu* Brown & Allen, 1989) in order to better understand its distribution patterns (i.e., long-term databases, larger spatial scales).

A physical - biological coupling given by the variability in reproduction and delivery of propagules, hydrodynamic conditions (waves, turbulences, currents, temperature, salinity and nutrient gradients), topography and substratum features (grain size, sorting and organic content), and biological interdependencies (competition, predation), is expected to generate significant spatial and temporal variation in pre and post-settlement mortality of sandy beach populations. However, the differential role of such processes in understanding recruitment dynamics of sandy beach populations (Defeo, 1993) has not been adequately assessed. Once again, the explicit inclusion of different space-time scales, shows an alternative approach concerning the study of population regulation and dynamics in exposed sandy beaches.

The study cases above mentioned also showed the critical role that humans could also play in explaining long-term patterns of harvested and unharvested stocks; these human-induced disturbances must be considered when evaluating the long-term variability of exposed sandy beach populations and communities (Defeo, this volume, Defeo & de Alava, 1995).

There are no explanations about the causative mechanisms that could potentially explain recruitment variability. For example, there is not enough information to verify the proposed mechanism of passive filtering of larvae out of the water column (Defeo, 1993). Because of the scarcity of field and laboratory experiments and the general lack of data, it is unclear how the conclusions

emanated from intertidal rocky and soft-bottom sheltered habitats apply to dissipative beaches. These facts emphasize the need for additional observations on the natural history and long term dynamics of exposed sandy beach populations, in order to confirm the significance of adult-larval interactions.

The dispersive abilities of planktonic larvae of the sandy beach populations are still unknown. The role of near-shore hydrodynamics in settlement/recruitment processes deserves more in depth studies in populations of sandy beaches. Studies of the planktonic component of the life cycle are particularly important to determine the scales at which the population dynamics is to be considered as an open process (see also Wade, 1968, Ansell, 1983, Defeo, 1993). This topic has crucial importance to define if exposed sandy beach populations could be considered as self-sustaining, with relative isolation of the rest of the species distribution. The inclusion of physical-oceanographic information related to larval dispersal would be of importance in this context.

It will be desirable to evaluate the incidence of environmental variables in explaining recruitment variability through space and time. Up to now, the absence of long data series and the intricate combination of regulatory mechanisms make the evidences only fragmentary. A time series of recruitment and spawning stock estimates, together with a set of appropriate environmental variables that may affect this relationship, may be useful to predict recruitment levels.

Multivariate analyses traditionally performed in studies of sandy beach populations and communities only provide a framework within which to focus on those variables that are most likely to be important in understanding the observed patterns of the species distribution, but not a cause-effect relationship between stock and recruitment abundance and environmental variables. Scale-dependent experimental manipulations of population density are needed to test specific questions on this important topic.

Fisheries development in exposed sandy beaches might determine a considerable amount of technological effects that impact not only the targeted species, but also the magnitude and strength of ecological

interdependencies as well (Defeo & de Alava, 1995). Thus, it will be desirable to know about by-catch processes and ecological-side effects of fishing, as well as the magnitude of habitat modification as a result of the harvesting process. Ecological field experiments, including the exclusion of humans as top predators, will be needed to quantify these effects.

#### ACKNOWLEDGMENTS

Financial support by Instituto Nacional de Pesca of Uruguay, Centro de Investigación y Estudios Avanzados del IPN, Mérida (México) CSIC Uruguay and CONICYT-Uruguay (Project N° 1018) is acknowledged.

#### LITERATURE CITED

- ANDRE C & R ROSENBERG (1991) Adult-larval interactions in the suspension-feeding bivalves *Cerastoderma edule* and *Mya arenaria*. *Marine Ecology Progress Series* 71: 227-234.
- ANDRE C, PR JONSSON & M LINDEGARTH (1993). Predation on settling bivalve larvae by benthic suspension feeders: the role of hydrodynamics and larval behaviour. *Marine Ecology Progress Series* 97: 183-192.
- ANSELL AD (1983) The biology of the genus *Donax*. In McLachlan A & T Erasmus (eds) *Sandy beaches as ecosystems*: 607-636. The Hague, W. Junk.
- ARNTZ WE, T BREY, J TARAZONA & A ROBLES (1987) Changes in the structure of a shallow sandy-beach community in Peru during an El Niño event. In Payne AI, JA Gulland & KH Bink (eds) *The Benguela and comparable ecosystems*. *South African Journal of Marine Science*: 645-658.
- BALLY R (1983a). Factors affecting the distribution of organisms in the intertidal zones of sandy beaches. In McLachlan A & T Erasmus (eds) *Sandy beaches as ecosystems*: 391-403. The Hague, W. Junk.
- BALLY R (1983b) Intertidal zonation on sandy beaches of the west coast of South Africa. *Cahiers de Biologie Marine* 24: 85-103.
- BARNES RB & AM WENNER (1968) Seasonal variation in the sand crab *Emerita analoga* (Decapoda Hippidae) in the Santa Barbara area of California. *Limnology and Oceanography* 13: 465-475.
- BARRY JP & PK DAYTON (1991) Physical heterogeneity and the organization of marine communities. In Kolasa J & STA Pickett (eds) *Ecological heterogeneity*: 270-320. Springer-Verlag, Berlin.
- BLACK R & CH PETERSON (1988) Absence of preemption and interference competition for space between large suspension-feeding bivalves and smaller infaunal macroinvertebrates. *Journal of Experimental Marine Biology and Ecology* 120: 183-198.
- BOTSFORD LW (1986a) Population dynamics of Dungeness crab (*Cancer magister*). In: Jamieson GS & N Bourne (eds) *North Pacific Workshop on stock assessment and management of invertebrates*. Canadian Special Publication of Fisheries and Aquatic Sciences 92: 140-153.
- BOTSFORD LW (1986b) Effects of environmental forcing on age - structured populations: northern California Dungeness crab (*Cancer magister*) as an example. *Canadian Journal of Fisheries and Aquatic Sciences* 43: 3245-2352.
- BRANCH GM (1984) Competition between marine organisms: ecological and evolutionary implications. *Oceanography and Marine Biology Annual Review* 22: 429-593.
- BRENCHLEY GA (1982) Mechanisms of spatial competition in marine soft-bottom communities. *Journal of Experimental Marine Biology and Ecology* 60: 17-33.
- BROWN AC (1983) The ecophysiology of sandy beach animals - a partial review. In: McLachlan A & T Erasmus (eds) *Sandy beaches as ecosystems*: 575-605. The Hague, W. Junk.
- BROWN AC & A McLACHLAN (1990) *Ecology of sandy shores*. Elsevier, Amsterdam.
- BROWN BJ & TFF ALLEN (1989) The importance of scale in evaluating herbivory impacts. *Oikos* 54: 189-194.
- BUTMAN CA (1987) Larval settlement of soft-sediment invertebrates: the spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamical processes. *Oceanography and Marine Biology Annual Review* 25: 113-165.
- CADDY JF (1966) Some aspects of the biology of *Macoma balthica* (L.). Ph.D. Dissertation, University of London: 284 pp.
- CADDY JF (1986) Modelling stock-recruitment processes in crustacea: some practical and theoretical perspectives. *Canadian Journal of Fisheries and Aquatic Sciences* 43: 2330-2344.
- CADDY JF (1989a) A perspective on the population dynamics and assessment of scallop fisheries, with special reference to the sea scallop *Placopecten magellanicus* Gmelin. In Caddy JF (ed) *Marine invertebrate fisheries: their assessment and management*: 559-590. J. Wiley & Sons, New York.
- CADDY JF (1989b) Recent developments in research and management for wild stocks of bivalves and gastropods. In Caddy JF (ed) *Marine invertebrate fisheries: their assessment and management*: 665-700. J. Wiley & Sons, New York.
- CAFFEY HM (1985) Spatial and temporal variation in settlement and recruitment of intertidal barnacles. *Ecological Monographs* 55: 313-332.
- CAPUTI N (1993) Aspects of the stock-recruitment relationships, with particular reference to crustacean stocks; a review. *Australian Journal of Marine and Freshwater Research* 44: 589-607.
- CASTILLA JC & R DURAN (1985) Human exclusion from the rocky intertidal zone of Central Chile: the effects on *C. concholepas* (Mollusca: Gastropoda: Muricidae). *Oikos* 45:391-399.
- CASTILLA JC (1990) La problemática de la repoblación de mariscos en Chile: diagnóstico, estrategias y ejemplos. *Investigaciones Pesqueras* 35: 41-48.
- COBB JS & JF CADDY (1989) The population biology of decapods. In: Caddy JF (ed) *Marine invertebrate fisheries: their assessment and management*: 327-374. J. Wiley & Sons, New York.
- COE WR (1953) Resurgent populations of littoral marine invertebrates and their dependence on ocean currents and tidal currents. *Ecology* 34: 225-229.
- COE WR (1956) Fluctuations in populations of littoral marine invertebrates. *Journal of Marine Research* 15: 212-232.
- CONNELL JH (1961) The influence of interspecific competition and other factors on the distribution of

- the barnacle *Chthamalus stellatus*. *Ecology* 42: 710-723.
- CONNELL JH (1963) Territorial behavior and dispersion in some marine invertebrates. *Research in Population Ecology* 5: 87-101.
- CONNELL JH (1985) The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *Experimental Marine Biology and Ecology* 93: 11-45.
- COOKE JG (1984) Glossary of technical terms. In May RM (ed) *Exploitation of marine communities*: 341-348. Springer-Verlag, Berlin.
- CRISP DJ (1984) Overview of research on marine invertebrate larvae, 1940 - 1980. In Costlow JD & RC Tipper (eds) *Marine biodeterioration: an interdisciplinary study*. Naval Institute Press, Annapolis: 103-126.
- CRISP DJ & EW KNIGHT-JONES (1953) The mechanism of aggregation in barnacle populations. *Journal of Animal Ecology* 22: 360-362.
- CROKER RA & EB HATFIELD (1980) Space partitioning and interactions in an intertidal sand-burrowing amphipod guild. *Marine Biology* 61: 79-88.
- CROKER RA, RP HAGER & KJ SCOTT (1975) Macroinfauna of northern New England marine sand. II. Amphipod dominated intertidal communities. *Canadian Journal of Zoology* 53: 42-51.
- CROWE WA, AB JOSEFSON & I SVANE (1987) Influence of adult density on recruitment into soft sediments: a short-term *in situ* sublittoral experiment. *Marine Ecology Progress Series* 41: 61-69.
- CROWL TA & GD SCHNELL (1990) Factors determining population density and size distribution of a freshwater snail in streams: effect of spatial scale. *Oikos* 59: 359-367.
- CUBIT J (1969) Behaviour and physical factors causing migration and aggregation of the sand crab *Emerita analoga* (Stimpson). *Ecology* 50: 118-123.
- CUSHING DH (1988) The study of stock and recruitment. In: Gulland JA (ed) *Fisheries population dynamics*: 105-128. J. Wiley & Sons, New York.
- DAYTON PK (1984) Processes structuring marine communities: are they general? In: Strong Jr. DR, D Simberloff, LG Abele & AB Thistle (eds) *Ecological communities: conceptual issues and the evidence*: 181-197. Princeton University Press, Princeton.
- DAYTON PK & JS OLIVER (1980) An evaluation of experimental analyses of population and community patterns in benthic marine environments. In: Tenore KR & BC Coull (eds) *Marine benthic dynamics*: 93-120. University of South Carolina, Columbia.
- DENLEY EJ & AJ UNDERWOOD (1979) Experiments on factors influencing settlement, survival, and growth of two species of barnacles in New South Wales. *Journal of Experimental Marine Biology and Ecology* 36: 269-293.
- DE ALAVA A (1989) Dinámica poblacional y estructura espacio-temporal de *Excirolana armata* y *Excirolana braziliensis* (Isopoda: Cirolanidae) en playas del litoral atlántico uruguayo. B. Sc. Thesis, Universidad de la República, Montevideo, xvi + 112pp.
- DE ALAVA A (1993) Interdependencias ecológicas entre dos bivalvos simpátricos en una playa arenosa de la costa atlántica uruguayo. M.Sc. Thesis, Cinvestav Mérida, México, xi + 75 pp.
- DE ALAVA A & O DEFEO (1991) Distributional pattern and population dynamics of *Excirolana armata* (Isopoda: Cirolanidae) in a uruguayan sandy beach. *Estuarine, Coastal and Shelf Science* 33: 433-444.
- DEFEO O (1987) Consideraciones sobre la ordenación de una pesquería en pequeña escala. *Biología Pesquera* 16: 47-62.
- DEFEO O (1989) Development and management of artisanal fishery for yellow clam *Mesodesma mactroides* in Uruguay. *Fishbyte* 7: 21-25.
- DEFEO O (1993) The effect of spatial scales in population dynamics and modelling of sedentary fisheries: the yellow clam *Mesodesma mactroides* of an Uruguayan exposed sandy beach. Doctoral Dissertation, CINVESTAV-IPN Unidad Mérida, México: xxi + 308 pp.
- DEFEO O & A DE ALAVA (1995) Effects of human activities on long-term trends in sandy beach populations: the wedge clam *Donax hanleyanus* in Uruguay. *Marine Ecology Progress Series* 123: 73-82.
- DEFEO O, C LAYERLE & A MASELLO (1986) Spatial and temporal structure of the yellow clam *Mesodesma mactroides* (Deshayes, 1854) in Uruguay. *Medio Ambiente* 8(1): 48-57.
- DEFEO O, E ORTIZ & JC CASTILLA (1992) Growth, mortality and recruitment of the yellow clam *Mesodesma mactroides* in Uruguayan beaches. *Marine Biology* 114: 429-437.
- DEFEO O, A DE ALAVA, V VALDIVIESO & JC CASTILLA (1993) Historical landings and management options for the genus *Mesodesma* in coasts of South America. *Biología Pesquera* 22: 41-54.
- DE VILLIERS G (1975) Growth, population dynamics, a mass mortality and arrangement of white sand mussels, *Donax serra* Röding, on beaches in the south-western Cape Province. Investigation Report. Sea Fisheries, South Africa 109: 1-131.
- DONN TE (1990) Zonation patterns of *Donax serra* Röding (Bivalvia: Donacidae) in southern Africa. *Journal of Coastal Research* 6: 903-911.
- EFFORD IE (1970) Recruitment to sedentary marine populations as exemplified by the sand crab, *Emerita analoga* (Decapoda, Hippidae). *Crustaceana* 18: 293-308.
- ERTMAN SC & PA JUMARS (1988) Effects of siphonal currents on settlement of inert particles and larvae. *Journal of Marine Research* 46: 797-813.
- FOGARTY MJ (1989) Forecasting yield and abundance of exploited invertebrates. In Caddy JF (ed) *Marine invertebrate fisheries: their assessment and management*. 710-724. J. Wiley & Sons, New York.
- FOGARTY MJ, MP SISSEWINE & EW COHEN (1991) Recruitment variability and the dynamics of exploited marine populations. *Trends in Ecology and Evolution* 6: 241-246.
- FOGARTY MJ, AA ROSENBERG, & MP SISSEWINE (1992) Fisheries risk assessment, sources of uncertainty. A case study of Georges Bank haddock. *Environmental Science & Technology* 26: 440-447.
- FRECHETTE M & D LEFAIVRE (1990) Discriminating between food and space limitation in benthic suspension feeders using self-thinning relationships. *Marine Ecology Progress Series* 65: 15-23.
- GAINES SD & J ROUGHGARDEN (1985) Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. *Proceedings of the Natural Academy of Sciences (USA)* 82: 3707-3711.
- GROSBURG RK (1981) Competitive ability influences habitat choice in marine invertebrates. *Nature* 290: 700-702.
- GROSBURG RK (1982) Intertidal zonation of barnacles: the influence of planktonic zonation of larvae on vertical distribution of adults. *Ecology* 63: 894-899.
- GÜNTHER CP (1992) Dispersal of intertidal invertebrates: a strategy to react to disturbances of different scales? *Netherlands Journal of Sea Research* 30: 45-56.

- HALL MA (1983) A spatial approach to the population dynamics of the manila clam (*Tapes philippinarum*). Ph.D. Thesis, University of Washington, 244pp.
- HANCOCK DA (1973) The relationship between stock and recruitment in exploited invertebrates. *Rapports et Procès-Verbaux des Réunions Conseil International pour l'Exploration de la Mer* 164: 113-131.
- HANCOCK DA (1979) Population dynamics and management of shellfish stocks. *Rapports et Procès-Verbaux des Réunions Conseil International pour l'Exploration de la Mer* 175: 8-19.
- HILBORN R (1986) A comparison of alternative harvest tactics for invertebrate fisheries. In: Jamieson GS & N Bourne (eds) North Pacific Workshop on stock assessment and management of invertebrates. Canadian Special Publication of Fisheries and Aquatic Sciences 92: 313-317.
- HILBORN R & CJ WALTERS (1992) Quantitative fisheries stock assessment. Choice, dynamics and uncertainty. Chapman & Hall, New York.
- HILL AE (1991) Advection-diffusion-mortality solutions for investigating pelagic larval dispersal. *Marine Ecology Progress Series* 70: 117-128.
- HOLM ER (1990) Effects of density-dependent mortality on the relationship between recruitment and larval settlement. *Marine Ecology Progress Series* 60: 141-146.
- HUGHES TP (1990) Recruitment limitation, mortality, and population regulation in open systems: a case study. *Ecology* 71: 12-20.
- JARAMILLO E (1987a) Community ecology of Chilean sandy beaches. Ph.D. Thesis, University of New Hampshire, 179pp.
- JARAMILLO E (1987b) Sandy beach macroinfauna from the Chilean coast: zonation patterns and zoogeography. *Vie et Milieu* 37: 165-174.
- JARAMILLO E, M PINO, L FILUN & M GONZALEZ (1994) Longshore distribution of *Mesodesma donacium* (Bivalvia: Mesodesmatidae) on a sandy beach of South Chile. *The Veliger* 37: 192-200.
- JENSEN KT & LD KRISTENSEN (1990) A field experiment on competition between *Corophium volutator* (Pallas) and *Corophium arenarium* Crawford (Crustacea: Amphipoda): effects on survival, reproduction and recruitment. *Journal of Experimental Marine Biology and Ecology* 137: 1-24.
- KEOUGH MJ & BJ DOWNES (1982) Recruitment of marine invertebrates: the role of active larval choices and early mortality. *Oecologia (Berl.)* 54: 348-352.
- LASIAK T (1991) The susceptibility and/or resilience of rocky littoral molluscs to stock depletion by the indigenous coastal people of Transkei, southern Africa. *Biological Conservation* 56: 245-264.
- LEVIN LA (1984) Life history and dispersal patterns in a dense infaunal polychaete assemblage: community structure and response to disturbance. *Ecology* 65: 1185-1200.
- LEVIN LA (1986) The influence of tides on larval availability in shallow waters overlaying a mudflat. *Bulletin of Marine Science* 39:224-233.
- LOOSANOFF VL (1966) Time and intensity of setting of the oyster, *Crassostrea virginica*, in Long Island Sound. *Biological Bulletin* 130: 211-227.
- MANN R (1986) Sampling of bivalve larvae. In: Jamieson GS & N Bourne (eds) North Pacific Workshop on stock assessment and management of invertebrates. Canadian Special Publication of Fisheries and Aquatic Sciences 92: 107-116.
- MARELLI DC (1990) Recruitment of the estuarine soft-bottom bivalve *Polymesoda caroliniana* and its influence on the vertical distribution of adults. *Veliger* 33: 222-229.
- MAURER D (1983) The effect of an infaunal suspension feeding bivalve *Mercenaria mercenaria* (L.) on benthic recruitment. *P.S.Z.N.I. Marine Ecology* 4: 263-274.
- McLACHLAN A (1980) Exposed sandy beaches as semi-closed ecosystems. *Marine Environmental Research* 4: 59-63.
- McLACHLAN A (1983) Sandy beach ecology - a review. In: McLachlan A & T Erasmus (eds) Sandy beaches as ecosystems: 321-380. The Hague, W. Junk.
- McLACHLAN A (1988) Behavioural adaptations of sandy beach organisms: an ecological perspective. In: Chelazzi G & M VANNINI (eds) Behavioral adaptation to intertidal life: 449-475. Plenum Publishing Corporation.
- McLACHLAN A (1990) Dissipative beaches and macrofauna communities on exposed intertidal sands. *Journal of Coastal Research* 6: 57-71.
- McLACHLAN A & CG BATE (1983) Sandy beach ecology - Workshop report. In: McLachlan A & T Erasmus (eds) Sandy beaches as ecosystems: 569-572. The Hague, W. Junk.
- McLACHLAN A & P HESP (1984) Faunal response to morphology and water circulation of a sandy beach with cusps. *Marine Ecology Progress Series* 19: 133-144.
- McLACHLAN A, E JARAMILLO, T DONN & F WESSELS (1993) Sandy beach macrofauna communities and their control by the physical environment: a geographical comparison. *Journal of Coastal Research* 15: 27-38.
- MENGE BA (1991) Relative importance of recruitment and other causes of variation in rocky intertidal community structure. *Journal of Experimental Marine Biology and Ecology* 146: 69-100.
- MENGE BA & JP SUTHERLAND (1987) Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *American Naturalist* 130: 730-757.
- MIKKELSON PS (1981) A comparison of two Florida populations of the coquina clam, *Donax variabilis* Say, 1822. (Bivalvia: Donacidae). I. Intertidal density, distribution and migration. *The Veliger* 23: 230-239.
- MILEIKOVSKY SA (1971) Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a reevaluation. *Marine Biology* 10: 193-213.
- MÖLLER P (1986) Physical factors and biological interactions regulating infauna in shallow boreal areas. *Marine Ecology Progress Series* 30: 33-47.
- OLAFSSON EB (1988) Inhibition of larval settlement to a soft bottom benthic community by drifting algal mats: an experimental test. *Marine Biology* 97: 571-574.
- OLAFSSON EB (1989) Contrasting influences of suspension-feeding and deposit-feeding populations of *Macoma balthica* on infaunal recruitment. *Marine Ecology Progress Series* 55: 171-179.
- OLIVA D & JC CASTILLA (1986) The effect of human exclusion on the population structure of keyhole limpets *Fisurella crassa* and *Fisurella limbata* on the coast of central Chile. *Marine Ecology* 7: 201-217.
- OLSON RR (1985) The consequences of short-distance larval dispersal in a sessile marine invertebrate. *Ecology* 66: 30-39.
- ORENSANZ JM (1986) Size, environment, and density: regulation of a scallop stock and its management implications. In: Jamieson GS & N Bourne (eds) North Pacific Workshop on stock assessment and management of invertebrates. Canadian Special Publication of Fisheries and Aquatic Sciences 92: 195-227.

- ORENSANZ JM, AM PARMA, & OO IRIBARNE (1991) Population dynamics and management of natural stocks. In: Shumway SE (ed) *Scallops: biology, ecology and aquaculture*. Developments in Aquaculture and Fisheries Science, 21: 625-713.
- OSMAN R, RB WHITLATCH & RN ZAJAC (1989) Effects of resident species on recruitment into a community: larval settlement versus post-settlement mortality in the oyster *Crassostrea virginica*. *Marine Ecology Progress Series* 54:61-73.
- PALMER AR & RR STRATHMANN (1981) Scale of dispersal in varying environments and its implications for life histories of marine invertebrates. *Oecologia (Berl.)* 48: 308-318.
- PASCUAL MA & H CASWELL (1991) The dynamics of a size-classified benthic population with reproductive subsidy. *Theoretical Population Biology* 39: 129-147.
- PAULY D (1980) A new methodology for rapidly acquiring basic information on tropical fish stocks: growth, mortality and stock-recruitment relationship. In: Saila SB & PM Roedel (eds) *Stock assessment for tropical small-scale fisheries: 154-172*. Proceedings International Workshop at the University of Rhode Island.
- PENN JW & N CAPUTI (1986) Spawng stock-recruitment relationships and environmental influences on the tiger prawn (*Penaeus esculentus*) fishery in Exmouth Gulf, Western Australia. *Australian Journal of Marine and Freshwater Research* 37: 491-505.
- PENN JW, NG HALL & N CAPUTI (1989) Resource assessment and management perspectives of the penaeid prawn fisheries of western Australia. In: Jamieson GS & N Bourne (eds) *North Pacific Workshop on stock assessment and management of invertebrates*. Canadian Special Publication of Fisheries and Aquatic Sciences 92: 115-140.
- PETERSON CH (1977) Competitive organization of the soft-bottom macrobenthic communities of southern California lagoons. *Marine Biology* 43: 343-359.
- PETERSON CH (1979) Predation, competitive exclusion, and diversity in the soft-sediment benthic communities of estuaries and lagoons. In: Livingston RJ (ed) *Ecological processes in coastal and marine systems: 233-264*. Plenum Press, N.Y.
- PETERSON CH (1982) The importance of predation and intraspecific competition in the population biology of two infaunal suspension-feeding bivalves, *Protothaca staminea* and *Chione undatella*. *Ecological Monographs* 52: 437-475.
- PETERSON CH (1990) On the role of ecological experimentation in resource management: manging fisheries through mechanistic understanding of predator feeding behaviour. In: Hughes RN (ed) *Behavioural mechanisms of food selection: 821-846*. Springer-Verlag, Berlin.
- PETERSON CH & HC SUMMERSON (1992) Basin-scale coherence of population dynamics of an exploited marine invertebrate, the bay scallop: implications of recruitment limitation. *Marine Ecology Progress Series* 90: 257-272.
- PETERSON CH & R BLACK (1987) Resource depletion by active suspension feeders on tidal flats: influence of local density and tidal elevation. *Limnology and Oceanography* 32: 143-166.
- PHILLIPS BF & RS BROWN (1989) The west australian rock lobster fishery: research for management. In Caddy JF (ed) *Marine invertebrate fisheries: their assessment and management*. 115-140. J. Wiley & Sons, New York.
- POSSINGHAM HP & J ROUGHGARDEN (1990) Spatial population dynamics of a marine organism with a complex life cycle. *Ecology* 71: 973-985.
- RAIMONDI PT (1988) Settlement cues and determination of the vertical limit of an intertidal barnacle. *Ecology* 69: 400-407.
- RAIMONDI PT (1990) Patterns, mechanisms, consequences of variability in settlement and recruitment of an intertidal barnacle. *Ecological Monographs* 60: 283-309.
- RHOADS DC (1974) Organism-sediment relations on the muddy sea floor. *Oceanography and Marine Biology Annual Review* 12: 263-300.
- RHOADS DC & DK YOUNG (1970) The influence of deposit-feeding organisms on sediment stability and community trophic structure. *Journal of Marine Research* 28:150-178.
- RICKER WE (1954) Stock and recruitment. *Journal of the Fisheries Research Board of Canada* 11: 559-623.
- ROUGHGARDEN J & Y IWASA (1986) Dynamics of a metapopulation with space-limited sub-populations. *Theoretical Population Biology* 29: 235-261.
- ROUGHGARDEN J, S GAINES & Y IWASA (1984) Dynamics and evolution of marine populations with pelagic larval dispersal. In: May RM (ed) *Exploitation of marine communities: 111-128*. Springer-Verlag, Berlin.
- ROUGHGARDEN J, Y IWASA & C BAXTER (1985) Demographic theory for an open marine population with space - limited recruitment. *Ecology* 66: 54-67.
- ROUGHGARDEN J, S GAINES & H POSSINGHAM (1988) Recruitment dynamics in complex life cycles. *Science* 241: 1460-1466.
- SAILA SB, CW RECKSID & MH PRAGER (1988) Basic fishery science programs. A compendium of micro-computer programs and manual of operation. *Developments in aquaculture and fishery science* 18. Elsevier, Amsterdam. 230 pp.
- SASTRE MP (1985) Aggregated patterns of dispersion in *Donax denticulatus*. *Bulletin of Marine Science* 36: 220-224.
- SHELTEMA RS (1974) Biological interactions determining larval settlement of marine invertebrates. *Thalassia Jugoslavica* 10: 263-296.
- SHELTEMA RS (1986) On dispersal and planktonic larvae of benthic invertebrates: an eclectic overview and summary of problems. *Bulletin of Marine Science* 39: 290-322.
- SHELTEMA RS, IP WILLIAMS, MA SHAW & C LOUDON (1981) Gregarious settlement by the larvae of *Hydroides dianthus* (Polychaeta: Serpulidae). *Marine Ecology Progress Series* 5: 69-74.
- SHEPHERD JG (1982) A versatile new stock-recruitment relationship for fisheries, and the construction of sustainable yield curves. *Journal du Conseil International pour l' Exploration de la Mer* 40: 67-75.
- SINCLAIR M (1987) *Marine populations*. Univ. Washington Press, Seattle.
- SISSEWINE M, MJ FOGARTY & WJ OVERHOLTZ (1988) Some fisheries management implications of recruitment variability. In: Gulland JA (ed) *Fisheries population dynamics: 129-152*. J. Wiley & Sons, New York.
- SOLOW AR (1990) Testing for density dependence: a cautionary note. *Oecologia (Berl.)* 83: 47-49.
- STRATHMANN RR (1974) The spread of sibling larvae of sedentary marine invertebrates. *American Naturalist* 108: 29-44.
- STRATHMANN RR (1986) What controls the type of larval development? Summary statement for the evolution session. *Bulletin of Marine Science* 39: 616-622.
- SUTHERLAND JP (1990) Recruitment regulates demographic variation in a tropical intertidal barnacle. *Ecology* 71: 955-972.

- TANG Q (1985) Modification of the Ricker stock recruitment model to account for environmentally induced variation in recruitment with particular reference to the blue crab fishery in Chesapeake Bay. *Fisheries Research* 3: 13-21.
- THORSON G (1950) Reproduction and larval ecology of marine invertebrates. *Biological Review* 25: 1-45.
- THORSON G (1966) Some factors influencing the recruitment and establishment of marine benthic communities. *Netherlands Journal of Sea Research* 3: 267-293.
- THRUSH SF (1991) Spatial patterns in soft-bottom communities. *Trends in Ecology and Evolution* 6: 75-79.
- TODD CD & RW DOYLE (1981) Reproductive strategies of marine benthic invertebrates: a settlement timing hypothesis. *Marine Ecology Progress Series* 4: 75-83.
- TREMBLAY MJ & M SINCLAIR (1990) Sea scallop larvae *Placopecten magellanicus* on Georges Bank: vertical distribution in relation to water column stratification and food. *Marine Ecology Progress Series* 61: 1-15.
- TREMBLAY MJ & M SINCLAIR (1992) Planktonic sea scallop larvae (*Placopecten magellanicus*) in the Georges Bank region: broadscale distribution in relation to physical oceanography. *Canadian Journal of Fisheries Aquatic Sciences*. 49: 1597-1615.
- UNDERWOOD AJ & EJ DENLEY (1984) Paradigms, explanations and generalizations in models for the structure of intertidal communities on rocky shores. In: Strong DR et al. (eds) *Ecological communities: conceptual issues and the evidence*. 151-180. Princeton University Press, Princeton.
- WADE BA (1968) Studies on the biology of the West Indian beach clam, *Donax denticulatus* Linne. 2. Life history. *Bulletin of Marine Science* 18: 876-901.
- WIENS JA (1990) Spatial scaling in ecology. *Functional Ecology* 3: 385-397.
- WILLIAMS JG (1980) The influence of adults on the settlement of spat of the clam, *Tapes japonica*. *Journal Marine Research* 38: 729-741.
- WILSON WH (1981) Sediment-mediated interactions in a densely populated infaunal community: the effects of the polychaete *Abarenicola pacifica*. *Journal of Marine Research* 39: 735-748.
- WILSON WH (1983) The role of density dependence in a marine infaunal community. *Ecology* 64: 295-306.
- WILSON WH (1984) An experimental analysis of spatial competition in a dense infaunal community: the importance of relative effects. *Estuarine, Coastal and Shelf Science* 18: 673-684.
- WILSON WH (1991) Competition and predation in marine soft-sediment communities. *Annual Reviews in Ecology and Systematics* 21: 221-241.
- WOOLDRIDGE T (1981) Zonation and distribution of the beach mysid, *Gastrosaccus psammodytes*. *Journal of Zoology, London* 193: 183-189.
- WOODIN SA (1976) Adult-larval interactions in dense infaunal assemblages: patterns of abundance. *Journal of Marine Research* 34: 25-41.
- WOODIN SA (1986) Direct observations of field swimming behavior in larvae of the colonial ascidian, *Ecteinascidia turbinata*. *Bulletin of Marine Science* 39: 279-289.