Factors affecting settlement and post-settlement processes in littoral marine fishes, focusing on Aidablennius sphynx

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FACTORS AFFECTING SETTLEMENT AND POST-SETTLEMENT PROCESSES IN LITTORAL MARINE FISHES, FOCUSING ON AIDABLENNIUS SPHYNX

A dissertation submitted to the SWISS FEDERAL INSTITUTE OF TECHNOLOGY ZURICH for the degree of Doctor of Natural Sciences

presented by Ulrike Zika
Dipl. Natw. ETH citizen of Austria

accepted on the recommendation of Prof. Dr. A. Zehnder, examiner Dr. A. Peter, co-examiner Prof. Dr. E. Macpherson, co-examiner

1999
To the 740 sacrificed blennies,
may it aid their species.
# Table of contents

Summary ....................................................................................................................... 5

Zusammenfassung ......................................................................................................... 7

Chapter 1 Introduction ................................................................................................. 9

Chapter 2 Defining and sampling settlement and recruitment:  
A conceptual approach for reef fish ecology ......................................................... 14

Chapter 3 The influence of physical and oceanographic parameters on  
settlement of littoral fish ......................................................................................... 28

Chapter 4 Temporal and spatial variability of settlement success and recruitment  
level in three blennoid fishes in the northwestern Mediterranean ............... 48

Chapter 5 The importance of unaliased time series of settlement to estimate  
post-settlement losses ............................................................................................. 74

Chapter 6 Nutritional status, body size, and abundance of settlers and their  
implications on post-settlement survival ............................................................... 98

Chapter 7 'Recruitment limitation' or 'competition regulation'?  
The case of a temperate, rocky shore fish ............................................................. 114

Chapter 8 References ............................................................................................... 120

Acknowledgements .................................................................................................. 140

Curriculum vitae ....................................................................................................... 142
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Zika, U., T. Granata, and E. Macpherson The influence of physical and oceanographic parameters on settlement of littoral fish. Limnology and Oceanography (Chapter 3)

Zika, U., E. Macpherson, and G. Agell The importance of unaliased time series of settlement to estimate post-settlement losses. Ecology (Chapter 5)

Zika, U., T. C. Granata and E. Macpherson Nutritional status, body size, and abundance of settlers and their implications on post-settlement survival. Marine Ecology Progress Series (Chapter 6)

One manuscript is in preparation:

Zika, U. and E. Macpherson 'Recruitment limitation' or 'competition regulation'? The case of a temperate, rocky shore fish. Trends in Ecology and Evolution (Chapter 7)
Summary

Most littoral marine fishes have a pelagic stage, usually larval, resulting in a life history with two distinct phases. The pelagic and littoral stages differ in almost all characteristics and settlement is the process that connects the pelagic to the littoral phase. The focus of this work was to investigate: 1) if larval input (settlement) is the limiting factor for local populations and if variation in larval supply is reflected by subsequent variation in juvenile densities (i.e. recruitment limitation); or 2) if processes onshore (i.e. post-settlement processes) regulate juvenile densities.

Factors affecting settlement and post-settlement processes, and their impact on populations, were quantified, compared, and assessed. The study species, the rocky shore fish Aidablennius sphynx (family Blenniidae), is a typical representative of temperate fish and one of the most common species along the Mediterranean coast. Settlement and survival were measured in the NW Mediterranean littoral zone by daily collections and weekly observations, respectively, for three settlement seasons (1996 - 1998).

The variability in settlement was a result of spatial and temporal differences in the pelagic environment and physiological differences (morphological and nutritional) in the characteristics of pelagic larvae. Settlement patterns reflected the high variability in the pelagic stage. On large to intermediate scales (100 km - 10 m), no spatial differences in settlement were found. On small spatial scales (1 m), the maximum density of settlers only depended on the availability of the preferred substrate. To resolve temporal patterns, the frequency of post-settlement losses defines how frequent settlement needs to be sampled. For A. sphynx, no daily losses or diel cycles in settlement were found. Time series of daily settlement were correlated with oceanographic events occurring before and during the seasons. On the largest scales, mesoscale processes, including eddies and shelf-slope fronts, determined the duration of settlement seasons and probably also regulated settlement on geographic scales. On intermediate scales, settlers arrived in episodic peaks enhanced by physical transport mechanisms, especially waves, which probably aided onshore transport of larvae.

Differences between settlement and survivor time series showed post-settlement losses were density-dependent until a carrying capacity was reached and thereafter, were density-independent of numbers surviving. Physiological characteristics were only weakly related to post-settlement survival. These two findings suggest pelagic and benthic processes are decoupled. Contrary to the general belief in reef fish ecology, densities of A. sphynx are not recruitment limited since littoral habitat is saturated.
Instead, intraspecific competition is the most likely factor regulating population dynamics.
Zusammenfassung


1. Introduction

Ecologist are generally interested in demographic processes which influence population dynamics and how these demographic processes themselves are influenced by environmental factors. Ecological theories in population and community dynamics mainly focus on organisms with a simple life cycle, however, most organisms have a complex life cycle with at least two stages (Roughgarden et al. 1988). Dispersal is a strategy used by many plants and animals on land and in water to either escape or discover an environment during a phase of their life (Begon et al. 1990). Consequently, dispersal and subsequent settlement can have a significant influence on the dynamics of populations. Given that developmental stages could be dispersed over large geographic areas, it is crucial to understand scale and coupling among these spatially separated sites (Roughgarden et al. 1988), as well as the temporal and spatial scales of underlying processes.

THE LIFE-CYCLE OF LITTORAL, MARINE FISHES

Most littoral, marine fish have a dispersal stage, usually larval, resulting in a life history with two distinct and very different phases (Roughgarden et al. 1988, Hughes 1990, Sale 1991) (Fig. 1.1). The pelagic phase and littoral phase differ in almost all characteristics, from the morphology to the food, and the behavior of fish (e.g. Leis 1991a, McCormick and Makey 1997). Settlement connects the pelagic to the littoral phase and is defined as the arrival of a new individual from the pelagic to the benthic habitat with a transition from a planktonic larvae to a benthic juvenile.

Pelagic phase

The pelagic phase begins when eggs or larvae are transported offshore. Developing larvae may seek food and protection from benthic predators in offshore waters with some water masses being more favorable than others for development (Doherty and Fowler 1994). Once in offshore waters, larvae may be dispersed by prevailing currents to new locations far from the spawning sites of the parental population (Bailey 1981, Leis 1986, Bailey et al. 1997). Geographical barriers, retention features, and high mortality rates of dispersed larvae are likely to restrict gene flow as a result of larval drift (Bailey et al. 1997). Larvae and pelagic juveniles of reef fishes have been found distributed from waters over a coral reef (Leis 1991a) to the open ocean many hundreds of kilometers from any reef (Leis 1986, Victor 1987), therefore, pre-settlement losses are mainly caused by pelagic processes (Doherty 1991, Jones 1991).
To compensate for these losses, large numbers of offspring are produced to spread the risk over repeated spawning events (Begon et al. 1990).

Fig. 1.1. Life-cycle of a marine, rocky shore fish.

**Littoral phase**

The transition of fish larvae into benthic, reef-associated populations can be extremely variable in space and time (Underwood and Fairweather 1989, Sale 1990, Doherty 1991). If larvae are transported and settle far from their spawning grounds, local settlement of individuals into the adult habitat is decoupled from the reproductive activity of the parental population (Doherty and Fowler 1994). Of particular importance to the settlement process is the blend of passive transport and active swimming responses to water flow near the settlement habitat (Breitburg et al. 1995). Thus, settlement patterns may depend upon large scale processes, such as ocean currents or tides, as well as other physical and biological processes (Kingsford et al. 1991, Leis 1991a, Breitburg et al. 1995). Individuals surviving some arbitrary time after settlement are referred to as recruits (Connell 1985). In this study, individuals are recruits when they join the adult population (García-Rubies and Macpherson 1995). The small scale processes that influence settlement and recruitment are microhabitat selection (Sale et al. 1984, Carr 1994, Macpherson 1994, García-Rubies and Macpherson 1995, Tolimieri 1995) and the presence or absence of resident organisms, especially conspecifics (Sweatman 1988, Sweatman and St. John 1990).

Most of the studies on settlement and recruitment have been carried out on coral reefs and are therefore strongly influenced by the characteristics of these tropical and subtropical systems. Temperate reefs and coastal zones globally provide large areas of habitat for benthic marine fishes. The habitat in temperate zones is usually more continuous and homogenous than corals, but is characterized by a much higher seasonality (Eberling and Hixon 1991, Carr 1994). Temperate, marine fishes typically settle or recruit in pulses, usually in the spring and summer months (Doherty 1991, Kneib 1993, García-Rubies and Macpherson 1995, Secor and Houde 1995). Although there may be well-defined peaks in settlement and recruitment, e.g. schooling by larvae prior to settlement (Breitburg 1989, Macpherson et al. 1997), these processes can last for periods of months. This spread could be a result of variation in timing of spawning, variation in the duration in the plankton, differential survival during the pelagic stage, or a combination of all these (Pfister 1997).
OBJECTIVES OF THE DISSERTATION

The objectives of this dissertation were to define which factors affect settlement and post-settlement processes of a littoral, marine fish with two distinct life history stages. The blenny *Aidablennius sphynx* was chosen as a study species for three reasons: 1) the family Blenniidae is cosmopolitan, with tropical and temperate representatives, which facilitates comparisons of temperate and tropical studies; 2) Blennies are one of the most abundant families in the Mediterranean littoral (Corbera et al. 1996); and 3) *A. sphynx* is the most abundant blenny. All the above makes *A. sphynx* a logical study species and a model for settlement and post-settlement. Data on settlement and recruitment of benthic coastal fishes, especially in the Mediterranean Sea, are scarce (Vigliola et al. 1998). Most of the Mediterranean blenniid species live in the upper littoral and, since there are very low amplitude tides (< 10 cm amplitudes) (Albérola et al. 1995), settlers are restricted to a rather narrow intertidal zone which simplifies sampling. Consequently, this work was conducted along the rocky shore of the Northwestern Mediterranean Sea (Spanish coast). Although they are so frequent in littoral waters, very little is known of the ecological role of blennies. This study should lead to a better understanding of settlement and post-settlement processes in general, since many factors influencing the study species could apply to other marine fishes, especially in temperate zones.

Factors studied

To determine the influence of settlement and post-settlement processes on population dynamics, it is necessary to resolve settlement patterns and levels on several temporal and spatial scales. The sampling methods and frequency of sampling are dependent upon the settlement strategy of the study species. Different definitions for settlement and recruitment are used in the literature along with disparate sampling frequencies. The concept of sampling appropriate temporal scales for species with different settlement strategies is presented in Chapter 2.

Physical processes acting on the pelagic phase could impact settlement patterns. Physical and oceanographic processes occurring on different temporal and spatial scales in nearshore waters during, before, and after three settlement seasons were related to settlement patterns onshore (Chapter 3). The objective was to determine the factors linked to the high temporal variability in settlement of *Aidablennius sphynx*.

The hypothesis that habitat influences settlement success and recruitment level was tested over different spatial scales (Chapter 4). The objectives were to determine which habitat characteristics significantly influence settlement and to evaluate the importance
of spatial and temporal variations. Suitable habitats were determined for *Aidablennius sphynx* and two other species, co-occurring in the same zone.

The role settlement and post-settlement processes play in regulating population densities was studied in Chapter 5. The objectives were to evaluate if post-settlement processes are able to modify settlement patterns created by larval input, and which factors are significant for determining densities of *Aidablennius sphynx*.

Predation, starvation, competition, and risk partitioning may all influence the probability of post-settlement survival. The hypothesis that nutritional status, body size, and numbers of settlers are related to settlement and subsequent post-settlement survival was evaluated in Chapter 6.

The overall conclusions (Chapter 7) integrate the factors affecting settlement and post-settlement processes with current ecological theories. It is suggested that availability of suitable habitat is the determining factor for population densities of *Aidablennius sphynx*, and not larval supply as is generally believed. The necessity of future studies in habitat limitation is discussed based on appropriate sampling designs.
2. **Defining and sampling settlement and recruitment: A conceptual approach for reef fish ecology**

**ABSTRACT**

Recent articles reporting time series of settlement or recruitment were reviewed in order to determine which sampling frequencies are necessary to resolve temporal patterns of settlement and recruitment for species using different strategies. Of the studies analysed, 70% were conducted on coral reefs and 30% in littoral, temperate zones. Two dominant strategies in settlement were found. Most coral reef species show periodic cycles (lunar and diurnal) but littoral temperate species have episodic settlement. While many authors define settlement as the arrival of a pelagic larvae and its transition to a benthic juvenile, several definitions are used for recruitment. The most commonly used methods for sampling settlement and recruitment were collections and visual surveys, respectively, though sampling frequencies varied between studies.

Based on dominant settlement strategies, two model time series of settlement were analyzed, representing coral reef species (periodic) and temperate species (episodic). For periodic settlement, only 47% of the time series needed to be sampled daily around new moon to account for 80% of the settlers. In contrast, for episodic settlement, a much greater sampling effort (81% of the time series) is needed to account for 80% of the settlers.

To assess the effects of settlement and recruitment on population demography, standard definitions of settlement and recruitment are necessary to avoid overlap in time scales and to reduce confusion in the literature. For settlement, the estimation of temporal patterns requires sampling initial patterns before their alteration by post-settlement losses. Consequently, the frequency of post-settlement losses defines how often settlement needs to be sampled. The rule of thumb is to resolve the smallest temporal scale but sample long enough to encompass the whole seasonal pattern.
INTRODUCTION

The complex spatial and temporal variability in abundance of reef fish populations are not solely explainable by traditional theories of resource-based concepts of equilibrium (Doherty and Williams 1988). In fisheries, to assess population sizes, egg production is related to number of fish recruiting to the population (Hilborn and Walters 1992). However, this relationship only applies in closed systems where mortality is either density- or stock-dependent. For example, the Beverton-Holt and Ricker models (Hilborn and Walters 1992) predict recruitment from spawning stock size in sockeye salmon in a river, where adults after their dispersal stage return to spawning grounds. Benthic reef fish have a complex life cycle also with a dispersal stage, usually larval, which ends with settlement on benthic reef habitats (Roughgarden et al. 1988, Hughes 1990, review of Sale 1991). Dispersion of larvae decouples larval supply from local populations, since larvae do not return to parental spawning grounds, making local, reef fish dynamics an open system (e.g. review of Caley et al. 1996). When onshore habitat is not limited and population densities exist below carrying capacity, a non-equilibrium situation exists where enhanced settlement should augment densities of local populations (review of Doherty 1991). This idea that densities of reef populations are limited by the rate at which larvae settle and recruit at a site is known as recruitment limitation (Doherty 1983, Victor 1986a, Doherty and Fowler 1994). If local abundances are really only limited by larval supply, survival of individuals after settlement should be completely independent of local densities and predictable from recruitment statistics (Doherty and Fowler 1994). However, post-settlement mortality was observed to be both, density independent (Doherty 1982, Victor 1986a, Levin 1994a, Doherty and Fowler 1994, Sano 1997) and density dependent (van der Veer 1986, Myers and Cadigan 1993, Macpherson et al. 1997, Schmitt and Holbrook 1999). In some species, density dependence in mortality only occurred in the first 24 hours after settlement (Hixon and Carr 1997, Caselle 1999) and therefore, infrequent sampling or back-calculation of settlement dates from otolith data may miss initial density dependence, leading to the false conclusion of density independence in post-settlement mortality (Hixon and Carr 1997). Additionally, high mortality after the first days of settlement can alter settlement patterns (e.g. Connell and Jones 1991, Tupper and Boutilier 1997, Houde 1997, Macpherson et al. 1997, Chapter 5).

Since different species experience a range of different scales in ecological systems, the key to predicting and understanding patterns in such systems lies in the knowledge of relevant scales which depend on underlying processes (Levin 1992). For the recruitment limitation model, the relevant processes are larval supply, recruitment, and post-settlement losses, which combined regulate population densities. These processes
operate on different spatial and temporal scales (e.g. Sponaugle and Cowen 1997) and
sampling defines the limits of resolution, thus acting as a filter on patterns. If the filter is
too coarse, then observations may influence the description of patterns. If the filter is
fine but too small, patterns can not be extrapolated to larger scales (Levin 1992, Sale
1998). Therefore, to determine population dynamics of reef fishes, two things must be
considered: 1) it is indispensable to define settlement and recruitment processes based on
their scales; and 2) the sampling methods, i.e. the filters used, should take into
consideration strategies of settlement and recruitment.

Spatial scales

For coral reef fish, the importance of spatial scales have been shown (e.g. Caselle
and Warner 1996) and two recent reviews (Chesson 1998, Sale 1998) discussed the
question of appropriate spatial scales for studies of reef fish ecology. The consensus of
these reviews is that reef systems are multi-scalar systems and there is no single correct
scale on which to sample, but it is important to sample spatial scales: 1) relevant to the
organisms to determine variability; 2) relevant to the population unit to resolve density
dependence; 3) relevant to the processes of interest (i.e. environment, predation, etc.);
and 4) relative to geographical regions, to resolve habitat patchiness. Generally, spatial
dependence of results must be taken into consideration. Since the recent reviews of
Chesson (1998) and Sale (1998) cover the spatial scales of settlement and recruitment,
only temporal patterns will be considered hereafter.

Temporal scales

Despite an increasing number of studies on settlement, variability in larval supply,
and recruitment of marine organisms, very little is known about whether temporal
variations in settlement have an important effect on populations (but see Jones 1990,
Doherty and Fowler 1994, Pfister 1996). Definitions of settlement and recruitment in the
literature often overlap in their time scales, which is a problem in reef fish ecology. For
recruitment, the importance of temporal scales on demographic effects has been
addressed by Robertson and Kaufmann (1998), who emphasized that frequent
monitoring (i.e. small time intervals) is necessary to estimate accurate patterns. In
addition, we should consider temporal scales of settlement which define the initial input
of larvae that later recruit to the local population. Even weekly intervals between
settlement measurements may obscure the actual mechanisms determining recruitment
patterns given the high mortality the first days after settlement (Doherty and Sale 1985,
Sampling of appropriate temporal scales in pelagic systems is well known to biological oceanographers (Müller-Karger 1990, Taylor and Howes 1994, Wiggert et al. 1994), though seldom considered for settlement studies of littoral fish. Undersampling could lead to underestimation of the role of post-settlement processes (Connell 1985, Frederick 1997) and predation (e.g. Hixon and Carr 1997, Steele 1997a, 1998). To determine these post-settlement processes, it is necessary to estimate true or unaliased patterns of settlement by frequent monitoring. This high frequency sampling must be maintained over sufficient durations to encompass the settlement (and recruitment) process. Booth (1991) concluded that frequent sampling with removal of settlers would most closely estimate true settlement rates and that less frequent censuses without removal may provide closer estimates of the size of the recruit cohort that will enter the juvenile population. Results of different studies are difficult to compare because of: 1) different strategies of species; 2) different definitions of settlement and recruitment used by authors; and 3) incongruous sampling frequencies and methods used to determine settlement and recruitment patterns. The goal of this study is to critically review the literature in order to determine which sampling frequencies are necessary to resolve temporal patterns of settlement and recruitment for species using different strategies.

SEARCH CRITERIA AND METHODS

Recent articles reporting time series of settlement or recruitment of any duration, and conducted on natural habitats, were considered. Experimental studies with manipulations of either habitat (including predator removal, adjustment of local population densities, transplanting of individuals to different habitats, manipulation of food resources, etc.) or environmental factors (i.e. chemical cues, temperature, currents) were excluded, since the purpose of this review is to focus on sampling frequencies needed to resolve natural patterns and levels of settlement and recruitment. The different sampling methods (collection of individuals versus observation), however, were not considered to modify habitat or environmental parameters.

Based on settlement strategies reported in the literature, two model patterns were proposed and analyzed. The first model was periodic settlement (lunar and diurnal) and the second episodic settlement. Both were considered for a 128 day settlement season with 330 settlers. Time series of 256 points (128 days sampled twice daily) were demeaned, detrended and a 15% taper applied. Variance-frequency distributions of time series were calculated from power spectral densities using fast Fourier transform (FFT) algorithms with a Hamming weighting (STATISTICA manual 1994). All calculations were done with STATISTICA for the Macintosh, Version 4.1.
RESULTS

Strategies of settlement and recruitment

Of the studies analysed, 70% were conducted on coral reefs. Periodicity in settlement or recruitment was reported in 48% of the coral reef studies where either lunar or semi-lunar cycles dominated, the latter connected to tidal cycles (Table 2.1). Many coral reef species had diel periodicity with settle occurring during the night (e.g. Robertson et al. 1988, Millicich et al. 1992, Dufour and Galzin 1993, Thorrold et al. 1994a) and peak settlement on the darkest nights of the new moon, which has been explained as an adaptation to reduced predation on settling fish (e.g. review of Doherty 1991).

For the 30% of the studies conducted in temperate zones, no periodicity was reported in settlement or recruitment and all showed seasonality (Table 2.1). Many species display continuous settlement or recruitment over months with conspicuous episodic peaks superimposed on lower, background fluctuations (e.g. Jenkins et al. 1997, Sano 1997, Chapter 4), which may be explained by spreading the risk of encountering unfavorable conditions between events. No day/night differences in settlement have been observed for temperate species (Breitburg 1991, Chapter 5). Clumped distributions, including schooling and shoaling behavior and transient groups, were observed for both, temperate (Breitburg 1989, 1991, Sano 1997, Macpherson 1998, Vigliola et al 1998) and coral reef species (McFarland et al. 1984, Shulman and Ogden 1987, Robertson 1988, Planes et al 1993).

Definitions and measurements of settlement and recruitment

Most authors agree that settlement is defined as the arrival of a pelagic larvace and its transition to a benthic juvenile (Table 2.1 A). The most commonly used method for estimating settlement was collection of newly settled individuals (Table 2.1 A). However, sampling frequencies for the determination of settlement vary between studies. The smallest sampling intervals were hourly, carried out by collections of individuals using permanently moored nets or manually. The largest sampling intervals were monthly observations or collections and, in some studies, the exact dates of settlement were back-calculated from otolith data.

Definitions for recruitment were highly variable and three main groups were distinguishable (Table 2.1 B). The first group includes studies in which recruitment and settlement were similarly defined, i.e. the two terms were synonymous, and had overlapping time scales (Table 2.1 B1). Individuals that arrived from the pelagic and settled into the benthic or juvenile habitat were considered recruits. The frequencies of
sampling and methods ranged from manual or net collections twice daily to twice a year. The most commonly used method for sampling recruitment was visual surveys. Back-calculations of exact settlement dates from otolith data were also done in some studies. The second group of recruitment definitions included studies where recruitment was considered to represent an arbitrary period of time that juvenile fish survived after settlement (Table 2.1 B2). This arbitrary time period ranged from 0 days to 1 year, and fish were either collected or censused. The third group lists studies that defined recruitment as the addition of a new young to the established population, based on the cohort of the year class or the fish length (Table 2.1 B3). Sampling frequencies for this group ranged from biweekly to yearly, with either collections or observations. The definitions of recruitment from groups 2 and 3 included post-settlement mortality.
Table 2.1. Definitions of A) settlement and B) recruitment; Freq. = highest sampling frequencies (sampled per days); Dur. = duration sampled for one season (days); Method, c = collection, o = observation, b = back-calculation of settlement date from otolith data; Species and strategies of fish; and Authors investigating temporal aspects in settlement and recruitment.

<table>
<thead>
<tr>
<th>Definition of:</th>
<th>Freq.</th>
<th>Dur. (days)</th>
<th>Method</th>
<th>Species and strategies</th>
<th>Authors</th>
</tr>
</thead>
<tbody>
<tr>
<td>A) Settlement</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arrival of a new individual from the pelagic to the benthic habitat and its transition from a planktonic larva into a benthic oriented juvenile</td>
<td>24/d</td>
<td>1</td>
<td>c</td>
<td>50 families CR, d, l</td>
<td>Dufour and Galzin 1993</td>
</tr>
<tr>
<td></td>
<td>12/d</td>
<td>2</td>
<td>c</td>
<td></td>
<td>Booth 1991</td>
</tr>
<tr>
<td></td>
<td>3/d</td>
<td>8</td>
<td>c</td>
<td></td>
<td>Shenker et al. 1993</td>
</tr>
<tr>
<td></td>
<td>5/d</td>
<td>2</td>
<td>o</td>
<td>Dascyllus albisella (domino damselfish) CR, d, sd, (g)</td>
<td>Thorrold et al. 1994*</td>
</tr>
<tr>
<td></td>
<td>4/d</td>
<td>75</td>
<td>c</td>
<td>53 taxa CR, 97% d, semi-l, l, some c</td>
<td>Colin et al. 1997</td>
</tr>
<tr>
<td></td>
<td>2/d</td>
<td>79</td>
<td>c</td>
<td></td>
<td>This work (Chapter 5)</td>
</tr>
<tr>
<td></td>
<td>2/d</td>
<td>2</td>
<td>c</td>
<td>Epinephelus striatus (grouper) CR, d, l, t, s</td>
<td>Robertson et al. 1988</td>
</tr>
<tr>
<td></td>
<td>2/d</td>
<td>80</td>
<td>c</td>
<td>Aulableniunys sphynx (blenny)</td>
<td>Victor 1986</td>
</tr>
<tr>
<td></td>
<td>1/d</td>
<td>20</td>
<td>c</td>
<td></td>
<td>Robertson 1992</td>
</tr>
<tr>
<td></td>
<td>2/d</td>
<td>12</td>
<td>c</td>
<td>Stegastes partitus (damselfish) CR, l, s</td>
<td>Robertson et al. 1993</td>
</tr>
<tr>
<td></td>
<td>1/d</td>
<td>365</td>
<td>c</td>
<td></td>
<td>Williams 1983</td>
</tr>
<tr>
<td></td>
<td>1/d</td>
<td>365</td>
<td>c</td>
<td>Thalassoma bifasciatum (bluehead wrasse) CR, l, (l)</td>
<td>Sale and Ferrell 1988</td>
</tr>
<tr>
<td></td>
<td>1/d</td>
<td>365</td>
<td>c</td>
<td>7 pomacentrids, 3 acanthurids, 1 labrid, 1 chaetodontid, 2 pomacanthids, and 1 canthigasterid</td>
<td>McGeehe 1995</td>
</tr>
<tr>
<td></td>
<td>1/d</td>
<td>365</td>
<td>c</td>
<td>6 Caribbean damselfishes CR, 5 species</td>
<td>Vigliola et al. 1998</td>
</tr>
<tr>
<td></td>
<td>1/d</td>
<td>49</td>
<td>o</td>
<td>pomacentrids CR, ad</td>
<td>Macpherson and Zuka 1999</td>
</tr>
<tr>
<td></td>
<td>1/2d</td>
<td>93</td>
<td>o</td>
<td>56 species CR</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1/7d</td>
<td>365</td>
<td>o</td>
<td>Stegastes planifrons, S. partitus, S. variabilis (threespot, cocoa, bicolor damselfish, resp.) CR, ad</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1/7d</td>
<td>365</td>
<td>o</td>
<td>S. leucosticus (beaugregory) CR</td>
<td></td>
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<tr>
<td></td>
<td>1/7d</td>
<td>365</td>
<td>o</td>
<td>Diplodus puntazzo, D. sargus, D. vulgaris (Sparids) TR, (s, th)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1/7d</td>
<td>98</td>
<td>o</td>
<td>Tripterygion tripteronotus (triplefin), Aulableniunys sphynx, Parableniunys incognitus (blennies)</td>
<td></td>
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<tr>
<td></td>
<td>1/8.5d</td>
<td>51</td>
<td>c (b)</td>
<td>Rhombosolea tapirina (flounder) TR, s</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1/14d</td>
<td>365</td>
<td>c (b)</td>
<td>Heteroclinus sp. (Scott's Weedfish) TR, s</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1/14d</td>
<td>90</td>
<td>c (b)</td>
<td>Sillaginodes punctatus (King George whiting) TR, s</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1/40d</td>
<td>160</td>
<td>c (b)</td>
<td>primarily pomacentrids and labrids</td>
<td>CR, l, sd</td>
</tr>
<tr>
<td></td>
<td>1/30d</td>
<td>365</td>
<td>o</td>
<td>Acanthurus bahianus, A. chirurgus, A. coeruleus (surgeonfishes) CR, l, feeding sh</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1/30d</td>
<td>365</td>
<td>o</td>
<td>Thalassoma bifasciatum (bluehead wrasse) CR, l, c, t</td>
<td></td>
</tr>
</tbody>
</table>
### B) Recruitment

1) Larvae that have ended their dispersive stage and begin their reef-associated stage (newly settled fish)

<table>
<thead>
<tr>
<th>24/d</th>
<th>8</th>
<th>c</th>
<th>120 species (50 families) CR, l, d</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-2/d</td>
<td>60</td>
<td>c</td>
<td>92 taxa</td>
</tr>
<tr>
<td>1/30</td>
<td>150</td>
<td>o</td>
<td>Thalassoma bifasciatum (bluehead wrasse) CR, l, (s)</td>
</tr>
<tr>
<td>1/d</td>
<td>3</td>
<td>c</td>
<td>(b) Sillaginodes punctata (King George whiting) TR, s</td>
</tr>
<tr>
<td>1/3d</td>
<td>57</td>
<td>c</td>
<td>(b) Sillaginodes punctata (King George whiting) TR, s</td>
</tr>
<tr>
<td>1/5d</td>
<td>365</td>
<td>o</td>
<td>Dascyllus abisella (domino damselfish) CR, g, (d, sd)</td>
</tr>
<tr>
<td>1/3d</td>
<td>236</td>
<td>o</td>
<td>Haemulon flavolineatum (French grunts) CR, semi-l, s, t, (d, not sd, sh)</td>
</tr>
<tr>
<td>1/7d</td>
<td>325</td>
<td>o</td>
<td></td>
</tr>
<tr>
<td>1/11d</td>
<td>300</td>
<td>o</td>
<td></td>
</tr>
<tr>
<td>1/60d</td>
<td>365</td>
<td>c</td>
<td>26 species of 9 families, mostly Tripterygiidae (triplefins) and Gobiesocidae (clingfishes) TR, s, sd</td>
</tr>
</tbody>
</table>

- settle into benthic juvenile habitats

- larval recruits in intertidal pools

2) Juvenile fish surviving an arbitrary period of time after settlement: 0-16 d - to the time of sampling

| 1/7d | 284 | o | Haemulon flavolineatum (French grunt) CR, d, not sd, sh, (semi-l, s) |
| 1/14d | 70 | o | Coryphopterus glaucofraenum CR, l, (s) (bridled goby), Gnatholepis thompsoni CR, l, (s) (goldspot goby) |
| 1/14d | 70 | o | Halichoeres bivittatus, H. radiatus, H. poeyi, H. garnoti, H. pictus, H. maculipinna all CR, l, t, s, and Thalassoma bifasciatum (bluehead wrasse) and "other species" CR, l |
| 1/14d | 168 | c | (b) Thalassoma bifasciatum CR, l, (t, s) (bluehead wrasse) and "other species" CR, l |
| 1/14d | 60 | o | Chaetodon rainfordi CR (butterflyfish) |
| 1/d | 365 | c | 6 species of Caribbean damselfishes CR, no s, sd |
| 1/30d | 365 | o | 6 species of Caribbean pomacentrids, 1 Pacific blenniid, and 2 Pacific damselfishes |
| 1/14d | 365 | o | 6 species of Caribbean damselfishes CR, no s, sd |
| 1/7 | 98 | o | Sagitta genetonia (annual goby) TR, g |

- anywhere from days to months - to the end of the lunar cycle in which they settled

- to the end of the settlement season

---

Dufour and Galzin 1992  
Williams and Sale 1981  
Victor 1986  
Jenkins et al. 1996*  
Jenkins et al. 1997*  
Booth 1992  
McFarland et al. 1984  
Willis and Roberts 1996  
Shulman and Ogden 1987*  
Sponaugle and Cowen 1994  
Sponaugle and Cowen 1997  
Caselle and Warner 1996  
Fowler et al. 1992  
Robertson 1992, 1995  
Robertson et al. 1993  
Robertson 1990*  
Sano 1997  
Macpherson and Zika 1999 (Chapter 4)
- to the end of the recruitment season
- one year

3) Observed addition of a new young to the established population

- juveniles more than 50% the length of post larvae size
- until recruits to adult or demersal population

- fishes smaller than 20 mm standard length

- proportion of the population represented by the year class in question

<table>
<thead>
<tr>
<th>Time</th>
<th>Event</th>
<th>Duration</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>1/365</td>
<td>160</td>
<td>c, o</td>
<td>Pomacentrus amboinensis (damselfish) CR see above</td>
</tr>
<tr>
<td>1/40d</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1/14d</td>
<td>365</td>
<td>o</td>
<td>Pomacentric damselfish: Stegastes partitus CR, s, (l) (bicolor), S. leucosticus CR, s (beaugregory), S. variabilis CR, s (cocoa), S. planifrons CR, s (3-spot), S. diencaeus CR, s (longfin); and Chromis cyanea CR, l, s (blue chromis), C. multilinea CR, l, s (brown chromis)</td>
</tr>
<tr>
<td>1/14d</td>
<td>168</td>
<td>o</td>
<td>86 taxa, CR, d but only diurnal species, sh were s, none-sh species not s</td>
</tr>
<tr>
<td>1/7d</td>
<td>365</td>
<td>o</td>
<td>24 litoral species TR, s</td>
</tr>
<tr>
<td>1/14d</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1/30</td>
<td>240</td>
<td>o</td>
<td>Ophiohilemnis atlanticus (redlip blenny) CR, s, sd</td>
</tr>
<tr>
<td>1/30d</td>
<td>365</td>
<td>o</td>
<td>Oligocottus maculosus, Clinocottus globiceps, C. embryum (intertidal sculpins) TR, s, sd</td>
</tr>
<tr>
<td>1/30d</td>
<td>365</td>
<td>o</td>
<td>families: Serranidae, Apogonidae, Chaetodontidae, Labridae, Scaridae, Acanthuridae CR</td>
</tr>
<tr>
<td>1/d</td>
<td>30</td>
<td>o</td>
<td>see above</td>
</tr>
<tr>
<td>1/42d</td>
<td>60</td>
<td>o</td>
<td></td>
</tr>
<tr>
<td>1/365d</td>
<td>365</td>
<td>o</td>
<td>Clinocottus spp. and Oligocottus spp. (tide pool sculpins) TR, s, sd</td>
</tr>
<tr>
<td>1/365</td>
<td>365</td>
<td>o, c (b)</td>
<td>Pomacentrus moluccensis (damselfish) CR, sd</td>
</tr>
<tr>
<td>1/365d</td>
<td>365</td>
<td>o, c (b)</td>
<td>Semicossyphus pulcher (sheephead) TR-CR</td>
</tr>
<tr>
<td>1/365</td>
<td>365</td>
<td>o</td>
<td>10 common species of labroids CR</td>
</tr>
</tbody>
</table>

Note: footnotes in parentheses indicate information taken from other articles; * = no explicit definition given; CR = Caribbean, coral and tropical reef fishes; TR = temperate reef fishes; d = diurnal cycle; most settle/recruit between dusk and dawn; l = lunar cycle; t = tidal cycle; s = seasonal; sd = "sedentary": little movement after settlement, inhabit restricted area; sh = schools or shoals: clumped distributions; g = transient groups

Jones 1990
Williams et al. 1994
Robertson 1988 *
Booth and Beretta 1994
Planes et al. 1993
García-Rubies and Macpherson 1995
Hunte and Côté 1989
Pfister 1997
Lewis 1997
Williams 1983
Pfister 1996
Doherty and Fowler 1994
Cowen 1985
Eckert 1984 b
Model species and sampling strategies

Since the two most common settlement strategies are periodic (diel & lunar) and episodic, simple model patterns (time series) are proposed to estimate the variability of the strategy relative to the sampling scales.

The settlement time series for a model species with lunar and diurnal periodicity, representing coral reef species, is shown in Fig. 2.1 A. Day/night cycles in settlement are superimposed on peaks during the new moon. The settlement time series for a model species with episodic settlement, representing temperate reef species, is shown in Fig. 2.1 B. No difference in day/night settlement exists and peaks are random throughout the season.

![Settlement time series and variance-frequency distributions](image)

Fig. 2.1. Settlement time series for model species with A) lunar and diurnal periodicity, representing coral reef species, and B) episodic settlement, representing temperate reef species. Variance-frequency distributions for C) periodic settlement and D) episodic settlement. Filled circles in A and B represent new moon.
The length of the settlement season and the number of fish settling were the same for both models, the variance was similar (9.3 for periodic and 8.9 for the episodic time series), but the kurtosis differed (15.3 for the periodic and 28.0 for the episodic time series), such that the data distribution for the episodic time series was more strongly asymmetrical compared to the periodic time series. The variance-frequency distribution of the periodic settlement time series (Fig. 2.1 C) shows two dominant peaks. Most of the variability was around the monthly (new moon) and daily frequencies. The variance-frequency distribution of the episodic settlement time series (Fig. 2.1 D) had no dominant peaks, rather the variance was spread over all frequencies.

DISCUSSION

Definitions and methods from the literature

Larval supply and juvenile recruitment are both thought to have strong effects on the abundances and distributions of adult reef fishes (e.g. Doherty 1983, review of Caley et al. 1996). To assess which one (initial larval input or recruitment, including post-settlement mortality) regulates population dynamics, it is important to determine the magnitude of these processes separately. As shown in Table 2.1, definitions of recruitment in reef fish vary widely and are often based on arbitrary time scales, similar to the definitions used in fisheries. Hilborn and Walters (1992) define recruitment as the number of individuals still alive at any specified time after the egg stage. In their review, Robertson and Kaufmann (1998) emphasized the necessity of using non-arbitrary time scales to define recruitment. They suggested use of a standard definition based on the biology of the species, such as the time to maturity or the adult half-life. Without such standard definitions, it is impossible to compare demographic effects of recruitment among species with different longevities and to access relationships between recruitment and abundances of reef fishes. Estimates of abundances of reef fishes should also account for fluctuations over the various time scales. Visual recruitment surveys have the advantage that they are non-destructive and, consequently, do not change the natural conditions of the environment. Therefore, surveys without removal of individuals may provide close estimates of the size of the recruit cohort entering the juvenile population (Booth 1991). The disadvantage of visual surveys is the diminishing accuracy and precision with increasing sampling area, especially for newly settled fish that are easily overseen (review of Doherty 1991). Such surveys are not useful in estimating settlement if there are high post-settlement losses between surveys. Therefore, recruitment patterns only equal settlement patterns when there are no losses.
To estimate larval supply, Booth (1991) concluded that only frequent collection of settlers provide true settlement rates. A popular method is also the back-calculation of settlement dates from otolith increments (e.g. Thresher et al. 1989, May and Jenkins 1992, Jenkins and May 1994) under the assumption that over short periods, back-calculations resolve settlement patterns better than visual censuses (review of Doherty 1991). There is a critical flaw in this assumption. Just as infrequent sampling does not account for losses, back-calculations of settlement dates from otoliths have the same problem, since reconstructions are based on the ages of survivors and not on the initial abundances of settlers. Magnitudes of back-calculated settlement events are inappropriate to compare since recent settlers have not yet suffered the seasonal losses to the same extent as have older recruits (review of Doherty 1991). To estimate true settlement (i.e. unaltered settlement patterns), it is indispensable to sample frequencies higher than the time scales of post-settlement losses, such as mortality and migrations (Frederick 1997). Of the studies in Table 2.1, 44% seemed to resolve settlement patterns on the appropriate time scales, based on criteria such as the frequency of collections, the definition used for settlement, and the assumption that significant losses do not occur the first day after settlement. This percentage would decrease if post-settlement losses are significant on a smaller time scales but would increase if the sampling frequency was greater than the frequency of losses. Sampling durations set the time window of the filter applied to the settlement patterns. Only by sampling the entire season, at the appropriate frequencies, can the influence of settlement be assessed on population dynamics. Collections of settlers, on the other hand, have the disadvantage that they may change environmental conditions. Settlement will be underestimated if arriving settlers are attracted by already settled individuals, an effect shown for adults (Sweatman 1985) and conspecific groups (e.g. Jones 1987a, Forrester 1990), in which case collections would remove a significant settlement cue. Removal of settlers would overestimate settlement if habitat availability is a limiting factor for settlers and a carrying capacity is not reached (Hunte and Côté 1989, Chapters 4, 7).

Combining strategies and sampling frequencies

Coral reef species differ from littoral temperate species in that many have periodic cycles and not episodic patterns. To resolve day/night differences in settlement, dusk and dawn sampling is necessary (minimum twice daily), until sufficient data are collected to establish the cycles. During diel cycles, post-settlement losses could occur, making more frequent observations necessary (Hixon and Carr 1997, Caselle 1999) to estimate diel patterns of settlement. But, if nightly post-settlement losses are low and settlement is nocturnal, only sunrise sampling is necessary to determine seasonal patterns. The important issue is to quantify on what time scale losses occur. In lieu of frequent
sampling, another possibility to establish losses is by marking fish individually and tracking them. To resolve settlement patterns of species with lunar and nocturnal periodicity, sampling should be at least once a month for a duration of about 7 days around settlement peaks (one week before and after new moon at dawn). The daily frequency is dependent on post-settlement processes as discussed above. Daily sampling of the periodic model for 7 days around settlement peaks would account for 80% of the settlers but only encompass 47% of the settlement season (a total of 60 days).

The situation is more hopeless for the episodic strategy, since there is no way to predict peak settlement. Thus, continuous, high frequency sampling throughout the whole season is needed. For the episodic model to account for 80% of the settlers 81% of the settlement season must be sampled (a total of 104 days). Further, the frequency of post-settlement losses will define how often settlement needs to be sampled. For example, if losses are low in the first 24 hours, then sampling once per day is sufficient.

**How can research be improved?**

To address the issue of how to improve settlement/recruitment research, I propose several steps are needed, some basic and requiring little effort and others more complex and work intensive. These steps are outlined below.

First, standard definitions of settlement and recruitment are needed to avoid their overlapping in time scale and to reduce confusion in the literature. Most authors consider settlement as the transition of a pelagic larva to a benthic organism, i.e. the moment a pelagic larva settles into the benthic habitat. As Leis (1991b) points out in his review, larva is a morphological/developmental term and pelagic an ecological term (denoting open water) and the two terms are not synonymous. After settling, fish are post-settlers. Metamorphosis is the transition from larva to juvenile and may be abrupt or gradual (Leis 1991b). Therefore, the term juvenile includes all stages (settlers to recruits) before adulthood. The definition of recruits should not be based on arbitrary time scales but on biological aspects of the fish, as suggested in the review of Robertson and Kaufmann (1998). Without such standard definitions, separating settlement and recruitment, it is impossible to assess which of the two processes affects population demography.

Second, since the key to predicting and understanding patterns lies in the knowledge of relevant scales which depend on underlying processes, sampling must be designed to resolve these processes. Some basic rules to follow are:
1. If larval supply is limiting population densities, then an intense effort has to be put into sampling settlement patterns.

2. If habitat is limiting, then the sampling effort has to be put into recruitment observations.

3. If post-settlement losses are to be resolved for specific time periods, then settlement still has to be sampled frequently.

4. Where to start? Start on the smallest scale and work upward i.e. start resolving at the smallest temporal scale. Consequently, determine if there are diel cycles in settlement and in losses by intense sampling over 24 hours. If not, less frequent sampling may be used to check for weekly patterns and finally the monthly and seasonal patterns.

5. Lastly, sample long enough to encompass entire process.

For both the settlement and recruitment process, the frequency of sampling must be adjusted to the definition of the process studied and the strategy used by the study species. For estimation of temporal patterns in settlement, the important issue is to sample initial patterns before their alteration by post-settlement losses. This is especially pertinent when correlating settlement with environmental time series such as physical and oceanographic parameters. Therefore, the frequency of post-settlement losses will define how often settlement needs to be sampled. The rule of thumb is to resolve the smallest temporal scale but long enough to see the whole pattern, i.e. seasonal variability in settlement.

The hope of this review and conceptual model is to provide a more standard framework for determining processes affecting reef fish populations. Considerations of sampling, in combination with clear definitions, are critical to advance our knowledge in reef fish ecology.

ACKNOWLEDGEMENTS

Thanks to A. Peter, E. Macpherson, A. Zehnder, and T.C. Granata for discussions and comments that improved the manuscript.
3. The influence of physical and oceanographic parameters on settlement of littoral fish

ABSTRACT

Physical processes have been shown to facilitate onshore movements of pelagic larvae and therefore may aid in the settlement of benthic fish. Oceanographic processes known to influence settlement are tidal currents, wind driven currents, fronts, and waves. In this study, we relate temporal variations in settlement of the rocky shore fish Aidablennius sphynx with oceanographic events occurring before and during the settlement season. Three years of settlement data, collected daily in the NW Mediterranean Sea, were correlated with high frequency physical data sets, including wind speed and direction, wave height, sea surface temperature (SST) from satellite images, in situ sea surface temperature (ISST), lunar and day/night cycles.

The length of the settlement seasons varied each year and appeared to be related to the development of frontal and mesoscale structures. For all three years, settlement began in the early summer when mesoscale features, including eddies, approached the coastline and ended in the late summer when structures dissipated or eddies moved down the coast. A likely mechanism for the formation of these eddies is entrainment of colder, less saline water from river outflows by the Catalan current and deflection of the current by headlands and bottom topography along this rugged rocky shoreline. Temperature anomalies, however, were not related to settlement patterns indicating that nearshore temperatures may not reflect the complex circulation of water masses along the coast or may not reflect settlement if larval fish actively swim the last stretch to their settlement habitat.

Spring tides were not related to settlement since no lunar periodicity in settlement was found. Diurnal tides in the Mediterranean Sea are weak which is confirmed by the lack of day/night differences in settlement. Surface Ekman currents along the coast were only correlated with settlement for the 1998 season. Settlement peaks were positively correlated with significant wave heights, and negatively with barometric pressures, suggesting that waves aided onshore larval transport. Different wave processes acting on different scales could be responsible for inshore larval transport, and thus settlement, including cliff waves, surface convergence zones created by internal waves, and edge waves. The steep cliffs, headlands with interspersed bays, and nearshore submarine canyons of this coast could all modify wave fields producing onshore-offshore currents and promoting settlement. The combination of mesoscale transport and wave processes
are the two most prominent mechanisms that explain the temporal variability in settlement of *A. sphynx*. 
INTRODUCTION

Many littoral, marine fishes have a pelagic stage with eggs or larvae in offshore waters. After completing their pelagic development phase, larvae return onshore to settle and recruit to the adult population. Populations of marine organisms are believed to be limited by larval supply (Doherty and Williams 1988, Doherty and Fowler 1994), which can be extremely variable in space and time (Underwood and Fairweather 1989, Sale 1990, Doherty 1991). The variability in larval settlement may be a result of different interacting processes. The capability to swim and to actively modify their pelagic distribution (Champalbert and Koutsikopoulos 1995, Leis et al. 1996, Stobutzki and Bellwood 1997) distinguishes fish larvae of both, temperate and coral species, from other marine larvae that are mainly passively transported. On the other hand, physical processes are of considerable importance because they have been shown to facilitate onshore movements, thus, increasing the likelihood of larvae returning to reef habitats (Kingsford and Choat 1986).

Processes known to influence settlement are tidal currents, wind driven currents, fronts, and waves. For some tidal systems, it has been shown that flood tides transport settlement-stage fishes onshore (Shenker et al. 1993, Thorrold et al. 1994b), and can aid night time recruitment (Colin et al. 1997). Peak onshore movements of recruits were also observed for nights when winds and currents had strong cross-shelf components (Shenker et al. 1993). Distributions and movements of pre-settlers around a coral reef were associated with tidally induced fronts and Langmuir circulations cells driven by winds (Kingsford and Choat 1991). However, the link between wind stress and larval supply appears to be habitat-dependent (Milicich 1994). Lunar and semi-lunar settlement cycles occur for many coral reef fish, which also tend to settle at night (e.g. Leis 1991b, Dufour and Galzin 1993, Thorrold et al. 1994a). Kingsford and Finn (1997) found that the lunar phase in combination with wind explained more variability than the lunar phase alone. Onshore winds were significantly related with reef transport of larvae for some taxa (Thorrold et al. 1994b). Onshore advection by Ekman transport could also be important by bringing water masses with eggs and larvae nearshore, favoring settlement of juveniles and increasing subsequent recruitment strength (Bailey 1981, Castonguay et al. 1992, Castillo et al. 1994). The timing of recruitment in shelf-slope waters was found to be determined by the onset of dissipation of a surface temperature front (Hare and Cowen 1996). Another mechanism of larval transport could be passive drift back to reefs connected to mesoscale eddy/current systems which entrain and entrap larvae (Bailey et al. 1997, Dickey-Collas 1997, Kingsford and Choat 1986, Lobel and Robertson 1988, Sabatés 1990, Sabatés and Olivar 1996). Drift alone does not always explain distributions of larvae, suggesting that self-motile mechanisms may be more
important (Lobel and Robinson 1986). Larval swimming abilities contributed to active choice of habitat beginning in the planktonic stage (Doherty et al. 1996) and during the colonization of reefs (Sancho et al. 1997) and some larvae even prefer low-flow areas near the settlement habitat (Breitburg et al. 1995). The idea that the blend of passive transport and active responses have a particular importance for the settlement process was proposed by Breitburg et al. (1995) and confirmed by Thorrold and Williams (1996) who suggest that active aggregation rather than passive accumulation results in patch generation and that settlement occurs when such patches encounter reef habitats. In addition to physical processes, the high interannual variability could reflect variations in the timing of spawning, variations in the duration in the plankton, differential survival during the pelagic stage, or a combination of all these (Pfister 1997). Therefore, to explain the variation in larval supply, knowledge is required on production, length of pre-settlement phase, swimming abilities and behavior, biological and physical phenomena influencing survival (Kingsford and Finn 1997).

One of the principal problems in studies that relate oceanographic conditions to settlement is an accurate estimation of the number of larvae arriving and the pattern during the settlement season. New settlers can suffer high losses during the first days after settlement, generally caused by predation (e.g. Carr and Hixon 1995, Beets 1997, Steele 1997a, 1998, Connell 1998). Sampling must quantify these losses to determine accurate relationships between settlement patterns and oceanographic processes. The sampling frequency reported by various authors for different species ranges mainly from weekly to monthly (e.g. Robertson 1988, Thresher et al. 1989, Booth 1992, Meekan et al. 1993, Williams et al. 1994, Jenkins et al. 1997, Vigliola et al. 1998), though some are on smaller scales of days or less (Williams and Sale 1981, Victor 1986a, Robertson et al. 1988, Booth 1991, Dufour and Galzin 1993, Thorrold et al. 1994a, Danilowicz 1997). Recent studies demonstrated that, in species with episodic settlement, the description of the settlement pattern needs at least a daily periodicity to resolve the true pattern (Booth 1991, Chapters 2, 5). For three years we studied the daily arrival of new settlers to a rocky zone in the NW Mediterranean Sea in order to relate settlement with some oceanographic events occurring before and during settlement period.

The NW Mediterranean coast features an indented topography, characterized by abrupt cliffs and three submarine canyons, < 100 km apart, intersecting the broad shelf. The major current in this region is the Catalan current which flows SW along the coast (Salat and Font 1987, Castellón et al. 1990), generally inshore of the shelf break. Filaments and mesoscale eddies often develop in the vicinity of the shelf front, approximately 35 km offshore (Tintoré et al. 1990). Inshore flows have been shown to
meander based on vorticity changes over nearshore canyons (Masó et al. 1990, Masó and Tintoré 1991). However, Rojas et al. (1995) found that typical flow patterns can be reversed in the upper layer after the development of spring stratification. Predominant wind forcing is offshore from the NW-N and can augment the alongshore transport (García-Ladona and Djenidi 1991), but is not significant enough to generate mesoscale activity (Font 1990). While few studies have been done on wave-current interactions, alongshore currents are known to be generated by waves obliquely encountering the coast (Longuet-Higgins 1970) and by coastally trapped waves (Bryan and Bowen 1998). The importance of flow modification along this shelf has been shown for phytoplankton and larval fish distributions (Sabatés and Olivar 1996, Olivar et al. 1998).

We chose as our study species Aidablennius sphynx because it is relatively abundant. Generally, blennids (Family Blennidae) form one of the most common groups of the Mediterranean rocky shore fishes (Corbera et al. 1996). Eggs are laid onshore (Kraak 1996), but once hatched larvae of Blenniidae disperse away from reefs (Brogan 1994, Sabatés 1994), therefore, the distribution of larval blenniids may not be determined by the proximity of shore (Kingsford and Choat 1989). In this paper, we relate daily settlement to physical and oceanographic processes occurring during three settlement seasons. Since offshore dispersal of larvae along the western Mediterranean coast appears to be limited by the geographical position of the shelf-slope front (Sabatés and Olivar 1996) and since larvae of A. sphynx are in the surface layer (< 10 m depth, A. Sabatés personal communication), we examine hydrodynamic and physical conditions affecting the surface layer between the coastline and shelf-slope. This species settles in the summer from June to September, with highly variable (episodic) timing, necessitating high frequency sampling, and a high interannual variability in settlement (Chapter 5). By combining high frequency physical datasets with settlement time series, we test the hypothesis that temporal variations in settlement are a result of physical processes.

MATERIALS AND METHODS

This study covered three settlement seasons, from mid-June to the end of September for the years of 1996, 1997, and 1998. The study site was the littoral zone of the rocky coast of Northeastern Spain, in an open bay in Blanes (41° 40' - 41° N, 02° 47' - 48° E) (Fig. 3.1).
Fig. 3.1. A map of the rocky coast of northeastern Spain showing the locations of the sampling stations: wind speeds and directions (L' Estartit), wave heights (Palamós and Tordera delta), and settlement (Blanes).

Settlement time series

Settlers were collected along 3 transect walls daily or twice daily (sunrise and sunset) to determine temporal patterns of settlement, except when precluded by weather and sea conditions. Collections were carried out with handnets, passing one hand over the rocky substrate and scaring fish out of crevices while snorkelling along transects. Newly settled fish were translucent and easily distinguishable from already settled individuals (Chapter 5). Sampling was done for 194 dives (in 92 days), 147 dives (in 105 days), and 104 dives (in 93 days) for the settlement seasons of 1996, 1997, and 1998, respectively. Numbers of settlers were standardized per m$^2$ suitable habitat (Chapter 4) and differences between transects tested with analysis of variance (ANOVA). Homogeneity of variances and normal distribution of data were checked. Day and night patterns were similar, and no differences in the mean number of settlers arriving during
the day and night were found for all three settlement seasons (Chapter 5). Additionally, no differences in settlement densities between transects were found for the settlement seasons of 1996, 1997 and 1998. Therefore, day/night and transect data were pooled for daily analyses.

**Physical and oceanographic parameters**

To detect relationships between settlement and lunar cycles, time series containing lunar months of all three seasons were used to obtain a sufficient number of lunar cycles.

Significant wave heights (mean one third of the highest amplitudes measured) were obtained from surface wave buoys (Wave Riders) at two different locations along the coast, 30 km apart. The first buoy was moored in 70 m water off Tordera delta (41° 38.8' N, 02° 48.9' E) 3 km from the study site, and the second buoy was moored in 90 m of water off Palamós (41° 49.8' N, 03° 11.2' E) 30 km from the study site (Fig. 3.1). Data from Palamós, averaged to 1 hour time bins, were available for all three settlement seasons, whereas data from Tordera, averaged to 3 hour time bins, were only available for the settlement season of 1996 and half the settlement season of 1997. Cross-correlations between daily averaged wave heights for Palamós and Tordera showed highly correlated wave events between the two locations ($r > 0.75$ for 1996 and 1997 at 0 day lag). Given this result and the fact that the two buoys were about 30 km apart (less than 1 hour difference based on the group wave speed of 30 km h⁻¹), Palamós data were used to evaluate settlement processes in Blanes since Tordera time series were incomplete. The portion of swell waves relative to wind waves was represented by the quotient of maximum energy of the wave spectrum and the total energy of the spectrum.

Daily averaged barometric pressures in Blanes for 1996 were measured by an automated meteorological station and also manually each day for 1996 and 1997. Pressure data were then correlated with settlement and significant wave height time series.

Wind directions and speeds were from L’Estartit (42° 3.28' N, 03° 12.15' E), about 40 km north of the Palamós buoy (Fig. 3.1) and were averaged every three hours. Alongshore, onshore, and offshore time series of wind speed were plotted and cross-correlated to settlement time series. Ekman current speed ($V_0$) in the surface layer (Pond and Pickard 1983) was estimated from a 45° clockwise rotation of wind direction, given by:
\[ V_0 = \frac{\sqrt{2\pi C_d(w)\rho_{air}w^2}}{s\sin|\phi|\rho_{water}\left| f_{coriolis}\right|} \]  

(3.1)

where \( w = \text{wind speed \,[m \, s^{-1}]}; \rho_{air} \text{ and } \rho_{water} = \text{density of air and water \,[kg \, m^{-3}];} \phi = \text{degrees latitude; } C_d \text{ is the drag coefficient, which is dependent on wind speed (Smith 1980 in Pond and Pickard 1983):)}

\[ C_d(w) = 6 \times 10^{-3} + 0.6 \times 10^{-3}w \quad \text{if } w > 5 \text{ m/s} \quad (3.2a) \]

\[ C_d(w) = 0.0009 \quad \text{if } w < 5 \text{ m/s} \quad (3.2b) \]

and the Coriolis parameter is:

\[ \left| f_{coriolis} \right| = 2\Omega\sin|\phi| \quad \Omega = 7.29 \times 10^{-5} \, [\text{rad \, s}^{-1}] \]  

(3.3)

In situ sea surface temperatures (ISSTs) were measured daily about 200 m offshore from the settlement site. ISST time series were first corrected for seasonal heating by subtracting a linear trend from the raw data and then differenced to detect temperature anomalies. Advanced very high resolution radiometry (AVHRR) satellite images of sea surface temperatures (SSTs) with 1.1 km resolution were obtained for the settlement seasons of 1997 and 1998, where 13 and 15 SST images were usable, respectively. Additional satellite images of 4 km resolution were obtained for the 1996 settlement season and day 152 of the 1997 season. All images were resized, some rotated, and scaled to grey shades from 0 to 255, however, not all images were calibrated to the same temperature ranges. For this study, cooler waters are lighter and warmer waters are darker grey shades, and clouds and land have been masked.

All cross-correlations between settlement time series and different physical parameters were done with STATISTICA for the Macintosh, Version 4.1 for time lags of ± 7 days. For all physical data, missing values for < 2 days were filled by interpolation of adjacent points. For large gaps in data, however, the settlement time series was truncated to match physical time series (seen in Table 3.1).
RESULTS

Seasonal and lunar periodicity

The length of the settlement seasons varied each year. The total number of settlement days for the 1996 season was 55, for 1997 it was 98, and in 1998 it was 53, all based on the days the first and the last settler was caught. The diel settlement time series for 1996, 1997, and 1998 showed no relationship with the lunar cycles (Fig. 3.2) and no significant cross-correlations at any time lag (Table 3.1).

Fig. 3.2. Time series of daily settlement of Aidablennius sphynx for the settlement season in 1996 (lunar months 1 - 3.5), 1997 (lunar months 3.5 - 6.5), and 1998 (lunar months 6.5 - 9.5). Lunar phase is indicated by filled (new moon) and open (full moon) circles.

Barometric pressure

Negative correlations were found between settlement and barometric pressure, with lags of 2 - 6 days for the seasons of 1996 and 1997. The highest coefficients are shown in Table 3.1. The maximum difference in pressure between two successive days was 16.2 mbar. Time series of wave height and barometric pressure also showed a significant relationship. Waves lagged barometric pressure by 2 - 6 days in 1996 (r = -0.311 to -0.432), and 1 - 5 days in 1997 (r = -0.258 to -0.486).
Table 3.1  Summary of cross-correlation statistics between settlement and physical time series. N is the number of days, r is the highest correlation coefficient based on the standard error (S.E.) and the day lag of settlement peaks. ns means not significant at the 95% confidence level.

<table>
<thead>
<tr>
<th>Physical parameters</th>
<th>Settlement seasons</th>
<th>N</th>
<th>r</th>
<th>S.E</th>
<th>Day lag</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lunar cycles</td>
<td>1996-1998</td>
<td>252</td>
<td>ns</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Significant wave height</td>
<td>1996</td>
<td>76</td>
<td>0.4836</td>
<td>0.1222</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>1997</td>
<td>90</td>
<td>0.3541</td>
<td>0.1179</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>1998</td>
<td>60</td>
<td>0.343 (ns)</td>
<td>0.1826</td>
<td>0</td>
</tr>
<tr>
<td>Barometric pressure</td>
<td>1996</td>
<td>74</td>
<td>-0.435</td>
<td>0.1231</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>1997</td>
<td>89</td>
<td>-0.330</td>
<td>0.0933</td>
<td>7</td>
</tr>
<tr>
<td>Surface Ekman current speed</td>
<td>1996</td>
<td>77</td>
<td>ns</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1997</td>
<td>105</td>
<td>ns</td>
<td></td>
<td></td>
</tr>
<tr>
<td>alongshore (up the coast)</td>
<td>1998</td>
<td>63</td>
<td>0.3293</td>
<td>0.1374</td>
<td>4</td>
</tr>
<tr>
<td>In situ SST anomalies</td>
<td>1996</td>
<td>76</td>
<td>ns</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1997</td>
<td>92</td>
<td>ns</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1998</td>
<td>71</td>
<td>ns</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Significant wave height

For all three settlement seasons, the characteristics of the waves were similar. Mean values of significant wave height were from 3.3 - 3.8 m, with maximum wave heights from 5 - 6 m. Wave spectra had mean periods around 5 s and maximum periods from 8.7 - 9.8 s. Swell waves amounted to 90% of the wave energy. Wave events were episodic and peaks in settlement of *Aidablennius sphynx* lagged wave events (Fig. 3.3 A-C).

Significant cross-correlation coefficients occurred at lags of 0 - 4 days in 1996 and 2 - 5 days in 1997 (Table 3.1). In 1998, the highest correlation coefficients had lags of 0 - 1 day, though were not statistically significant (Table 3.1). However, time series of significant wave height for 1998 was shorter than for the other seasons as a result of missing data, thus, standard errors and confidence levels are higher than for 1996 and 1997 settlement seasons.
Fig. 3.3. Time series of daily settlement of Aidablennius sphynx (AS) and significant wave heights (Hs) for A) 1996, B) 1997, and C) 1998 settlement season. Time is in Julian days and days of year begin from January 1.
Ekman transport

Surface Ekman currents were most important in the onshore direction and alongshore from northeast to southwest (down the coast) (Fig. 3.4 A-C).

Fig. 3.4. Time series of Ekman surface current speeds for the settlement seasons A) 1996, B) 1997, and C) 1998. Onshore (−), offshore (+) directions (solid lines) and alongshore directions, from downcoast (−) to upcoast (+)(broken lines), are shown. Days of year begin from January 1.
Currents down the coast reached mean speeds of 0.35 m s\(^{-1}\) for the 1996 settlement season, 0.23 m s\(^{-1}\) for 1997, and 0.32 m s\(^{-1}\) for 1998. Relative transport perpendicular to the coast was mainly onshore with means of 0.2 m s\(^{-1}\) for 1996, 0.07 m s\(^{-1}\) for 1997, and 0.1 m s\(^{-1}\) for 1998. A relationship between Ekman current for different directions and settlement events was only found for 1998 when settlement peaks were significantly correlated to upcoast transport with a 4 day lag (Table 3.1).

**Sea surface temperatures**

*In situ* sea surface temperatures ranged from 17-26°C during all three settlement seasons. Maximum temperatures anomalies were 3°C for 1996 and 1997, and 2°C for 1998. The diel settlement time series from 1996 to 1998 showed no relationship with temperature anomalies and no significant cross-correlations at any time lag (Table 3.1). Satellite images show the development of mesoscale structures over the seasons. In early spring before settlement began, no horizontal stratification of SST was noted (Fig. 3.5 Julian days 152 - 155). Coincident with the onset of the settlement season and peaks in settlement (Fig. 3.5, Julian days 185 -198), high SST variability occurred along the coast and continued for the duration of the settlement season (Fig. 3.5, Julian days 195 - 203). By late summer (Fig. 3.5, Julian days >260), settlement ended and warm water extended over the whole coastal zone. The high SST variability was often associated with mesoscale eddies, whose structure can be clearly seen in images for days 199 and 203 of 1997 and 1998, respectively (Fig. 3.6.A, B), where the line is a transect perpendicular to the Blanes coast. The cold water, originating from outflow of the Rhône River, and entrained by the eddies, is clearly visible in the images as light grey bands. In 1997, the eddy drifted down the coast with a translation speed up to 10 km d\(^{-1}\), but then stalled after day 206. In 1998, the translation speeds ranged from 3 to 5 km d\(^{-1}\). The diameters of both eddies, for 1997 and 1998, were about 150 km.
Fig. 3.5. Satellite images of northeastern Spain showing sea surface temperatures (SST) for spring to summer 1996, 1997, and 1998. In spring, before the onset of the settlement season, Julian days 155, 152, and 152 are shown. Peaks in settlement occurred on days 185, 187, and 198, and settlement seasons continued through days 195, 199, and 203. Days 265, 262 and 264 represent late summer, after the end of the settlement seasons. Cooler waters are lighter grey shades and warmer waters darker shades, images however are not calibrated to the same temperature scale. Clouds and land are masked.
DISCUSSION

Mesoscale processes

For different geographical regions, larval stages of pelagic fish have varying durations (Victor 1986b). The durations of our three settlement seasons varied in length by as much as 45 days (Chapter 5), however, no geographical differences were observed on scales of 10's of kilometers (Chapter 3). The varying lengths of the settlement seasons could be a result of mesoscale processes, such as eddies and fronts, which influence large portions of this coastline. In the western Mediterranean Sea, off the northeastern Spanish coast, flows over the shelf are also highly variable in space and time (Masó and Tintoré 1991). The most dominant feature is a permanent shelf slope front (Font et al. 1988), associated with the Catalan Current, which flows along the coast from the northeast to the southwest with a mean speed of about 0.3 m s⁻¹ (Castellón et al. 1990). The water mass of the shelf slope front is characterized by density gradients with lower salinity water originating from outflow of the Rhône River in the spring and manifest on the shelf side as a plume of cold water moving southward from the Gulf of Lion (Sabatés and Masó 1990). The plume's temperature gradients are evident in our SST images. It has been previously shown that mesoscale dynamics are favored by strong density gradients, i.e. baroclinic processes (Strass et al. 1992). The critical
background level for baroclinic forcing of mesoscale activity in the open ocean can be estimated from the vertical scale of stratification \((H = 10 \text{ m})\) relative to the 'Rhine length scale' for the mean flow \((u)\) acting over the \(\beta\)-plane (i.e. \(L_{RH} = \sqrt{\frac{H}{u/\beta}}\)) such that \(H/L_{RH} = \frac{H}{\frac{H}{u/\beta}^{1/2}} = 10^{-4}\) (Strass et al. 1992). Using the local vorticity \((\zeta)\) of a typical eddy in the northwestern Mediterranean Sea, instead of the beta approximation across ocean basins, we estimate that baroclinic forcing is on the order of \(H/|u/\zeta| = 10^{-3}\) for \(u = 0.2\) m s\(^{-1}\) and \(\zeta = 2 \times 10^{-5}\) s\(^{-1}\) (based on Granata et al. 1995), meaning that summer stratification is a major contributor to mesoscale processes along this coast. On the continental shelf, shedding dipole eddies and energetic filaments are visible at the leading edge of the plume and are associated with the southward spreading of cold, plume water (La Violette et al. 1990). A likely mechanism for the formation of these filaments is the deflection of the cold, less saline water by the nearshore submarine canyons (La Violette et al. 1990) and headlands along this rugged rocky shoreline. The frontal filaments and eddies on the NW Mediterranean coast are thought to play an important role in shelf transport of water, and probably larvae, though the underlying physical processes which lead to the water exchange on the shelf remain poorly understood (La Violette et al. 1990). Maximum abundances of larval fish were usually located in the slope front (Sabatés 1990, Sabatés and Masó 1990, 1992, Sabatés and Olivar 1996, Olivar et al. 1998).

Large scale oceanographic features are known to be important for transport in coastal zones. Thorrold and Williams (1996) found mesoscale patterns of larval and pelagic juvenile fish which they suggest were generated by hydrographic phenomena acting over scales of at least 50 km in both alongshore and cross-shelf directions. Victor (1984) showed that the planktonic patch size of bluehead wrasse larvae was at least 46 km wide, which was the upper limit of his spatial resolution. The spatial patterns of cold filaments in the Californian Current were found to vary seasonally with the main flow meandering onshore-offshore in spring while in summer, mesoscale eddies developed (Strub et al. 1991). At the surface in the Californian Current, biological communities were often separated by a jet-like front, with phytoplankton pigments and nutrients on the inshore side, and pigment maxima near the center (Strub et al. 1991).

Other studies have shown that organisms react selectively to physical and biological gradients created or modified by fronts and eddies. For example, aggregations of phytoplankton and zooplankton concentrations are located in dynamic zones such as freshwater fronts (Owen 1981), tidal fronts and upwelling systems (MacKenzie and Leggett 1991), and mesoscale eddies (Lobel and Robinson 1988, Canino et al. 1991). Thus, fish might not be directly associated with circulation features, but rather by feeding
advantages as a result of higher prey abundances in frontal zones (Owen 1981). Eddies could therefore function as larval nursery grounds, especially when residence times are sufficiently long for pelagic development of reef fish species (Lobel and Robinson 1986). Eddies can also protect larvae from offshore transport (Bailey 1997). Entrainment and entrapment of nearshore larvae and particles have been observed during and after eddy formation (Lobel and Robinson 1986, Bailey 1997) but it is unclear if larvae were actively or passively transported. Swimming abilities and behavior of pelagic, juvenile fish were insufficient to explain their shift offshore and could only be explained by transport within a gyre with current speeds of 0.2 m s^{-1} (Dickey-Collas 1991). For eddies with current speeds of up to 0.5 m s^{-1} only the larvae in later stages, which are thought to be the most adept swimmers, were abundant in outer swirls whereas larval abundances increased from the eddy's center to the periphery, contrary to the pattern exhibited by zooplankton (Lobel and Robinson 1988). Patches with assemblages of different species were characteristic only for late stage larvae and pelagic juveniles, which lead Thorrold and Williams (1996) to conclude that aggregations are active rather than passive. Swimming capabilities of A. sphynx larvae are discussed below.

Thorrold and Williams (1996) found that major settlement peaks occurred when patches of larvae collided with the coast. For all three years of this study, the settlement seasons started when mesoscale structures, including eddies, reached the coastline and ended when structures dissipated or eddies moved down the coast. Thus, mesoscale processes appear to set-up the settlement season. In addition, the duration of the season corresponds to the transition time of passing eddies (~ 50 days). The longer settlement season in 1997 coincided with a stalled mesoscale eddy that remained off the coast for several months. Dynamic frontal zones have been shown to account for larval fluxes by either transporting them onshore or offshore (Govoni 1993). Blenny larvae in their pelagic phase were found in the spring (May and early June) between 10 km to 50 km offshore and were associated with colder, lower salinity water which limited their offshore distribution (Sabatés and Olivar 1996). By late spring (end of June), storms with large volumes of continental run-off displaced frontal structures farther offshore. As a consequence, blenny larvae were dispersed from near the coast to distances > 50 km offshore (Sabatés and Olivar 1996). This wide distribution of larvae over the shelf may have been the result of eddies or mesoscale structures formed during periods of strong stratification.

Nearshore processes

For all three years of our data, settlement peaks were positively correlated with significant wave heights. In a shallow bay Jenkins et al. (1997) found negative
correlations between wave heights and periodic settlement as a result of waves breaking up patches of settlers. The difference seems to be that waves play different roles in open and closes systems such as bays and open coasts. On the open NW Mediterranean coast, nearshore wave processes probably aid onshore transport of larvae.

Different wave processes could be responsible for inshore larval transport and thus, settlement over different scales. On the largest scale, cliff waves could create alongshore currents when waves oblique to steep cliffs are trapped (Longuet-Higgins 1970). On an intermediate scale, surface convergence zones created by internal waves could trap larvae. Further, internal waves are sensitive to vertical current shear and to density gradients, both of which are intensified along the fronts (Owen 1981). On the smallest scale, edge waves trap wave energy against the shore (Bryan and Bowen 1998), existing as standing waves or as waves travelling up and down the coast (Inman et al. 1976). The physical features of the Costa Brava, such as steep cliffs, bays, and nearshore submarine canyons, could all modify these wave fields, producing onshore-offshore currents, and promoting settlement.

Internal waves may have the ability to turn scattered distributions into regular patterns (Kingsford and Choat 1986) with the consequence that aggregations of presettlement fish in slicks may be transported onshore (Shanks 1983, Kingsford and Choat 1986). In the NW Mediterranean, storms with high winds commonly generate large surface and internal waves (Salât et al. 1992). Organisms at the surface, such as larvae of Aidablennius sphynx (A. Sabatés, personal communication), could be accumulated in surface convergence zones of these waves which have a tendency to move onshore (Shanks 1983, 1995). These convergence zones appear as light bands or slicks on the surface, moving at speeds of 0.01-1 m s\(^{-1}\) (Owen 1981). Sampling long period waves requires instrumentation unavailable to us during our study. However, aerial photographs and SAR images clearly show the convergence zones of these features. Accumulation of larvae in convergence zones have been demonstrated in other areas. Higher densities of pelagic fish larvae, invertebrates, and zooplankton were found in slicks of internal waves (Zeldis and Jillett 1982, Shanks 1983, Kingsford et al. 1991), 6 to 40 times more concentrated than in surface waters between the slicks (Shanks 1983). Larval and presettlement fish were also observed in association with surface drift algae in these convergent features (Kingsford and Choat 1985, 1986, Kingsford and Millicich 1987). In addition to advection, fish may actively select convergence zones because of higher food densities (Kingsford et al. 1991), which is advantageous since the composition and abundance of zooplankton may influence survival of presettlement fish (Kingsford 1989).
Episodic storm-events, which drive short-term variability in wind and currents could be the mechanism leading to variability in settlement (Shenker et al. 1993). Changes in air pressure drive high winds which generate waves given sufficient wind duration and fetch. Thus, it is not surprising that settlement of *A. sphynx* was not only positively correlated with significant wave heights but also negatively with barometric pressure. For some larvae, including blennies, onshore movement was enhanced when winds and currents showed strong cross-shelf components (Shenker et al. 1993, Thorrold et al. 1994a). However, surface Ekman current speeds along our coast were not consistently correlated with settlement. It may be that an indirect relationship is responsible for the positive correlation in 1998, such as weakening of the counter current. The influence of the surface flow could be dependent on various factors including: 1) the appropriate direction relative to the position of the larvae (Hare and Cowen 1996); 2) the direction relative to habitat (Milicich 1994); 3) the magnitude of the flow (Hare and Cowen 1996); and 4) the combination with other transport mechanisms.

Tides affect recruitment for some pelagic juveniles which recruited with the incoming tide at night (Colin et al. 1997). In the Mediterranean, however, diurnal tides are not important (Albérola et al. 1995) and no day night differences in settlement were found for *Aidablennius sphynx* (Chapter 5). Further, spring tides were not important since no lunar periodicity in settlement was found.

**Swimming capabilities**

While offshore distributions of larval fish reflect passive transport by currents, inshore patterns probably required relatively active swimming by the animals (Leis 1982). Pelagic larvae of *Aidablennius sphynx* are characterized by early, well developed fins. Pectoral fins of later stages reach 59% of their body length and during postflexion larvae formed principal rays of the caudal fins (Sabatés 1994). These morphological characteristics indicate that larvae of *A. sphynx* are strong swimmers capable of actively determining their position (A. Sabatés personal communication). Pelagic stages of other reef fish were found to be competent swimmers and able to modify their dispersal (Stobutzki and Bellwood 1997), however, strong tidal currents (3 m s\(^{-1}\)) were suggested to overwhelm their swimming speeds, causing them to behave as passive particles (Jenkins and Black 1994). Larvae were able to swim against currents averaging 0.27 m s\(^{-1}\) (Sancho et al. 1997) and mean observed swimming speeds were greater than average speeds of ambient currents (Leis and Carson-Ewart 1997).

Leis et al. (1996) showed that late pelagic stages of reef fishes swim directionally and orientate themselves relative to the reef. Different cues for orientation are possible.
For pelagic juveniles with well developed sensory and motor capabilities, temperature gradients were suggested to be one of the cues used for identification of lagoonal habitats (Doherty et al. 1996). In our study, temperature anomalies were not related to settlement, however, nearshore temperatures may only reflect complex circulation patterns along the coast. *In situ* temperatures are not always related to small scale SST perhaps because of the low resolution of SST images and fact that SST and ISST were only measured once per day. Larvae could also be associated with different water masses offshore, not transported passively, but actively swimming the last stretch to their settlement habitat, following other cues.

**CONCLUSIONS**

This study provides an explanation of a mechanism for the strong interannual variability in settlement of *Aidablennius sphynx*. Observed mesoscale structures, including eddies, in late spring effected large scale settlement by determining the beginning and end of the settlement seasons. These mesoscale eddies were probably set-up by strong vertical stratification and surface run-off by rivers. The intraseasonal variability typifies episodic settlement which is enhanced by wave processes, the most likely of which is internal waves. It is possible that these physical processes only aid larval transport nearshore and that larvae of *A. sphynx* may actively swim directionally to shore.

**ACKNOWLEDGMENTS**

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4. Temporal and spatial variability of settlement success and recruitment level in three blennoid fishes in the northwestern Mediterranean

ABSTRACT

We studied the settlement success and recruitment level of three common species of blennoids (Aidablennius sphynx, Parablennius incognitus and Tripterygion tripteronotus) off the NW Mediterranean coast at three localities separated ca. 50 km apart, over a period of four years (1994 - 1997). Settlement success is defined as the maximum number of new individuals observed during the settlement period and recruitment level as the number of new individuals at the end of the settlement period. We also determined which descriptive variables of the substratum had a significant influence on settlement, and whether the presence of adults had an effect on settlement. The results from the stepwise multiple regression analysis indicated that the type of substrate cover and the presence of adult conspecifics played a significant part in the abundance of settlers and post-settlers on the rocky shore for all three species. The variation in the abundance of settlers of A. sphynx was best explained by the category “bare rock”. Settlement variance of P. incognitus and T. tripteronotus was mainly explained by the substrate covered with ”small turf of algae”. Field experiments demonstrated a strong relationship between ”bare rock” density and A. sphynx settlement and between ”small turf of algae” density and P. incognitus and T. tripteronotus settlement. However, the strong correlation between settlers and adult conspecifics in the stepwise multiple regression seems to be causal. For the three blennoids, preferences for a specific substratum type at settlement can explain, on the small scale, the abundance of new settlers in a locality. The maximum density of settlers was only dependent on the amount of preferred substrate available along a transect and independent of the size of a transect.

The spatial and temporal patterns of the recruitment level differed from those observed in settlement success. For A. sphynx, no significant temporal and spatial differences were found for settlement success but were for recruitment level. For P. incognitus, no significant differences were found for settlement success, but a significant spatial variation was observed for recruitment level. For T. tripteronotus, the most significant differences were found for settlement success between years, which appeared in patterns of recruitment level. This suggests that the interannual differences were very strong and are maintained throughout the post-settlement period. Also for this species, significant differences of settlement success were found between localities, however,
they were not maintained over the season. Our results demonstrate that post-settlement processes can alter settlement patterns.
INTRODUCTION

The input of new individuals to a population is one of the most important processes in the life-history of fishes and, to a large extent, affects their population dynamics (Cushing 1996). The addition of new individuals in most fish populations is determined by events occurring at settlement, defined as the period when pelagic larvae reach the bottom, and between this period and recruitment, defined as the time at which the juveniles remaining at the end of the settlement period incorporate to the adult populations (see the review of Caley et al. 1996).

The number of larvae that reach the bottom is affected by a variety of abiotic [e.g. currents, wind, waves (Cowen 1985, Leis 1994, Kingsford et al. 1991, Sabatés and Masó 1992, Breitburg et al. 1995, Sabatés and Oliver 1996)], and biotic [e.g. predation, starvation (Bailey et al. 1995, MacKenzie and Leggett 1991)] processes and could be responsible for the year-class strength (Milicich et al. 1992). However, recent studies have demonstrated the importance of the processes occurring during the post-settlement period (e.g. habitat limitation, predation, competition) in recruitment strength and consequently in the final incorporation of new individuals to populations (e.g. Bailey 1994, Beets 1997, Booth and Beretta 1994, Carr 1994, Connell 1997, Hixon and Carr 1997, Macpherson et al. 1997). For these reasons, the identification of these processes and how they affect settlement success and recruitment level is one of the main goals in the study of fish populations (Doherty and Fowler 1994, Caley et al. 1996).

In recent years, studies on fish settlement and recruitment processes have become more abundant on coral and temperate rocky reefs (see the reviews of Jones 1991, Caley et al. 1996). Some of these studies have demonstrated the positive/negative or neutral influence of habitat factors, among them the selection of substratum characteristics (Shulman et al. 1983, Jones 1991, Levin 1994a, García-Rubies and Macpherson 1995). The presence or absence of conspecifics has also proven to be of great importance in determining the level of settlement and recruitment success for fish (Jones 1987b, Sweatman and St John 1990). The influence of these variables has also been demonstrated in the settlement and post-settlement processes of marine invertebrates (Raimondi 1990, Lopez et al. 1998, Uriz et al. 1998) emphasising the importance of these factors in the study of benthic population dynamics.

The adequate study of the relationship between habitat variables and settlement success and recruitment level can permit the analysis of their spatial and temporal variability, facilitating our understanding of the role of these events in the dynamics of fish communities (Caley et al. 1996). Most studies on settlement and recruitment
processes of fishes have been conducted on small spatial and temporal scales (see Doherty 1991, Jones 1991 and references therein), however, studies conducted on scales of kilometres along the coast and over a number of years are rare (Fowler et al. 1992, Tolimiieri 1995, 1998, Caselle and Warner 1996, Levin et al. 1997, Vigliola et al. 1998). As several authors have pointed out (e.g. Dayton and Tegner 1984), the scale of a study may influence the patterns that emerge. Therefore, research on these processes should include their spatial and temporal variation at different scales. This procedure would allow to determine whether patterns observed at small scales are also exhibited at larger scales (Levin et al. 1997).

In this paper, we have studied the settlement success and recruitment level of three common benthic littoral species of blennoids (*Aidablennius sphynx*, *Parablennius incognitus* and *Tripterygion tripteronotus*) from the NW Mediterranean Sea (Macpherson 1994). Three localities were studied separated ca. 50 km from each other over a period of four years. We selected these species because they are taxonomically close, they live in the same littoral zone and habitats, and they settle to the bottom and recruit to the adult population at nearly the same time. These similarities can provide interesting information about the generality of the patterns observed.

The objectives of this study are the following: 1) to determine which habitat characteristics have a significant influence in settlement, considering the descriptive variables of the substratum and the presence of adult conspecifics and 2) once the habitat variables that affect settlement have been delimited, to analyse the importance of spatial and temporal variations of settlement success and recruitment level. We have considered the settlement success to be the maximum number of new individuals observed during the settlement period and recruitment level to be the number of new individuals at the end of the settlement period that will incorporate into adult populations.

**STUDY SPECIES AND AREA**

Blennids and three-fin blennids (Families Blenniidae and Tripterygiidae, respectively) form one of the most common groups of the Mediterranean rocky shore fishes (Corbera et al. 1996). On the coast of the NW Mediterranean Sea one finds about 18 species, along the shallow zones of the littoral mainly in the upper 0 to 1 m below the surface (Zander 1986). The three most abundant species are *Aidablennius sphynx*, *Parablennius incognitus*, and *Tripterygion tripteronotus* with a maximum of 7 individuals of each species per m² (Illich and Kotrschal 1990, Macpherson 1994). It is these 3 species which will be considered in this work.
Some life history characteristics of these fishes are known (e.g. Koppel 1988, Abel 1993). The breeding season is from February until July. Mating males usually build nests during this season and attend the deposited eggs (e.g. Wirtz 1977, Almada and Santos 1995, Kraak 1996), which are laid on the rocky shoreline. Once hatched, larvae disperse offshore. Little information is available on this process and on the pelagic phase of the life cycle. For some Mediterranean blennoid species, larval development is known and described (Sabatés 1994). The larvae of the three studied species are differently distributed in the plankton: the larvae of Tripterygion tripteronotus hardly withdraw from the coast (ca. 100 - 300m), whereas the larvae of Aidablennius sphynx and Parablennius incognitus can be found various miles off shore (Sabatés 1994 and personal communication). Blennids and three-fin blennids, in general, have a short life span from 2 to 5 years (Gordina et al., 1972, Kotrschal and Goldschmid 1981 and unpublished data). Adults and juveniles of these common species are preyed upon by other fish species (e.g. Serranus cabrilla, Oblada melanura, personal observations).

Very little is known about settlement processes and the settler's habitat needs. The rocky substrate of the shallow zone along the Spanish coast of the NW Mediterranean is covered by the same dominant communities, mostly algae, barnacles (Chthamalus stellatus) and the bivalve Mytilus galloprovincialis (Ros et al. 1985). The most dominant species of the algal community are Corallina elongata, C. granifera, Cladophora spp., Rissoella verruculosa, Lithophyllum tortuosum, Ralfsia verrucosa, and Enteromorpha spp. and usually their abundances are maintained stable over the season when settlement takes place (Ros et al. 1985, Ballesteros 1987). Only a few species (e.g. Cystoseira mediterranea, Enteromorpha spp.) show alterations in their abundance between different months with higher abundances in May and June.

MATERIAL AND METHODS

This study is divided in three parts based on the two objectives above. First, we investigated the habitat characteristics that best explain the abundance of new settlers by a correlative approach. Second, to test the effects of the significant habitat characteristics (algal cover and presence of conspecific adults, see Results), we experimentally manipulated both variables to detect possible causal relationships with abundances of settlers. In the last part, settlement and recruitment were analysed for differences between localities and years.

Habitat selection

Three localities along the rocky shore of the Costa Brava, in the NW Mediterranean Sea, were sampled. The localities were Port de la Selva, the Medes
Islands, and Blanes, (Fig. 4.1), and are roughly 50 km apart. Data collection has been carried out along rocky walls, following transects between the surface and 1.5 m depth, during the four settlement seasons from 1994 to 1997.

Data on settlement and habitat were collected by sampling 14 transects in July and August of every year. Five transects were sampled by snorkelling in Port de la Selva, (totalling to 109 m²), 6 transects in the Medes Islands (52 m²), and 3 transects in Blanes (69 m²). The area of each transect varied between 6 and 46 m² because the number and length of the transects were limited by topographic characteristics of the locale and ease of access during the whole settlement season. Each wall was horizontally separated by discontinuities such as sandy beaches or deep intrusions, and vertically in depth by sandy bottoms or pebbles. While algal and barnacle communities were similar at the three localities, the bivalve *Mytilus galloprovincialis* was not present in Blanes.
Three dives per transect and year were carried out at each locality during the settlement season. Along each transect, the observer swam very slowly, from one end of the transect to the other, and a 1 m² square frame was gently placed on the bottom in order not to disturb and scatter the fishes. In each frame, divers recorded A) the percentage of each substratum type: 1) bare rock; 2) small turf algae, 0.5-1 cm; 3) long turf algae; 1-2 cm; 4) long turf algae > 2 cm; 5) Mytilus galloprovincialis; B) rugosity, 4 defined classes, using the chain method (Luckhurst and Luckhurst 1978); and C) slope, classified as gentle (0 to 15%), pronounced (16 to 30%), steep (31 to 60%), and very steep (> 60%). The substrate type "bare rock" included zones with the encrusting algae Ralfsia verrucosa and the occasional presence of short algae (< 0.5 cm in height, e.g. Enteromorpha clathrata). Individuals of all species (blenniid and three-fin blenniid) present in each 1 m² quadrant were counted and their sizes recorded, but only the three most abundant species, Aidablennius sphynx, Parablennius incognitus, and Tripterygion tripteronotus, have been analysed. Size was estimated by plastic trays bearing the silhouettes of individuals of different size-classes (0.5 cm increments) to minimize errors (e.g. Harmelin-Vivien et al. 1995; García-Rubies and Macpherson 1995). New settlers of the three species, with total length of about 1.0-1.5 cm, were easily distinguishable from each other: A. sphynx is practically unpigmented when settling, whereas P. incognitus was slightly pigmented similar to the adult color pattern. T. tripteronotus was recognisable by its body shape and a color pattern similar to adults.

A stepwise multiple regression analysis was made on each of the three localities to determine which habitat variable best explained the abundance of the new settlers. In total, nine independent variables were taken into consideration: the percentages of the five cover categories, rugosity, slope and the two fish variables (number of adult conspecifics and non-conspecifics). Normal probability plots were produced to check whether the assumption of normality is violated and means were plotted against standard deviations to check for outliers.

**Effect of substratum type and densities on settlement**

All of the following experiments were done on rocky walls in Blanes, Spain, in the upper littoral zone during the 1995 settlement season. Predominant winds and waves are from the north-east to the east and walls had nearly the same orientation, so that atmospheric and oceanographic conditions were the same along their whole length. Nearly homogenous walls, of little rugosity and without intrusions or extrusions, were selected. The experiments could only be conducted during the peak settlement period (for Aidablennius sphynx in July and for Parablennius incognitus and Tripterygion tripteronotus in August) to get a sufficient number of individuals.
Based on our preliminary results of 1994, "bare rock" was found to explain best the variation in settlement of *A. sphynx*, consequently, we manipulated the density of this substratum type to test its effect on settlement of this species. The same procedure was carried out in *P. incognitus* and *T. tripteronotus*, using "small turf algae (0.5-1 cm height)". To analyse the effect of substratum type, 1 m² quadrants were manipulated by scraping algae from surfaces, leaving selected densities (bare rock for *A. sphynx* and small turf algae for *P. incognitus* and *T. tripteronotus*) of different percentages: 20% (low); 50% (medium); and 80% (high); with 4 replicates for each density. A 1x1 m PVC frame, subdivided in 16 smaller squares, was used to quantify the percentage of substratum type. The distance between the quadrants was at least 5 m. Each quadrant was isolated from the adjacent areas by additionally scraping a 1.5 m wide section around the perimeter and then applying bleach so no living organism would remain. No artificial effect of bleach application was noted and no settlers were observed in the cleaned strips during the experiment. This procedure was used instead of artificial small rocks because it is believed to reflect a more natural condition that an individual finds when settling. All the adults and juveniles of blennoid species were removed from the quadrants to eliminate their possible effect on settlement. After 24 hours, the number of new settlers per m² was counted for each of the 3 densities and all 4 replicates. This procedure was repeated three times during the month of peak settlement for each species. No adults (conspecifics or non conspecifics) were observed in the quadrants or in the cleaned zone around the quadrants during the experiments.

The effects of algal densities and day of experiment on the abundance of settlers were determined in a two-factor ANOVA and differences among means were assessed using the Tukey HSD test.

**Effect of presence/absence of conspecifics on settlement**

To analyse the influence of the presence of conspecific adults on the abundance of new settlers, quadrants similar to those used above were used, but with constant substrate conditions in the presence or absence of adults. To test the effect on *Aidablennius sphynx*, quadrants of bare rock were used. For *Parablennius incognitus* and *Tripterygion tripteronotus*, a cover density of more than 80% of small turf algae (0.5-1 cm in height) was used. The density of each of these species is known to be from 1-5 ind./m² along this coast (Macpherson 1994). Given this, an adult density of 2 to 3 ind./m² was tested for its influence on settlement. For each of the species, 4 quadrants without and 4 with conspecifics were examined. To exclude possible migrations of settlers, quadrants with and without adults were situated on two different walls, separated horizontally on both sides by either deep and wide intrusions or sandy beaches, and vertically on the bottom
by sandy substrate or pebbles. The distance between the quadrants was 3 to 5 m. To avoid adult migrations from the nearby areas into the quadrants, all individuals on both walls were collected, leaving only the desired 2 to 3 adults per quadrant. Two days prior to the experiment, the number of adults per quadrant was observed and if the adult densities differed from 2-3 ind./m², their numbers were adjusted by replacing or removing individuals. In the majority of the cases the adults were males sitting in their nests which facilitated their remaining in the quadrant. Once verified that adult density remained stable in the quadrants, all juveniles were captured and 24 hours later the number of new settlers in each quadrant was counted. This experiment was repeated on 5 different days.

The effects of presence/absence of adult conspecifics and day of settlement were determined in a two-factor ANOVA and differences among means were compared using the Tukey HSD test.

Study of variations in settlement success and recruitment level between localities and years

To analyse a possible variation in settlement success and recruitment level between localities and years, and to quantify both events, the 14 transects were sampled weekly from June to first half of October, when permitted by the weather conditions. During each dive settlers of all three species were counted and their sizes noted as above. The maximum number of settlers observed per settlement season was assumed to indicate settlement success, for each transect and year. Recruitment level for each species was estimated using the number of individuals left after the end of the settlement season, when no new settlers (unpigmented or slightly pigmented fish) were observed.

Because of the different numbers of transects for each locality, data from transects within localities were pooled. As a result of the differences in lengths of these transects, numbers of settlers were standardized to ind./m² suitable substrate. Suitable habitat for Aidablennius sphynx was bare rock. For Parablennius incognitus and Tripterygion tripterontus cover of small turf algae (0.5 - 1 cm in height) were used. These algal covers were determined as the preferred substrate for each species (see Results). The variation of settlement and recruitment between localities and years was then determined in a two-factor ANOVA. The differences among means were assessed using the Tukey HSD test.

We also tested if settlement and recruitment success were influenced by the sizes of the transects. The same standardised data set as above was used. A general linear
regression model was applied to analyse the relationship between the abundance of settlers and recruits and the amount of suitable substrate available for each transect.

In addition to the statistics described above, we tested for outliers by plotting means versus standard deviations. Cochran's test was used to test for heterogeneity of variances. However, no transformations were effective, therefore raw data were used, since sample sizes were sufficiently large to minimize Type I error (Underwood 1997).

RESULTS

The weekly censuses showed that settlement season started in second half of June for Aidablennius sphynx, in the first half of July for Parablennius incognitus and Tripterygion tripteronotus, lasting until October for all three species. Settlement patterns were found to be similar for all three blennoids: few settlers per day and no shoal aggregations on the substrate. Once settled, fish remain benthic and live in the same habitats as adult conspecifics. Settlers of A. sphynx and T. tripteronotus remained on the surface of the rock, their colour pattern matching the substratum. Settlers of P. incognitus also have their colour matching the environment, although they used the rugosity of the rocks as hiding places. Peak settlement was recorded during the second half of August and first half of September, between 8 - 11 weeks after the arrival of the first settlers for A. sphynx, and 5 - 8 weeks for P. incognitus and T. tripteronotus. The last few settlers of P. incognitus and T. tripteronotus were observed in the last half of September, and of A. sphynx in the first half of October. No clear differences in the timing of first arrival of settlers was observed between localities and years.

Effect of habitat characteristics on settlement

The means of the 7 different substratum characteristics did not change significantly between each transect of each locality during the settlement season (Kruskal-Wallis test, p > 0.95, in all cases) or between years (Kruskal-Wallis test, p > 0.80, in all cases). This consistency was in a large part a result of the algae Corallina elongata which maintains a near constant coverage over years and within seasons (Ballesteros 1987). For this reason and in order to simplify further analysis for each locality, data from transects were pooled for each locality.

The results from the stepwise multiple regression analysis indicate that the type of algal cover and the presence of adult conspecifics significantly effect the abundance of settlers and post-settlers on the rocky shore of all three species (Table 4.1). However, the preferred substrate type and other wall characteristics differ between the species. The variation in the abundance of Aidablennius sphynx is best explained by the category
"bare rock". The amount of variance explained by the multiple regression of this type of cover is high in all three localities with the highest correlations occurring in Blanes and Port de la Selva. Negative correlations were obtained for long turf algae, *Mytilus galloprovincialis*, rugosity and slope in some localities.

**Table 4.1.** Stepwise multiple regression coefficients for sources of variation of settlement of A) *Aidablennius sphynx*, B) *Parablennius incognitus*, and C) *Tripterygion tripteronotus*, for different localities. The dependent variables are the 7 characteristics of the habitat (type of algal cover, *Mytilus galloprovincialis*, rugosity, and slope) and two fish variables (number of adult conspecifics and non-conspecifics). Only significant relationships are shown (**p < 0.001, *p < 0.01, *p < 0.05).**

<table>
<thead>
<tr>
<th>Independent variable</th>
<th>Blanes</th>
<th>Coefficient</th>
<th>$r^2$</th>
<th>p</th>
<th>Medes Islands</th>
<th>Coefficient</th>
<th>$r^2$</th>
<th>p</th>
<th>Port de la Selva</th>
<th>Coefficient</th>
<th>$r^2$</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>A) Aidablennius sphynx</strong></td>
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<td></td>
<td></td>
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</tr>
<tr>
<td>No to scarce algae</td>
<td>0.249</td>
<td>0.491 ***</td>
<td>0.855</td>
<td>***</td>
<td>0.350***</td>
<td>0.434</td>
<td>0.424</td>
<td>***</td>
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<tr>
<td>Long turf algae</td>
<td>-0.347</td>
<td>0.011 *</td>
<td></td>
<td></td>
<td>-0.715</td>
<td>0.105</td>
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<tr>
<td><em>Mytilus</em></td>
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<td></td>
<td></td>
<td></td>
<td>-1.150</td>
<td>0.011 *</td>
<td></td>
<td></td>
<td>-0.256</td>
<td>0.029 ***</td>
<td></td>
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<tr>
<td>Rugosity</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>-0.715</td>
<td>0.105</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Slope</td>
<td>-0.659</td>
<td>0.047 ***</td>
<td></td>
<td></td>
<td>-0.276</td>
<td>0.007 *</td>
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</tr>
<tr>
<td>Adult conspecifics</td>
<td>0.483</td>
<td>0.051 ***</td>
<td>0.208</td>
<td>***</td>
<td>0.027 ***</td>
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<tr>
<td><strong>B) Parablennius incognitus</strong></td>
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<td></td>
</tr>
<tr>
<td>Small turf algae</td>
<td>0.226</td>
<td>0.136 **</td>
<td>0.243</td>
<td>0.022</td>
<td>1.706</td>
<td>0.448</td>
<td>***</td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rugosity</td>
<td></td>
<td></td>
<td>0.591</td>
<td>0.323</td>
<td>0.607</td>
<td>0.022</td>
<td>***</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Adult conspecifics</td>
<td>0.095</td>
<td>0.087 **</td>
<td></td>
<td></td>
<td>0.348***</td>
<td>0.037 ***</td>
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<tr>
<td><strong>C) Tripterygion tripteronotus</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small turf algae</td>
<td>0.376</td>
<td>0.332 ***</td>
<td>0.090</td>
<td>0.251***</td>
<td>0.676</td>
<td>0.343</td>
<td>***</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Slope</td>
<td>-0.179</td>
<td>0.046 **</td>
<td></td>
<td></td>
<td>-0.149</td>
<td>0.119</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult conspecifics</td>
<td>0.168</td>
<td>0.171 *</td>
<td>0.243</td>
<td>0.069 ***</td>
<td></td>
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</tbody>
</table>

Settlement variance of *Parablennius incognitus* and *Tripterygion tripteronotus* was mainly explained by the substrate covered with "small turf of algae". In both species the amount of variance explained is higher in Port de la Selva than in the other localities. The importance of the other substrate characteristics differ between the species (e.g. rugosity is positively related with *P. incognitus*, slope negatively with *T. tripteronotus*).
Test of the effect of algal density on settlement

The results from the two-factor ANOVA show that only the percentage of algal cover explains the variance of abundance of settlers. No significant differences exist over time. Furthermore, algal cover and sampling date interaction show no significant relationship (Table 4.2), consequently data collected on different days were pooled for further analyses.

Table 4.2. Results of a two factor analysis of variance used to determine if the number of newly settled individuals of the species A) Aidablennius sphynx, B) Parablennius incognitus, and C) Tripterygion tripteronotus, is influenced by the algal density in the experimental quadrants (1 m²). Three different densities of algal cover per quadrant were tested: low (< 20%), medium (50%) and high (> 80%), with 4 replicates at each density. Selected algae cover varied between species, no algae to scarce small algae < 0.5 cm for A. sphynx, and small turf algae, 0.5-1.0 cm for P. incognitus and T. tripteronotus (see text for more explanations). Day refers to sampling days.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>A) Aidablennius sphynx</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Day (A)</td>
<td>2</td>
<td>0.282</td>
<td>2.096</td>
<td>0.100</td>
</tr>
<tr>
<td>Algal cover (B)</td>
<td>2</td>
<td>7.801</td>
<td>58.044</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>A x B</td>
<td>4</td>
<td>0.249</td>
<td>1.855</td>
<td>0.091</td>
</tr>
<tr>
<td>Error</td>
<td>45</td>
<td>0.134</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B) Parablennius incognitus</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Day (A)</td>
<td>2</td>
<td>0.238</td>
<td>1.007</td>
<td>0.414</td>
</tr>
<tr>
<td>Algal cover (B)</td>
<td>2</td>
<td>5.533</td>
<td>23.440</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>A x B</td>
<td>4</td>
<td>0.112</td>
<td>0.476</td>
<td>0.867</td>
</tr>
<tr>
<td>Error</td>
<td>45</td>
<td>0.236</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C) Tripterygion tripteronotus</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Day (A)</td>
<td>2</td>
<td>0.245</td>
<td>1.000</td>
<td>0.417</td>
</tr>
<tr>
<td>Algal cover (B)</td>
<td>2</td>
<td>1.718</td>
<td>7.018</td>
<td>0.002</td>
</tr>
<tr>
<td>A x B</td>
<td>4</td>
<td>0.102</td>
<td>0.418</td>
<td>0.904</td>
</tr>
<tr>
<td>Error</td>
<td>45</td>
<td>0.245</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Aidablennius sphynx settled in quadrants with high abundance of "bare rock" (80%). Settlement did not occur if this substrate type was less frequent than 50%. Mean abundances were significantly higher (Tukey HSD test) in quadrants with low algal densities, but high abundance of "bare rock" (high > medium > low, p = 0.0001), and no differences between medium and low densities of "bare rock" were found (p = 0.98, Figure 4.2). Parablennius incognitus preferred to settle on high algal densities (> 80%)
of "small turf of algae". Mean settlement abundances were significantly higher in quadrants with high algal densities than with medium (50%) and low (< 20%) densities (p = 0.04, Figure 4.2). *Tripterygion tripteronotus* showed an intermediate pattern, with no preference between medium and high densities of algal cover. When the densities of 50% turf algae and 50% bare rock could be selected, quadrants with low density cover (< 20%) were avoided (p = 0.0002, Fig. 4.2).

Based on results from experiments on algal densities and habitat characteristics, the hypothesis that algae cover on this coast effects settlement of larval fish is accepted. A strong effect of substrate type on settlement of *Aidablennius sphynx*, *Parablennius incognitus* and *Tripterygion tripteronotus* seems to exist.

![Graph showing the effect of three densities of preferred substrate on the density of blennoid settlers (mean ± SE).](image)

**Fig. 4.2.** Effect of three densities of preferred substrate on the density of blennoid settlers (mean ± SE). "Bare rock" cover type was tested for *Aidablennius sphynx* (AS), "small turf algae" cover type for *Parablennius incognitus* (PI), and *Tripterygion tripteronotus* (TT). Three different levels of preferred substrate densities (low 20%, medium 50%, and high >80% cover) were used.

**Test of the effect of presence/absence of conspecifics on settlement**

A significant relationship between conspecific presence or absence could not be found for any of the three species. Neither temporal variation or an influence of the combination factors detected a significant relationship with the abundance of settlers (two-factor ANOVA, Table 4.3).
Table 4.3. Results of a two factor analysis of variance used to determine if the number of newly settled individuals of the species A) Aidablennius sphynx, B) Parablennius incognitus, and C) Tripterygion tripteronotus, is influenced by the presence or the absence of adult conspecifics in the experimental quadrants (1 m²). Between 1 and 3 adults were present per quadrant. Day represents sampling days.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>A) Aidablennius sphynx</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Day (A)</td>
<td>2</td>
<td>0.038</td>
<td>2.096</td>
<td>0.100</td>
</tr>
<tr>
<td>Algal cover (B)</td>
<td>1</td>
<td>0.226</td>
<td>58.044</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>A x B</td>
<td>2</td>
<td>0.029</td>
<td>1.855</td>
<td>0.091</td>
</tr>
<tr>
<td>Error</td>
<td>30</td>
<td>0.087</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B) Parablennius incognitus</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Day (A)</td>
<td>2</td>
<td>0.124</td>
<td>1.007</td>
<td>0.414</td>
</tr>
<tr>
<td>Algal cover (B)</td>
<td>1</td>
<td>0.012</td>
<td>23.440</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>A x B</td>
<td>2</td>
<td>0.060</td>
<td>0.476</td>
<td>0.867</td>
</tr>
<tr>
<td>Error</td>
<td>30</td>
<td>0.167</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C) Tripterygion tripteronotus</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Day (A)</td>
<td>2</td>
<td>0.102</td>
<td>0.485</td>
<td>0.747</td>
</tr>
<tr>
<td>Algal cover (B)</td>
<td>1</td>
<td>0.004</td>
<td>0.195</td>
<td>0.890</td>
</tr>
<tr>
<td>A x B</td>
<td>2</td>
<td>0.034</td>
<td>0.162</td>
<td>0.956</td>
</tr>
<tr>
<td>Error</td>
<td>30</td>
<td>0.211</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Figure 4.3 shows the mean number of settlers in quadrants with adult conspecifics present or absent. Mean settler abundances were not found to be significantly different between quadrants (HSD Tukey test, p > 0.7). Thus, the hypothesis that settlement is directly affected by adult conspecifics, occupying the same habitat as settlers, is not accepted since no significant relationship was detected. The strong correlation between settlers and adult conspecifics in the stepwise multiple regression therefore, seems to be causal.
Variations in settlement success and recruitment level between localities and years

Settlement success of the three species studied for different localities and years is shown in Figure 4.4. For all analyses of variance Tukey HSD tests were carried out (see Material and Methods), but for simplicity only significant pairwise comparisons are noted. ANOVAs showed no spatial (between localities) or temporal (between years) differences in settlement success for *Aidablennius sphynx* or *Parablennius incognitus* (Table 4.4).
Fig. 4.4. Maximum density (mean per transect and $m^2 \pm SE$) of settlers for A) *Aidablennius sphynx*, B) *Parablennius incognitus*, and C) *Tripterygion tripteronotus* observed per locality and year. The maximum density is taken as an estimate of settlement success. Note that y-axes vary.
Table 4.4. Results of a two factor analysis of variance used to determine differences in settlement success and recruitment level of the species A) Aidablennius sphynx, B) Parablennius incognitus, and C) Tripterygion tripteronotus, between the four sampling years (1994-1997) and the three localities (Blanes, Medes Islands, and Port de la Selva)

<table>
<thead>
<tr>
<th>Settlement</th>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>A) Aidablennius sphynx</td>
<td>Day (A)</td>
<td>3</td>
<td>23.727</td>
<td>2.600</td>
<td>0.064</td>
</tr>
<tr>
<td></td>
<td>Algal cover (B)</td>
<td>2</td>
<td>27.410</td>
<td>3.004</td>
<td>0.060</td>
</tr>
<tr>
<td></td>
<td>A x B</td>
<td>6</td>
<td>3.842</td>
<td>0.421</td>
<td>0.861</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>44</td>
<td>9.123</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B) Parablennius incognitus</td>
<td>Day (A)</td>
<td>3</td>
<td>0.038</td>
<td>0.441</td>
<td>0.778</td>
</tr>
<tr>
<td></td>
<td>Algal cover (B)</td>
<td>2</td>
<td>0.226</td>
<td>2.588</td>
<td>0.118</td>
</tr>
<tr>
<td></td>
<td>A x B</td>
<td>6</td>
<td>0.029</td>
<td>0.333</td>
<td>0.835</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>44</td>
<td>0.575</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C) Tripterygion tripteronotus</td>
<td>Day (A)</td>
<td>3</td>
<td>3.740</td>
<td>13.564</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Algal cover (B)</td>
<td>2</td>
<td>1.399</td>
<td>5.074</td>
<td>0.010</td>
</tr>
<tr>
<td></td>
<td>A x B</td>
<td>6</td>
<td>0.286</td>
<td>1.038</td>
<td>0.414</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>44</td>
<td>0.276</td>
<td></td>
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</tr>
</tbody>
</table>

For Tripterygion tripteronotus, however, settlement success varied significantly between years, with higher settlement success in 1997 than in other years (Tukey HSD test, p < 0.007), and between localities, with higher settlement success in Medes (Tukey HSD test, p < 0.02). The number of recruits (A. sphynx $r^2 = 0.64$, P. incognitus $r^2 = 0.66$ and T. tripteronotus $r^2 = 0.86$, p < 0.00001 in all cases) was positively and significantly correlated with the maximum number of settlers for each species.

However, the two-way ANOVA performed on recruitment level data showed a different result than the results from settlement success (Table 4.4 continued, Fig. 4.5).
Recruitment for *Aidablennius sphynx* was significantly higher in Port de la Selva than in Blanes (Tukey HSD test, \( p = 0.05 \)), recruitment level of 1997 was significantly higher than in previous years (Tukey HSD test, \( p = 0.02 \)). For *Parablennius incognitus* spatial and temporal patterns of recruitment level were quite similar as for settlement success, the exception was Port de la Selva with significantly higher levels than Blanes (Tukey HSD test, \( p = 0.001 \)). For *Tripterygion triptonotus*, recruitment level did not vary significantly between localities, but was clearly different between years, with higher levels in 1997 than in previous years (Tukey HSD test, \( p = 0.0003 \)).

To test the relationship of the amount of suitable substrate on settlement success, a general linear regression between the maximum abundance of settlers per transect and the amount of suitable substrate available per transect was carried out. Data from all localities and years were pooled. A significant relationship was found for *Aidablennius sphynx* (\( r^2 = 0.79, p < 0.001 \)) and *Parablennius incognitus* (\( r^2 = 0.78, p < 0.001 \)) (Fig. 4.6 A, B). No relationship was found (\( r^2 = 0.19, p = 0.001 \)) for *Tripterygion triptonotus*. As noted from the statistical results above, for *T. triptonotus*, highest densities were found in Medes and in 1997. When a linear regression was repeated using

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<th>Source</th>
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<th>( F )</th>
<th>( p )</th>
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</thead>
<tbody>
<tr>
<td><strong>A) Aidablennius sphynx</strong></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Day (A)</td>
<td>3</td>
<td>17.778</td>
<td>3.276</td>
<td>0.029</td>
</tr>
<tr>
<td>Algal cover (B)</td>
<td>2</td>
<td>19.682</td>
<td>3.627</td>
<td>0.034</td>
</tr>
<tr>
<td>A x B</td>
<td>6</td>
<td>5.782</td>
<td>1.066</td>
<td>0.397</td>
</tr>
<tr>
<td>Error</td>
<td>44</td>
<td>5.426</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>B) Parablennius incognitus</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Day (A)</td>
<td>3</td>
<td>0.672</td>
<td>2.183</td>
<td>0.103</td>
</tr>
<tr>
<td>Algal cover (B)</td>
<td>2</td>
<td>2.309</td>
<td>7.500</td>
<td>0.002</td>
</tr>
<tr>
<td>A x B</td>
<td>6</td>
<td>0.416</td>
<td>1.350</td>
<td>0.256</td>
</tr>
<tr>
<td>Error</td>
<td>44</td>
<td>0.308</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>C) Tripterygion triptonotus</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Day (A)</td>
<td>3</td>
<td>1.494</td>
<td>19.123</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Algal cover (B)</td>
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<td>0.178</td>
<td>2.282</td>
<td>0.113</td>
</tr>
<tr>
<td>A x B</td>
<td>6</td>
<td>0.043</td>
<td>0.556</td>
<td>0.762</td>
</tr>
<tr>
<td>Error</td>
<td>44</td>
<td>0.078</td>
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</table>
only the data sets for Medes ($r^2 = 0.32$, $p < 0.01$) and for all localities in 1997 ($r^2 = 0.72$, $p < 0.001$), a better relationship was found (Fig. 4.6 C). The combination of the two gave the highest correlation between maximum numbers of settlers and amount of available suitable habitat ($r^2 = 0.95$, $p < 0.005$).

To test if settlement was lower on isolated patches of suitable habitat versus continuous, larger areas of suitable habitat, different models were applied on settlers, standardized by the area of suitable habitat (No./m$^2$ suitable habitat), and the amount of suitable habitat available per transect. No relationship was found for all three species. Thus, the abundance of settlers per surface area of suitable substrate is independent of the amount of the preferred substrate available along a transect (Fig. 4.7).
Fig. 4.5. Density (mean per transect and m² ± SE) of recruits for A) Aidablennius sphynx, B) Parablennius incognitus, and C) Tripterygion tripteronotus observed at the end of the settlement season per locality and year. Note that y-axes vary.
Fig. 4.6. Relationship between settlement success and suitable habitat available per transect for A) *Aidablennius sphynx*, B) *Parablennius incognitus*, and C) *Tripterygion tripteronotus*. For *A. sphynx* and *P. incognitus* all years and transects are shown, while for *T. tripteronotus* only 1997 is shown for all transects (see text for further explanations). Note that x- and y-axes vary.
Fig. 4.7. Relationship between settlers standardized by the area of suitable habitat and the amount of suitable habitat available per transect for A) Aidablennius sphynx, B) Parablennius incognitus, and C) Tripterygion triptonotus. For A. sphynx and P. incognitus all years and transects are shown, while for T. triptonotus only 1997 is shown for all transects (see text for further explanations). Note that x- and y-axes vary for the three species.
DISCUSSION

Substratum characteristics clearly influence the small-scale settlement of the three blennoid fishes. New individuals of Aidablennius sphynx occupied quadrants with a higher percent of rocky areas with no algal to scarce algal cover or covered by encrusting or occasional small algae. The other two species, Parablennius incognitus and Tripterygion triploteronotus, settled on clearly different substrata dominated by small turf algae. On the other hand, the presence or absence of adult conspecifics seems not to have a significant effect on settlement of the three species. Similar relationships have been described for other tropical and temperate fishes in which habitat characteristics influenced settlement (Sale et al. 1984, Doherty 1991, Levin 1991, Williams 1991).

Some authors have analysed the relationship between the density of new settlers and some substratum variables, finding different patterns. Marliave (1977) found that newly settling littoral fishes (e.g. Artedius lateralis, Leptocottus armatus) show substratum preferences based on tactile cues and light transmission. Carr (1991, 1994) demonstrated that spatial and temporal variation in the density of the giant kelp, Macrocystis pyrifera, explained much of the variation in the recruitment of Paralabrax clathratus as well as in other rockfish species. Macpherson (1998) found that settlers belonging to three species of the genus Diplodus showed a clear preference for specific habitats. A range of effects of adult conspecifics have been demonstrated, either a facilitation (Forrester 1990), inhibition (Shulman 1985, Tupper and Hunte 1994) or no effect on settlement (Doherty 1983, Sweatman 1985, Tupper and Boutilier 1995a). Levin (1993) demonstrated that resident conspecifics of Tautogolabrus adspersus did not affect small-scale variability in recruitment, where recruitment was higher in areas with dense understory of foliose and filamentous algae than in substrates covered by crustose algae. For this species, algal cover was an important predictor of variability in recruit abundance in one region, but not in others (Levin et al. 1997). Booth (1992) found that juveniles of Dascyllus albisella do not interact with adults, being conspecific juvenile density a major factor influencing settlement. The presence of conspecifics reduced settlement in Stegastes planifrons, but the percent cover of corals can affect significantly settlement dynamics (Tolimieri 1995).

Microhabitat choice at settlement of the three species matched quite well the pattern of adult conspecific distribution. Therefore, the substrate selection could confer a greater fitness on preferred microhabitat, as it has been observed in Stegastes planifrons, S. leucostictus and S. variabilis from the Caribbean Sea (Wellington 1992, Tolimieri 1995). Settlers of the three blennoid species showed similar behaviour as adults (Zander 1986, Abel 1993), remaining in the same type of habitats. Similar behaviour patterns were observed by other authors in littoral species (Marliave 1977). The overlap between
adult and settler distributions for the three species suggests that the selected habitat at settlement can provide some advantages for the species, for example protection and food. Several authors (Levin 1993, Tolimieri 1995) suggested that for species where adults and juveniles shared the same habitats, their co-occurrence indicated suitable zones for an adequate development. Consequently, differences in the adult abundances can be attributed to differential settlement (Fowler et al. 1992, Risk 1997). In the present study, the relationship between settlers, recruits, and adult distributions has not been evaluated as it has in other studies (e.g. Wellington 1992) and further studies with more detail need to be done. Gibson (1993) emphasised that future studies should be conducted on settlement distribution patterns, analysing if they are the result of an initial choice by larvae or if preferred substratum is chosen after a random settlement, or if it is simply an elimination of individuals from unfavourable habitats (also see Connell and Jones 1991).

For the three blennoids studied here, preferences for a specific substratum type at settlement can explain, on the small scale, the abundance of new settlers in a locality. This abundance will be related to the availability of habitat suitable for the species and, additionally, will be independent of the rocky reef size. Similar results have been provided by other authors in coral reef fishes (Williams 1991, Fowler et al. 1992, Tolimieri 1995, Risk 1997). Although the variations in habitat can explain much of the variation in settlement success and recruitment (Carr 1994), some important considerations should be taken into account in order to understand the variability on different spatial and temporal scales. The amount of suitable habitat accounts for some of the variation of settlement success, thus, the large variability observed in maximum settler density for the three blennoids suggests that, additionally, other processes are influencing settlement and later recruitment.

Numerous authors have emphasised the importance of analysing the relationship between settlement, recruitment, and habitat availability at different scales, in order to know how well patterns exhibited at small scales explain patterns observed at larger scales (Doherty 1991, Caley et al. 1996). This analysis is a central topic in ecological studies to determine the mechanisms influencing population dynamics of any species (Dayton and Tegner 1984). Unfortunately, comparisons of different spatial and temporal scales are rarely done in studies of fishes and invertebrates. Fowler et al. (1992), working on recruits of Chaetodon rainfordi at different spatial scales (from regions separated by hundreds of km at different sites on a coral reef), found that the distribution pattern of recruitment was consistent each year, and several regions always had higher recruitment rates than others. Tolimieri (1995) showed that microhabitat choice had consequences on the small-scale recruitment patterns of Stegastes planifrons, but not on
the large-scale variation. Levin et al. (1997) found that the variation in the densities of newly recruited individuals of *Tautogolabrus adspersus* was pronounced among sites (separated by 100 to 1000 m) and among localities (separated by ca 10 km), but this pattern was not geographically homogeneous but distinct to geographic regions. Vigliola et al. (1998) observed that for three species of *Diplodus* on a large scale (ca. 1000 km of coast line) the spatial variability of settlement was higher than the temporal variability, whereas on small scale, within localities, the temporal variability was higher. Settlement success patterns of *Aidablennius sphynx* and *Parablennius incognitus* did not differ between the three localities situated along 150 km coast line and separated ca. 50 km from each other. Furthermore, the settlement success did not show any significant differences among years. These results would suggest that processes affecting settlement success at small scale did not differ from patterns observed at larger scales. *Tripterygion tripteronotus*, however, showed temporal and spatial differences.

These different patterns could be driven by processes occurring at different stages in the life of fishes, during pre-settlement or at any time during and after settlement. The importance of pre-settlement versus post-settlement processes in determining year-class strength has been widely disputed. Larval supply to a locality is thought to be a major cause of variability in settlement success of fishes (Victor 1991) and it has been considered a primary factor in the population dynamics of many fish communities (Sale 1982, Doherty 1991, Cushing 1996). Larvae of *Aidablennius sphynx* and *Parablennius incognitus* have a distribution pattern clearly different than the one observed in *Tripterygion tripteronotus*. Larvae of the former species are distributed offshore, on the continental shelf and slope (Sabatés 1994), whereas larvae of *T. tripteronotus* are as in most Tripterygiidae (Leis 1994, Brogan 1994), located inshore, between the coastline and 100-200 m offshore (Sabatés, personal communication). These differences in larval distributions, could explain, at least partially, differences observed in the pattern of settlement success. Species situated on the continental shelf are influenced by mesoscale processes, as observed in other Mediterranean species, i.e. *Diplodus sargus* (Vigliola et al. 1998), which would result in a more homogeneous spatial pattern of settlement. On the other hand, settlement of *T. tripteronotus*, could be more dependent on microscale processes, quite common in the tortuous coast of the NW Mediterranean (Ros et al. 1985), and on local oceanographic events, e.g. currents, storms, waves (Kingsford and Choat 1989, Breitburg et al. 1995, Jenkins et al. 1997). The relationship between larval and settler distributions has been analysed by several authors (see above the mentioned references) for different areas, however, the above stated hypotheses need to be investigated further and the relevant physical oceanographic processes influencing settlement on this coast determined.
The differences observed between spatial and temporal variability in settlement success and recruitment levels for each blennoid species calls the attention to the interpretation of the results. Differences between settlement and recruitment patterns can provide a more complete view of the importance of post-settlement processes and the necessity for further research. The highest significant differences (yearly variability in *Tripterygion tripteronotus*) was reflected in both, settlement and recruitment patterns, which suggests that the interannual differences are very strong and are maintained throughout the post-settlement period. The minor differences of settlement success between localities for this species, however, were not maintained over the season. On the other hand, for *Aidablennius sphynx*, temporal and spatial differences were not found significant for settlement success but were significant for recruitment level. For *Parablennius incognitus* no significant differences were found for settlement success, but a significant spatial variation in recruitment level was observed. Although correlations between settlement success and recruitment are highly significant (by the order of magnitude), the results from the ANOVA (based on variance between means) demonstrate that post-settlement processes can alter patterns of settlement success and therefore, are able to change spatial and/or temporal recruitment patterns. The period following settlement can be dominated by high mortality, probably as a result of predation or competition (e.g. Pfister 1995, 1996, Booth 1995, Beets 1997, Hixon and Carr 1997, Macpherson et al. 1997, Connell 1998), which could easily alter settlement patterns and subsequent recruitment level. Recruitment patterns are believed to influence the dynamics of the adult population (Cushing 1996). The differences between patterns of settlement success and recruitment level presented in this study stress the complexity of processes occurring between the arrival of settlers and their recruitment.

ACKNOWLEDGEMENTS

Thanks are expressed to X. Turón, A. Gordoa, M. J. Uriz, A. García-Rubies, T. Granata, E. Sala, and anonymous reviewers for helpful comments and suggestions that improved the manuscript. Thanks are also expressed to E. Benavent and G. Agell for their assistance in collecting data. This research was funded by project DGCYdT PB94-0015 of the Spanish Government.
5. The importance of unaliased time series of settlement to estimate post-settlement losses

ABSTRACT

Disagreement exists over the relative importance of processes acting before, during, and after settlement of larval reef fish. To determine these processes, it is necessary to sample the appropriate temporal and spatial scales. To quantify the relative importance of settlement and post-settlement processes, we measured settlement and survival of the rocky shore fish Aidablennius sphynx in the NW Mediterranean sea over three years. We calculated short-term post-settlement losses from differences between numbers of twice daily to daily collected settlers and weekly censused survivors.

Spatial variability for both, settlement and survival time-series, was insignificant. Therefore, we focused on temporal processes and their relevant scales. No differences in the numbers settling during the day and night were found and the smallest sampling interval needed to determine unaliased settlement was daily. On the seasonal scale, temporal variability was large, resulting in episodic settlement with peaks occurring on different days each year. On the interannual scale, durations of the settlement seasons differed from year to year, though no differences among years in the total numbers of settlers at the end of the settlement seasons were found.

Post-settlement loss rates were high, approaching those of settlement rates. Weekly per capita loss rates were not density dependent, but the effects of episodic events lead to alterations of initial settlement patterns within the week. Survival patterns were therefore decoupled from settlement and losses only depended upon settlement patterns. Since survival among years was constant, we conclude that a carrying capacity was reached and therefore populations of A. sphynx are not limited by larval supply, but rather post-settlement survival determines their adult populations. We summarize that without such high frequency sampling, providing unaliased temporal settlement patterns, post-settlement losses can not be accurately determined and their impacts on populations assessed.
INTRODUCTION

In ecological studies it is often important to examine patterns and processes in an organism's life cycle to understand the distribution and abundance of the organism (Begon et al. 1990). Therefore, demographic rates, such as birth, mortality, and growth, must be measured. This is especially applicable for reef fishes where the concept of recruitment limitation suggests that rates of larval settlement are the leading determinant of subsequent population size (Doherty and Fowler 1994). Recently, however, it has also been discussed that better estimates of mortality schedules after settlement are needed for reef fishes in order to make robust predictions about the processes that shape both life-histories and population dynamics (Caley 1998, Levin 1998).

The majority of benthic and demersal marine organisms have a two-phase life cycle with a dispersive larval phase followed by a relatively sedentary adult phase (Roughgarden et al. 1988, Hughes 1990, Sale 1991). Unlike many marine larvae that are passively transported, both temperate and coral fish larvae are capable of horizontal and vertical changes in speed and direction (Champalbert and Koutsikopoulos 1995, Leis et al. 1996). Larvae end their pelagic phase when they settle, with survivors recruiting to the adult population. Despite an increasing number of studies on settlement, variability in larval supply, and recruitment of marine organisms, very little is known about whether temporal variations in settlement have an important effect on populations (but see Jones 1990, Doherty and Fowler 1994, Pfister 1996, 1997). The role that variation in larval input plays in creating variation in abundance among local populations is dependent on the extent to which post-settlement processes modify patterns created by larval settlement (Warner and Hughes 1988).

In temperate areas, some marine fishes settle or recruit in pulses, usually in the spring and summer months (Doherty 1991, Kneib 1993, Garcia-Rubies and Macpherson 1995, Secor and Houde 1995). Although there may be well-defined peaks in larval supply, e.g. schooling (Breitburg 1989, Macpherson 1998) prior to settlement when the majority of individuals return to the adult population, there is often a period of months over which recruits establish. The settler cohort can be modelled as a function of time and space, $N(t, x)$, with inputs and outputs as:

$$N(t, x) = N_{settled} - (N_{migration} + N_{death} + N_{growth}) = N_{in} - N_{out}$$  \hspace{1cm} (5.1)

If the temporal change is continuous and a function of linear rates, then:

$$\frac{dN}{dt} = N(r_{in} - r_{out})$$  \hspace{1cm} (5.2)
where \( r_{in} \) = settlement or recruitment rate, \( r_{out} \) = post-settlement loss rate, and \( \frac{dN}{dt} \) is the net increase of the cohort, i.e. the survival rate. This simple model shows that variations in settlement rate can affect recruitment strength (Williams and Sale 1981, Sale et al. 1984, Doherty 1987). However, high juvenile mortality and other losses can also modify initial recruitment patterns (Doherty and Sale, 1983, Victor 1986a, Eckert 1987, Shulman and Ogden 1987, Robertson 1988, Sale and Ferrell 1988, Macpherson et al. 1997, Steele 1997a), leaving subsequent calculations of loss underestimated.

Although early post-settlement mortality of reef fishes is known to be high (Shulman and Ogden 1987, Sale and Ferrell 1988, Connell and Jones 1991), the magnitude and variability of mortality relative to settlement is unknown for most species (Connell and Jones 1991). Post-settlement processes such as migration, predation, and growth are also capable of modifying settlement patterns and have strong influences on recruitment success (Jones 1990, Connell and Jones 1991). Thus, it is necessary to accurately determine settlement rates in order to estimate post-settlement mortality, and to separate this from pre-settlement processes. Unfortunately, infrequent measures of settlement and recruitment can underestimate the role of post-settlement losses (Connell 1985, Booth 1992, Levin 1998).

Sampling temporal processes not frequently enough to determine the underlying trend (or undersampling the trend) is a widespread problem called aliasing. For physical (e.g. Ray 1998) and biological oceanography (Müller-Karger 1990, Taylor and Howes 1994, Wiggert et al. 1994), the importance of sampling the appropriate temporal scales is well founded as are the errors resulting from temporal undersampling. In many ecological studies, however, the problem of aliasing is not addressed (but see Manuel and O’Dor 1997, Sancho et al. 1997). For the settlement model, \( \frac{\Delta N(t, x)}{\Delta t} \) must be sampled such that \( \Delta t \) the time interval between successive samples, captures the smallest temporal variations. Therefore, frequent monitoring with small time intervals, relative to the settlement process, is necessary to estimate accurate and unaliased patterns in settlement and losses. Especially when settlement is continuous, or episodic, recruitment surveys on short-term settlement dynamics are needed to quantify fluctuations in recruitment strength (Robertson and Kaufmann 1998). Even weekly intervals between settlement and a census may obscure the actual mechanisms determining recruitment patterns (Levin 1998) given the high mortality the first days after settlement (Doherty and Sale 1985, Victor 1986b, Sale and Ferrell 1988, Connell and Jones 1991, Houde 1997, Macpherson et al. 1997) and the influence of migrations (Frederick 1997).
In addition to temporal variations, the input of larvae into reef-associated populations of fishes can be extremely variable in space (Underwood and Fairweather 1989, Sale 1990, Doherty 1991). Sale (1998) emphasizes that it is important to sample at spatial scales that are relevant to the organisms and the processes of interest. Of particular importance on spatial scales of settlement processes is the blend of passive transport and active responses to water flow near the settlement habitat (Breitburg et al. 1995). Levin (1998) concludes that the importance of different demographic processes may change with scale, site or habitat. He therefore suggests that a pluralistic approach is required to explain the dynamics of populations of reef fishes, considering both, variability in pre- and post-settlement processes.

While numerous studies on settlement, recruitment, and post-settlement processes exist for coral reef fish, covering a wide range of time and space scales, very little is known for temperate reef fish. Further, many temperate species display continuous settlement over the season (e.g. Connell and Jones 1991, Carr 1991, 1994, Levin 1993, 1994a, b, Levin et al. 1997, Tupper and Boutilier 1995a, b, Jenkins et al. 1997, Pfister 1996, 1997, Sano 1997, Chapter 4) which is not comparable to lunar cycles of most coral reef fish. This is important since temperate rocky reefs constitute a large portion of the shallow marine environment, providing habitat for diverse assemblages of temperate reef fishes (Carr 1994) and the most common families in temperate zones (e.g. Mediterranean) include species with continuous settlement. Therefore, to extend our understanding of the dynamics on rocky shores and the role of fishes in these communities, it is necessary to further investigate variability in pre- and post-settlement processes.

While no large spatial differences in settlement occurred for our study species, the rocky shore fish Aidablennius sphynx (Chapter 4), habitat selection and habitat suitability strongly influenced settlement and recruitment on small spatial scales. Similar results were found for other species (e.g. Sale et al. 1984, Carr 1994, Macpherson 1998, García-Rubies and Macpherson 1995, Tolimeri 1995). Since habitat suitability was directly correlated to settler densities of A. sphynx (Chapter 4), spatial variation can be controlled for using multiple transects and standardizing by the amount of available suitable habitat. Consequently, in this study we will focus on temporal processes and their relevant scales.

We collected settlers at two different frequencies over the settlement season: twice daily and daily to: 1) quantify settlement over different temporal scales for a rocky shore fish with episodic settlement; and 2) determine what sampling frequency is necessary to
resolve temporal patterns of settlement. Survivorship was determined from separate weekly censuses at an adjacent site. Settlement and survivorship data were used to: 1) calculate post-settlement loss rates; 2) quantify to what extent post-settlement processes modify the patterns of settlement; and 3) examine how short-term post-settlement losses can alter and alias settlement patterns.

DESCRIPTION OF THE STUDY SPECIES

Blennids (Family Blenniidae) form one of the most common groups of the Mediterranean rocky shore fishes (Corbera et al. 1996). Aidablennius sphynx is one of the most abundant species with a maximum of 7 individuals per m² (Illich and Kotrschal 1990, Macpherson 1994). The breeding season starts at the end of April, when the water temperature reaches 14 - 15° C, and extends into August. The breeding male defends the same nest and receives eggs continuously throughout the season and no nesting cycles have been observed. Broods contain up to 7000 eggs from different females in different stages of development (Kraak 1996). Once hatched, larvae disperse and have been caught several kilometers offshore (Sabatés 1994). The settlement season starts in mid-June and lasts until late September - early October. Settlement is episodic, with few settlers per day and no shoal aggregations. A. sphynx prefer substrate with no to scarce algal cover, 0 - 0.5 cm height (e.g. Ralfsia verrucosa, Enteromorpha spp), and the presence of conspecific adults has little effect on habitat selection of A. sphynx (Chapter 4). Once settled, these blennies remain benthic and continue to live in the same habitat as the adults. New settlers of A. sphynx are translucent (personal observation) and remain in the surface (0 - 0.5 m depth) as do the adults (Illich and Kotrschal 1990).

METHODS

Site description and habitat measurements

This study took place in Blanes, Spain from mid-June to the end of September, encompassing the settlement seasons of 1996, 1997, and 1998. Blanes is located along the rugged coast of the Northwestern Mediterranean Sea (41° 40' N, 2° 47' - 48' E). The shoreline is rocky substrate and the superficial zone is covered by different communities, mostly algae and barnacles. We selected 6 horizontal transects along rocky walls between the surface and 1 m depth, covering areas from 9 m² to 20 m², depending on topographical conditions. The 6 transects were located in the same small bay and were split into two sites, with 3 transects per site (Fig. 5.1). Within a site, the transects had different exposures to the open coast, however, between sites, exposures were as similar as possible. The entrance to the bay is open and we assume that processes affecting settlement are the same for the entire area (i.e. for both sites). The
The distances between transects within the two sites was from 100 to 200 m, but the distances between the transects within the same site were (with one exception) no more than 5 m (Fig. 5.1). The amount of available suitable habitat for *Aidablennius sphynx* (see Description of the study species) on each transect was measured by placing a 1 m² square PVC frame, divided with string into sub quadrants of 25 cm², on the walls and the area of suitable substrate recorded.

**Fig. 5.1.** Map showing the location of the 6 transects within the study bay in Blanes, Spain. Transects 1 d, 2 d, and 3 d were sampled daily at site 1, while transects 1 w, 2 w, and 3 w weekly at site 2.

**Sampling Methods**

To determine the temporal pattern of settlement, all settlers were collected by snorkelling slowly along 3 transect walls (site 1), passing one hand over the rocky substrate from the surface to approximately 1 m depth to scare fish out of crevices for easier collection. For survival estimates, fish were visually censused by snorkeling along the 3 transects of site 2. Prior to data collection, both snorklers sampled the same
transect to insure that both counted the same number of fish at the end of a census. Thereafter, the same person always sampled the same transects, working with the same method. Sampling errors over the seasons were consequently minimized.

For the settlement time series, newly settled fish were collected with handnets twice daily (sunrise and sunset), except when precluded by weather and sea conditions. These settlers were translucent and easily distinguishable from immigrants which had already developed color patterns. This was verified by experiments noting the development of coloration patterns over time. Newly settled, transparent individuals were kept in dialyses bags and fixed to rocky substrates in the sea and in aquaria. Bags with control fish were fixed 1 m below the surface to lines on surface buoys in approximately a 5 m open water column. Color patterns were noted every three hours for 24 hours and the experiment was repeated on two different days. In total 19 fish were observed, 8 fish on the rocky shore, 12 fish in aquaria, and 10 fish as controls on buoys. Settlers on substrate developed color patterns after 14 - 18 hours, while fish in bags in open water stayed totally translucent. Based on the results from this experiment, only translucent individuals were caught and counted as new settlers.

To determine loss and migration immediately following settlement, a separate experiment was done. Newly settled fish were individually marked, released, and their position in the habitat observed for 24 hours. This experiment was repeated on two different days for a total of 19 fish. No fish were lost after 12 h and only 1 fish after 24 hours. Given the fact all fish were present for 12 hours and that there were no day/night differences in settlement (see Results), only daily sampling was done for the rest of the settlement seasons 1997 and 1998. Sampling consisted of 194 dives (in 92 days), 147 dives (in 105 days), and 104 dives (in 93 days) for the settlement seasons of 1996, 1997, and 1998, respectively. Initially, adults were removed during the 1996 season to reduce possible influences on settlement and released far from the transects. However, adults were refound on the transects within hours (personal observation). Either the same adults moved back or others immigrated from adjacent areas. Since conspecific adults had minor influence on settlement (Chapter 4), adults were left on the site for the last month of the 1996 season and the other two seasons.

For the survival time series, all fish present were censused weekly and 1 cm size classes, ranging from < 2 cm to 7 cm were noted. During the settlement seasons of 1996 and 1997, 9 weekly censuses were done, and in 1998, 11 weekly censuses were carried out. For the purpose of analysis, the total number of weeks considered for all seasons was 8, since no settlers came after week 8. To quantify the influence of migrations, we
individually marked 62 Aidablennius sphynx, ranging in size from 1.5 to 6.6 cm, at the beginning of this study. For one year (September 1996 - 1997) fish were surveyed monthly during the winter until May, and then weekly during summer.

Data Analyses

Diurnal and Nocturnal patterns — A total of 38 sunrises and 39 sunsets were sampled in the summer of 1996, 38 and 42 in 1997, and 26 and 28 in 1998, respectively. Numbers of collected settlers were standardized per m² suitable habitat and hours of daylight/darkness. After testing if data were normally distributed, a t test for independent samples was used.

Settlement rate — For the calculation of the settlement rate, the number of daily collected settlers was cumulated for the length of the settlement season. The total number of settlement days for the 1996 season was 55, for 1997 it was 98, and for 1998 it was 53, all based on the day the last settler was collected.

Difference between sampling methods — To determine possible differences resulting from the two sampling methods (censuses versus collection), the number of translucent settlers (new settlers) were simultaneously sampled on a weekly basis for a total of 29 days for the 3 settlement seasons. This was also done to verify that processes affecting settlement are the same for both sites (all transects). Data were analyzed by analysis of variance (ANOVA), comparing mean numbers of settlers between transects for the same day. Sampling days were nested within sites (sampling method) and both were considered random factors. Homogeneity of variances and normal distribution of data were tested for.

Survival, weekly losses and loss rates — The number of settlers lost over a weekly period (short-term losses) was calculated as the difference between the numbers from weekly censuses (weekly survivors) and the cumulated number of daily collected settlers. To account for losses as a result of growth, all size classes up to 4 cm were considered as survivors, since these classes were not present before the settlement season and no increase in size classes > 4 cm was observed during the seasons. For calculation of per capita (proportional) loss rates, weekly losses were divided by the number of settlers collected that week. Per capita loss rates were then standardized per day of each sampling week and compared over years by ANOVA. Additionally, the highest number of survivors observed during the settlement season and at the end of the season were compared for all three years by ANOVA. Homogeneity of variances and normal distribution of data were tested for.
Regression lines were fitted for curves of cumulative settlement and for weekly losses to determine mean rates of settlement and short-term losses. Statistical analyses were done using STATISTICA for the Macintosh, Version 4.1 and procedures in Zar (1984). Confidence bands at the 95% level were calculated and multiple comparison testing of slopes was done by analysis of covariance. Pairwise comparisons were conducted applying a double tailed t test (all from Zar 1984).

Analyses of variances — To determine if short-term post-settlement losses, calculated by subtracting the two time series, are statistically significant given the variance in time and space, we used a 3 factor ANOVA with a nested, mixed model design. For settlement, numbers of settlers from daily collections were summed for the week of survival censuses (group 1). Net weekly survival data were calculated from weekly increments in survival and also standardized per m² suitable habitat (group 2). Means between sampling weeks for both, settlement and net survival, were compared for the three years. Year was a fixed factor while sampling week (1-8) was nested within sampling group and both were considered random factors since they are a random sample of a larger population and possible levels (see Zar 1984, Bennington and Thaye 1994). To verify that no differences between transects exist, a 3 factor ANOVA with the same design as above was done, but using spatial data (transects) instead of temporal data (sampling weeks). In addition to testing for spatial variance for the settlement time series on a weekly basis, we also tested if transects were different on a daily basis using ANOVA. Homogeneity of variances and normal distribution of data were tested prior to all ANOVAs.

Following Levin et al. (1997), we estimated the degrees of association for our temporal ANOVA model for groups and week, where is an estimate of the degree of association between the effect of group and the dependent variable and where differences between groups represent losses. The number of levels of the sampling group is p, the number of levels of the week is q and SS and MS are the sum and mean squares, respectively.

For Group,\[ \rho_{1} = \frac{pMS_{group}}{SS_{total} + MS_{group} + pMS_{group \times year} + pMS_{week \times year} - pqMS_{error}} \] (5.3)

and for week,
\[
\rho_2 = \frac{SS_{total} + MS_{week} - MS_{error} + qMS_{group \times year} + qMS_{week \times year} - pqMS_{error}}{5.4}
\]

Quantification of aliasing — To examine how short-term post-settlement losses can alter settlement patterns and to quantify aliasing of the settlement time series, a cross-correlation analysis was carried out sequentially (for all three seasons).

RESULTS

Habitat measurements

The amount of preferred substrate type available to Aidablennius sphynx on each transect was found to be very consistent over the years. The yearly means for suitable habitat were 6.89 m² (SD ± 0.14), 2.22 m² (SD ± 0.23), 6.53 m² (SD ± 0.06) for transects 1 - 3 d, respectively (daily collection of settlers) from a total of 37 m² of transect surface; and 4.13 m² (SD ± 0.06) 15.33 m² (SD ± 0.29), 17.2 m² (SD ± 0.35) for transects 1 - 3 w, respectively (weekly censuses of survivors), from a total of 56 m². The fact that transects had different areas of habitat available had no effect on settler densities (Chapter 4).

Settlement patterns and rates

Diurnal and Nocturnal Patterns — For each season, day and night patterns were the same (not shown). No differences in the mean numbers settling during the day and night were found for the settlement seasons 1996, 1997, and 1998 (\(t = 0.042, p = 0.966; t = 0.737, p = 0.463; \) and \(t = 0.955, p = 0.344\)). The number of settlers collected bi-daily amount to 100% of the total number collected in 1996, 76% in 1997, and 98% in 1998. For further analyses, data from sunrise and sunset samples were pooled to represent diel sampling.

Daily patterns and rates — Cumulative curves for daily settlement are shown for each year (Fig. 5.2A). Data from the three transects were pooled, since no differences in daily settler densities between transects were found for the settlement seasons of 1996, 1997, and 1998 (Table 5.1). Daily settlement curves show that each year peaks occurred on different days, resulting in punctuated settlement. At the end of the season, the maximum number of settlers that arrived was similar with 13.40 fish/m² suitable habitat (SD ± 0.23) in 1996, 13.55 fish/m² suitable habitat (SD ± 0.44) in 1997, and 12.34 fish/m² suitable habitat (SD ± 0.36) in 1998, and no differences were found between years.
(df_{effect} = 2, MS_{effect} = 6.348, df_{error} = 6, MS_{error} = 0.130, F = 1.415, p = 0.314).

Settlement for each year started on different days and had different durations.

Cumulative numbers of settlers followed a linear relationship with time (p < 0.001), where the slope represents the settlement rate (Fig. 5.2 B). We also tried an exponential fit, but the linear model gave the best correlations. Daily settlement rates had significantly different slopes between the settlement seasons ($F_{(1, 195)}$, p < 0.001). The settlement rate for 1998 was higher than the rates for 1996 and 1997 ($t_{(2), 103}$, $t_{(2), 143}$, respectively, p < 0.001). The slopes for 1996 and 1997 were found to be parallel ($t_{(2), 149}$, p > 0.1), however, the elevations were significantly different ($t_{(2), 150}$).
p < 0.001). This difference in elevations is the result of the difference in duration of the settlement seasons, where the season for 1996 was significantly shorter than that for 1997. The intercepts were not zero because of episodic settlement.

Table 5.1. Summary of analysis of variance for differences in daily settler densities of *Aidablennius sphynx* between the three transects. Each year was analyzed separately.

<table>
<thead>
<tr>
<th>Source</th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Settlement season 1996</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Transect</td>
<td>0.057</td>
<td>2</td>
<td>0.028</td>
<td>0.461</td>
<td>0.631</td>
</tr>
<tr>
<td>Error</td>
<td>12.208</td>
<td>198</td>
<td>0.061</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Settlement season 1997</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Transect</td>
<td>0.124</td>
<td>2</td>
<td>0.062</td>
<td>0.824</td>
<td>0.440</td>
</tr>
<tr>
<td>Error</td>
<td>19.442</td>
<td>258</td>
<td>0.075</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Settlement season 1998</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Transect</td>
<td>0.264</td>
<td>2</td>
<td>0.132</td>
<td>1.013</td>
<td>0.365</td>
</tr>
<tr>
<td>Error</td>
<td>19.561</td>
<td>150</td>
<td>0.103</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

_Difference between sampling methods._ — To compare differences between sampling methods, it would be best to sample the exact same transects. Unfortunately that was not possible because one of the methods requires the daily collection of the settlers and the other their accumulation over time. However, no difference was found for mean numbers of translucent fish collected or censused the same day between transects for all three settlement seasons (Table 5.2). Therefore, censuses of settlers are as accurate as collection on a daily basis. Further, the spatial variability between the 6 transects is unimportant and processes affecting settlement are the same for all transects.
Table 5.2. Summary of analysis of variance for differences in densities of translucent settlers between transects collected or censused the same day. Groups represent the two different sampling methods (collection and censuses of settlers). Each year was analyzed separately.

<table>
<thead>
<tr>
<th>Source</th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
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<tbody>
<tr>
<td>Settlement season 1996</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Group</td>
<td>0.023</td>
<td>1</td>
<td>0.023</td>
<td>0.540</td>
<td>0.473</td>
</tr>
<tr>
<td>Day</td>
<td>0.675</td>
<td>16</td>
<td>0.042</td>
<td>2.649</td>
<td>0.008</td>
</tr>
<tr>
<td>Error</td>
<td>0.573</td>
<td>36</td>
<td>0.061</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Settlement season 1997</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Group</td>
<td>0.049</td>
<td>1</td>
<td>0.049</td>
<td>0.486</td>
<td>0.497</td>
</tr>
<tr>
<td>Day</td>
<td>1.422</td>
<td>14</td>
<td>0.102</td>
<td>3.253</td>
<td>0.003</td>
</tr>
<tr>
<td>Error</td>
<td>0.999</td>
<td>32</td>
<td>0.031</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Settlement season 1998</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Group</td>
<td>0.773</td>
<td>1</td>
<td>0.773</td>
<td>2.961</td>
<td>0.099</td>
</tr>
<tr>
<td>Day</td>
<td>5.741</td>
<td>22</td>
<td>0.261</td>
<td>1.060</td>
<td>0.419</td>
</tr>
<tr>
<td>Error</td>
<td>11.814</td>
<td>48</td>
<td>0.246</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Survival, short-term losses and loss rates

Cumulated settlers, starting from the first day of settlement are plotted in Fig. 5.3 with survivors for all three settlement seasons. Survival increased with settlement but then levelled off to near constant values about the same time as settlement. No differences in maximum numbers of survivors (df_{\text{error}} = 2, MS_{\text{effect}} = 0.012, df_{\text{error}} = 6, MS_{\text{error}} = 0.012, F = 0.975, p = 0.429) and in numbers of survivors observed at the end of the settlement seasons were found between years (df_{\text{effect}} = 2, MS_{\text{effect}} = 0.833, df_{\text{error}} = 6, MS_{\text{error}} = 0.771, F = 1.081, p = 0.397).
Fig. 5.3. Cumulative numbers of daily collected settlers of Aidablennius sphynx (AS), weekly observed survivors, and resulting losses for the three settlement seasons 1996, 1997, and 1998.

Calculated weekly losses were the difference in numbers between cumulated settlement and survival (Fig. 5.3). Since weekly losses showed a linear temporal relationship (p < 0.001), a linear model was chosen to describe the increasing numbers of settlers lost over the days of the settlement seasons, where slopes represent loss rates (Fig. 5.4). Significant differences between the slopes of the three seasons were found (F(1), 23, p < 0.001). Loss rates in 1998 were significantly higher than in 1997 (t(2), 15, P < 0.02). Slopes for 1996 and 1997 and for 1996 and 1998 were equal (t(2), 13, p > 0.2, t(2), 14, p > 0.05, respectively), however, the elevations were significantly different (t(2), 14, p < 0.005, t(2), 15, p < 0.02, respectively), again representing the difference in duration of the settlement seasons. Per capita loss rates were not dependent on density of all conspecifics, post-settlers or adults (Fig. 5.5 A, B).
Fig. 5.4. Linear regressions (± 95% confidence bands) of losses (cumulative numbers of settlers lost) for the three settlement seasons: 1996, 1997, and 1998 (P < 0.001), where slopes represent the loss rates.

Fig. 5.6 A shows that no significant differences in mean per capita loss rates were found between seasons (df_{effect} = 2, MS_{effect} = 0.002, df_{error} = 24, MS_{error} = 0.001, F = 1.691, p = 0.205). Within seasons, however, per capita loss rates were highly variable (Fig. 5.6 B).

Losses include mortality and migration. We note that migration must be significant, based on observations of marked fish. Only 35 of the originally 62 marked fish were refound, some after months without being seen. All sizes were represented and no relationship was found between size and distance travelled. Even the smallest individuals moved more than 45 m. For two of the smallest individuals marked (1.5 cm), one was refound after 4 months and 40 m from the release point, the other one after 5 months and 30 m from the release point. In one week, an 1.8 cm fish moved 35 m. Additionally, more settlers were found in the larger size classes (3 and 4 cm) than could have been accounted for by growth of settlers to these size classes. Based on these data we conclude that disappearing fish could be a result of migration and not solely mortality.
Fig. 5.5. Per capita loss rates of settlers (d⁻¹) for the three settlement seasons (1996, 1997, and 1998) A) as a function of post-settler density, size classes > 2 - 4 cm, and B) as a function of adult density, size classes > 4 cm. Densities standardized per m² suitable habitat.
Fig. 5.6. Per capita loss rates of settlers (d⁻¹) A) compared between settlement seasons (each box encloses 50% of the data, the line displays the median, top and bottom of box mark data limits of ± 25%, error bars represent values within acceptable range, and points are outliers), and B) as a function of time within the settlement seasons of 1996, 1997, and 1998. Densities standardized per m² suitable habitat.

Effect of post-settlement losses

The results of the temporal 3-factor ANOVA which compared groups (weekly settlement and net weekly survival), weeks, and years (settlement seasons) show that, despite the high temporal variance within seasons, weekly settlement differed from net weekly survival (Table 5.3 A). The variability between groups and the interaction of weeks and years were also significant. Far more variability was explained by differences
between groups ($\rho_1 = 0.10$) than by the weekly time-scale ($\rho_2 = 0.04$). For the spatial ANOVA (comparing transects), only groups showed significant differences (Table 5.3 B). This result confirms that transects for both sites were the same. Therefore, the ANOVA verified that: 1) spatial variance is unimportant on the scale of 1 m to 100 m; 2) fluctuations within seasons are important, represented by episodic settlement; and 3) mean weekly settlers differ significantly from net weekly survivors, as a result of post-settlement losses.

Table 5.3. Summary of analysis of variance for comparison between weekly settlement and net weekly survival of A) temporal and B) spatial variations in settlement densities. Groups represent the two different sampling methods (daily collection settlers and weekly censuses of survivors).

<table>
<thead>
<tr>
<th>Source</th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>$F$</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>A) Temporal</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Year</td>
<td>2.518</td>
<td>2</td>
<td>1.259</td>
<td>14.968</td>
<td>0.063</td>
</tr>
<tr>
<td>Group</td>
<td>24.731</td>
<td>1</td>
<td>24.731</td>
<td>9.886</td>
<td>0.007</td>
</tr>
<tr>
<td>Weeks (Group)</td>
<td>0.090</td>
<td>14</td>
<td>0.064</td>
<td>0.031</td>
<td>0.970</td>
</tr>
<tr>
<td>Year x Group</td>
<td>0.019</td>
<td>2</td>
<td>0.084</td>
<td>0.031</td>
<td>0.970</td>
</tr>
<tr>
<td>Year x Week (Group)</td>
<td>0.067</td>
<td>28</td>
<td>2.753</td>
<td>5.983</td>
<td>&lt; 0.0001</td>
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<tr>
<td>Year</td>
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<td>Group</td>
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<td>24.731</td>
<td>9.886</td>
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<td>Year x Group</td>
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<td>Error</td>
<td>152.893</td>
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</table>

Temporal fluctuations in weekly settlement patterns, i.e. episodic settlement, were not reflected in net weekly survival patterns, and no significant correlation between the two patterns was detected by the cross-correlation analysis. This indicates that short-term post-settlement losses significantly altered temporal settlement patterns and that these patterns were aliased, or under sampled by the weekly censuses. The magnitude of aliasing is shown in Figs. 5.7 A-D.
DISCUSSION

Settlement patterns and rates

Spatial scales — Studies on settlement and recruitment have been carried out on different spatial scales. Small scales are usually considered to be within meters (e.g. studies by Williams and Sale 1981, Victor 1986a, Fowler et al. 1992, Planes et al. 1993, Levin 1993, 1994a,b, Jenkins et al. 1997), intermediate scales from hundreds of meters to kilometers (Williams and Sale 1981, Victor 1986b, Fowler et al. 1992, Levin 1993, Planes et al. 1993, Jenkins et al. 1995, Levin et al. 1997, Vigliola et al. 1998), and large scales over geographic regions (Victor 1986b, Fowler et al. 1992, Doherty and Fowler 1994, Levin et al. 1997, Vigliola et al. 1998). The smallest spatial scale in our study was the meter distance between transects. No differences were found in numbers of settlers
of *Aidablennius sphynx* between transects. Our previous investigation over spatial scales from 150 km to 1 m already showed that, on small spatial scales, habitat is the determinant factor (Chapter 4), which is the reason why we standardized data per m² suitable habitat. This same study showed that no differences occurred on the largest scale, between localities. Additionally, in this study, we find no differences on intermediate spatial scales between the two sites in the bay. Thus, we conclude the variability in settlement is the result of temporal variation.

Temporal scales — The smallest temporal scale sampled was half day and time series of day versus night settlement were the same. Given that no significant differences were found between numbers of larvae settling during the night or day and that marked settlers were present up to 24 hours, we conclude that the smallest sampling interval needed to determine unaliased settlement was one day. Not all blenny larvae behave the same, however. Caribbean blenny larvae were caught at night 99% of the time (Thorrold et al. 1994). Many coral reef larvae show a lunar or semi-lunar cycle with settlement at night (e.g. Robertson et al. 1988, Milicich et al. 1992, Robertson 1992, Dufour and Galzin 1993, Thorrold et al. 1994, Sponaugle and Cowen 1994, 1997). However, for rocky shore fish, there are no other studies on diurnal settlement.

On the seasonal scale (weekly), temporal variability was larger than spatial variability. For another temperate species with similar behavior (no schooling or lunar cycle), Levin (1994a) also found highly variable recruitment on small temporal scales of 1 - 2 days, and speculated that episodic settlement could be responsible for much of this variation (Levin et al. 1997). For our species, peaks in settlement resulted in punctuated, episodic settlement, which occurred on different days each year, another indication that non-periodic processes must have a strong influence on settlement patterns of this rocky shore fish.

On the interannual scale, durations of the settlement seasons differed from year to year, though there were no differences among years in total numbers of settlers at the end of the settlement seasons. Victor (1986a), sampling daily, observed that only on large scales was settlement intensity consistent from year to year and was positively correlated with the exposure of the habitat to the onshore current. Therefore, Victor (1986a) concluded that settlement intensity is set by oceanographic processes. Our daily collections are frequent enough to resolve the influence of such processes on settlement, and will allow us, in the future, to discriminate between physical and biotic oceanographic processes effecting settlement. Since no differences were found in
numbers of translucent settlers between sites, it would appear that oceanographic processes acted equally on both sides of this open bay.

Settlement rates — Despite episodic settlement, settlement rates could be estimated by linear relationships for daily collections. These rates were the same in the first two seasons, but 40% higher for the last one. The prominent feature was that the length of the settlement season in 1997 was nearly twice that in the other two years, which could be caused by physical or biological processes. The result is that in 1998 settlers came in a shorter period, while in 1997 the rate of settlement was lower over a more extended season; 1996 was also a short settlement season, but strong initial settlement reduced the slope over the season. Curiously, the total number of settlers arriving was the same for all three years.

Survival, weekly losses and loss rates

Slopes of weekly losses approached those of the settlement rates, indicating high post-settlement losses. The loss rate for the last season was about 30% higher than for the other years but only showed significant differences to 1997. No difference in the number of maximum survivors during each season or at the end of the settlement season was found between years. This indicates that losses were constant over the three years. Mean per capita loss rates did not differ between years, however, the variability about the mean was high during the seasons, with rates ranging from 0.02 - 0.16 d\(^{-1}\). Similar losses (per capita mortality d\(^{-1}\)) in the first week of settlement were observed by Victor (1986a), while other authors reported rates that were 50% lower averaged over 2 weeks (Schmitt and Holbrook 1999), 65% lower over 50 days (McGehee 1995), and 91% lower over 30 days (Hixon and Carr 1997). Wider ranges were found by Macpherson et al. (1997) and Tupper and Boutilier (1997). The dissimilarities may stem from the fact that mortality rates were dependent on different parameters such as age of juveniles after settlement (Victor 1986a), predators (Hixon and Carr 1997), density (Macpherson et al. 1997, Schmitt and Holbrook 1999), microhabitat (Tupper and Boutilier 1997), seasonality (this study), and time interval after settlement (Victor 1986b, McGehee 1995, Macpherson et al. 1997, Shulman and Ogden 1987).

A running mean through the three years of our survival data shows that a constant density of about 2 post-settlers/m\(^2\) suitable habitat was reached. Maximum survival and survival at the end of the seasons were not different between years. This is substantiated with survival data from a previous study (Chapter 4) on the same site, which shows that survival at the end of the seasons 1994-1998 (with a mean of 1.7 m\(^{-2}\) suitable habitat) did not significantly differ. This suggests that a carrying capacity was reached. Since
survival remains fairly constant after week 5, loss rates are predominately determined by settlement rates. Thus, in 1998 survival was low but settlement rates were high leading to high loss rates. Similarly, periods of high episodic settlement have high losses. This suggests density dependence, however, no such relationship was found. Therefore, we conclude that habitat availability limits the density of post-settlers.

The variations in loss rates appear to be random, with the effects of episodic events on per capita losses leading to alterations of initial settlement patterns. High mortality has often been determined in the first days after settlement or transition (Doherty and Sale 1985, Victor 1986a, Sale and Ferrell 1988, Connell and Jones 1991, Houde 1997, Macpherson et al. 1997) and dramatic alteration of initial settlement patterns within a very short time have been observed (Connell and Jones 1991, Tupper and Boutilier 1997). Several authors also found density independent mortality (and survival) of juvenile fish (Doherty 1982, Victor 1986a, Levin 1994a, Doherty and Fowler 1994, Sano 1997). Doherty and Fowler (1994) concluded that density-dependent processes are rare and that the demography, at large spatial and temporal scales, can be almost entirely explained by variable recruitment interacting with density independent mortality. On the other hand, density dependent mortality and survival have also been demonstrated (e.g. van der Veer 1986, Myers and Cadigan 1993, Macpherson et al. 1997, Schmitt and Holbrook 1999). Hixon and Carr (1997) found that in the absence of predators, early mortality was virtually density independent, and concluded that predation on juveniles may naturally regulate species abundance. However, they pointed out that measuring larval supply at a site by sampling juveniles weeks to months after they have settled (or by back calculating settlement by using otoliths) may miss density dependence in the period shortly after settlement, therefore leading to the false conclusion that mortality after settlement is density independent.

In our study, losses were only observed on a weekly scale, therefore we can not state with certainty that no density depend losses occur shortly after settlement. Further we found that post-settlement losses are not only a result of mortality, but that migration is important since our study species is mobile. Settlers observed in the weekly censuses are considered to be survivors. However, Frederick (1997) pointed out that new settlers and immigrants can mask the loss of individuals and thereby inflate estimates of survivorship, or survivorship can be underestimated when new settlers emigrate and survive at another site. We observed more settlers in the larger size classes than could have been accounted for by growth of settlers to these size classes, indicating that survivorship is overestimated as a result of immigration. Sweatman and Robertson (1994) also observed that many fish recruiting to experimental structures were migrant
juveniles rather than settling larvae. Consequently, either post-settlement mortality or relocation "overrode" the effects of settlement patterns in determining the number of recruits and final adult abundances (Robertson 1988). When mortality or loss rates are capable of significantly altering settlement patterns, as shown here, it is impossible to distinguish between undersampling and underestimating. Basic information on time scales at which processes take place is vital for resolving and determining these or connected processes.

**Settlement and the effect of post-settlement losses**

Small temporal scale variations in settlement, such as punctuated or episodic peaks, must be resolved to estimate true settlement. Consequently, our high frequency monitoring, with small time intervals relative to the settlement process, leads to an unaliased estimate of settlement. Such an accurate estimate of settlement is needed to investigate the coupling of physical transport mechanisms and activities of larvae. These processes may have different temporal and spatial scales, thus, it is important to sample frequently enough to determine the dominant trend.

We showed that post-settlement processes can drastically change settlement patterns within a week. Thus, correlating larval supply and early recruitment level by weekly sampling (Milicich et al. 1992) might lead to the wrong conclusions. Therefore, arguments that annual recruitment surveys are good indicators for settlement patterns, estimated by censuses every month and a half (Williams et al. 1994), might not be true since they probably do not reflect initial settlement patterns but rather survival. Also back-calculations of settlement dates and reconstruction of settlement or recruitment patterns by otoliths (Victor 1982, Pitcher 1988, Thresher et al. 1989, Meekan et al. 1993, Sponaugle and Cowen 1994, 1997, Jenkins and May 1994, Caselle and Warner, 1996, Jenkins et al. 1997) might be connected with a high error, since otoliths are from individuals that survived to the collection day (or even a random subset of them) and not from all possible settlers. Correlating the back calculated settlement or recruitment patterns with oceanographic processes (Jenkins et al. 1997, Sponaugle and Cowen 1997), or other processes influencing settlement such as food supply (Thresher et al. 1989), could also result in the wrong conclusions. To answer the questions of which is more important in determining adult populations, pre-settlement or post-settlement processes, and if settlement reflects processes occurring within the benthic population, it is absolutely necessary to look at unaliased patterns and not those altered by post settlement processes. Therefore, it is important to match the sampling frequency with the frequency of the settlement process. The same applies for species with periodic settlement, e.g. lunar periodicity, where a higher sampling effort is required before and
after the event. For continuous and episodic settlement, a sustained effort is necessary to capture temporal patterns.

For our study, post-settlement losses were only dependent on settlement, while survival patterns were decoupled from initial settlement patterns. If survival reached a carrying capacity, as suggested from our data, then the population is not undersaturated as a result of low settlement rates. Instead, post-settlement survival is determining adult populations, as shown before for a coral reef species (Shulman and Ogden 1987). Therefore, we conclude that populations of the rocky shore fish *Aidablennius sphynx* are not limited by larval supply as suggested by the recruitment-limitation model (Doherty and Williams 1988, Doherty and Fowler 1994), but by processes determining post-settlement survival. Lastly, without high frequency sampling, which provides unaliased temporal settlement patterns, post-settlement losses can not be accurately determined and their impacts on populations assessed.

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6. **Nutritional status, body size, and abundance of settlers and their implications on post-settlement survival**

**ABSTRACT**

In this paper we address how characteristics of larvae surviving the pelagic phase influence survival after settlement, and therefore promote transition to the benthic phase. The characteristics measured were total length, RNA-DNA ratios, and stomach contents, representing conditions in the pelagic phase ranging from large to small temporal scales. Post-settlement survival was estimated from weekly observations and daily collections of settlers. Stomach contents of recently settled fish indicated that food was available nearshore. Although stomach contents displayed diurnal differences, RNA-DNA ratios lacked diel cycles probably because of the disparity in time scales. No seasonal differences were observed in either total length or nutritional status despite the warming of surface waters during the settlement season. RNA/DNA and total length of larvae were highly variable within the same day. The ratios were also highly variable within the same size classes and no relationship existed between RNA/DNA and total length. The high variability of RNA-DNA ratios probably reflected the high variability or patchiness of the food supply in the pelagic environment. Either RNA-DNA ratios do not integrate over sufficiently long time scales to resolve the whole growth history of larvae in the pelagic phase, or other environmental factors besides food supply, such as offshore temperature, are responsible for the high variability in size and nutritional status.

Post-settlement survival in the benthic phase was compared to RNA-DNA ratios, total length, and numbers of settler, where the size of settlers was more strongly related to survival than either nutritional status or abundance. The combination of all three factors explained 26% of the variance on survival, leading us to conclude that factors in the benthic phase play a more important role in post-settlement survival than characteristics from the pelagic phase. We suggest that habitat quality, including habitat limitation, competition, and predation, may be important factors. The most likely explanation is habitat limitation, since the majority of larvae settled at the beginning of the settlement seasons during episodic peaks, when habitat was still available. Further, most of the large fish arrived at the beginning of the season when survival probabilities were highest and therefore, it is difficult to state if size is really directly related to post-settlement survival.
INTRODUCTION

Factors influencing survival of fishes during different life stages are crucial for determination of population densities. Considerable interest exists in evaluating which individuals survive to the next life stage and why. One of the unanswered questions in benthic fish ecology is which characteristics of larvae surviving the pelagic phase influence survival after settlement, promoting transition to a benthic juvenile? We investigate this process by comparing morphological and nutritional characteristics of newly settled fish with post-settlement survival.

High mortality rates during the early life history stages may regulate the size and the variability of populations since larval input has been shown to strongly influence population densities (Doherty 1983, Victor 1986a, Doherty and Fowler 1994). During the pelagic phase, survival of fish larvae is dependent on physical factors, such as currents and retention features (e.g. Bailey et al. 1997), and on biological factors, such as predation and starvation (Houde 1987). The latter two are related processes since poor nutrition reduces larval growth rates, resulting in longer durations in the larval stage (Buckley 1984). One hypothesis is that smaller individuals are more vulnerable to predation (Cushing 1990, Rice et al. 1993, Meekan and Fortier 1996), yet no consistent survival advantages were found for larger larvae of the same age (Bertram and Leggett 1994). Good feeding conditions may influence larval survival directly, by eliminating starvation, or indirectly, by regulating the timing and rate of mortality resulting from predation (Leggett and DeBlois 1994). Additionally, a good nutritional status could function as a buffer against poor environmental conditions, such as unfavorable temperatures and food scarcities (Kerrigan 1996).

Larval durations in the plankton and body size at settlement have been found to vary geographically and temporally for the same species (Victor 1986b, McCormick and Mackey 1997). The variability in size and nutritional status at metamorphosis and settlement has largely been ignored in studies of reef fish population dynamics (McCormick 1998), but they are important because they reflect the link between pelagic and benthic environments (Boero et al. 1996). These two life-stages may not be independent and events and environmental conditions during the pelagic phase may impact the life stages following settlement (review of McCormick 1998). Survival after settlement on the benthic habitat has been correlated to different environmental factors, including habitat characteristics (Connell and Jones 1991, Shulman et al. 1983, Levin 1991, 1993, 1994a, Tupper and Boutilier 1995a, Chapter 5), competition (Pfister 1995, Steele 1998), and predation (e.g. Carr and Hixon 1995, Beets 1997, Steele 1997b, 1998, Connell 1998). If predation pressure on smaller individuals is enhanced (review of
Sogard 1997) as previously stated, then nutritional status, as well as size of fish could have important consequences for subsequent survival and transition to the next life stage (Canino et al. 1991). Further, these characteristics can function as key indices of fitness (see reviews of McCormick 1998, Suthers 1998). Different means exist for measuring nutritional status of individuals (review of Ferron and Leggett 1994). One method is the ratio between RNA and DNA, where the amount of RNA in the cell is directly proportional to the rate of protein synthesis and the amount of DNA reflects the number of cells. Therefore, this ratio can serve as an index of the cell’s metabolic intensity and as an indicator of the nutritional status of fish (reviews of Ferron and Leggett 1994, Suthers 1998).

The objectives of this study are to determine: 1) nutritional and morphological characteristics of larvae that survived their pelagic phase; and 2) the implications that these characteristics and numbers of settlers have on post-settlement survival. We did this by measuring the total length, RNA/DNA ratios, and stomach contents of settlers and correlated these factors with survival rates for a temperate, rocky shore fish. Survival rates were calculated from weekly censused post-settlers and settlement was estimated from daily collected settlers.

STUDY SPECIES AND AREA

Blennids form one of the most common groups of the Mediterranean rocky shore fishes (Corbera et al. 1996). On the coast of the NW Mediterranean Sea about 18 species are found in the shallow littoral zone, mainly in the upper 0 to 1 m (Zander 1986). One of the most abundant species is Aidablennius sphynx (Corbera et al. 1996), with a maximum of 7 individuals per m² (Illich and Kotschal 1990, Macpherson 1994). After hatching, larvae of A. sphynx disperse about 50 km offshore (Sabatés 1994, Sabatés and Olivar 1996). Settlement onshore takes place from June to September and shows episodic peaks, and preferred substrate is bare rock (Chapters 4, 5).

MATERIALS AND METHODS

Settlement

Settlement was measured by collecting A. sphynx larvae as described elsewhere (Chapter 5). Briefly, this method consisted of collecting newly settled fish with handnets twice daily or daily for the settlement seasons 1996-1998, except when precluded by weather and sea conditions. These settlers were translucent and easily distinguishable from immigrants which had already developed color patterns. Sampling consisted of 194 dives in 92 days for 1996, 147 dives in 105 days for 1997, and 104 in dives 93 days
for 1998 between June and September. The total numbers of settlement days for the
seasons of 1996, 1997 and 1998 were 55, 98, and 53, respectively, all based on the first
and last day settlers were found. Spatial variation was controlled by using three
transects. Standardization was done dividing the number of individuals by the amount of
suitable habitat per transect, since the amount of habitat had no effect on settler densities,
only suitable substrate was important (Chapter 4).

Survival

Survival was estimated by weekly censusing all fish present on three transects and
dividing them into 1 cm size classes. To account for losses as a result of growth, all size
classes up to 4 cm were considered as survivors, since these classes were not present
before the settlement season and no increase in size classes > 4 cm was observed during
the seasons (Chapter 5). During the settlement seasons of 1996 and 1997, 9 weekly
censuses were done, while in 1998, 11 weekly censuses were carried out. For the
purpose of analysis, the total number of weeks considered for all seasons was 8, since no
settlers came after week 8 of survival censuses. Numbers of observed survivors were
standardized per m² suitable habitat. For the calculation of per capita (proportional)
survival, the numbers weekly survivors were first divided by the number of settlers
collected that week and then divided by the number of days in each sampling week.

Size and stomach contents

Subsamples of settlers caught alive were killed by adding the chemical quinaldine
(settlement season 1996) or freezing by -20°C (seasons 1997 and 1998). For the 1996
season, weights and lengths were determined to the nearest µg and mm, respectively.
For the seasons of 1997 and 1998 only lengths were measured since the relationship
between weight and length was well described by an exponential function (r² = 0.84).
Stomachs from all settlers were removed, their contents analyzed under a light
microscope, and the rest of the sample used for biochemical assays. Removing stomachs
from the larvae also ensured that RNA-DNA ratios were not affected by nucleic acid
contents of prey (Lochmann et al. 1996), although no differences were found in RNA/
DNA of laboratory reared larvae with or without visible stomach contents (Clemmesen
1996).

Extraction of nucleoid acids

Chemicals — DNA Type I from calf thymus (highly polymerised form, D-1501)
and RNA Type III from baker's yeast (R-7125) were purchased from Sigma;
Ribonuclease A from bovine pancreas (124686) was obtained from Merck (Darmstadt,
Germany). DNase and magnesium chloride hexahydrate were purchased from Fluka (Buchs, Switzerland). Water saturated phenol (AquaPhenol), pH 7.5, was obtained from Appligene (Illkirch, France). Ethidium bromide (EB), EDTA, and sodium dodecyl sulphate (SDS) were bought from Panreac (Barcelona, Spain).

Solutions — The RNase was dissolved in Tris-HCl buffer (pH 7.5) to a final concentration of 10 mg ml\(^{-1}\) (stock solution) and heated to 100°C for 15 min to destroy any DNase present. After cooling to room temperature, the solution was split into 25 µl aliquots and stored at -20°C until further use. For the RNase working solution, the stock solution was diluted with Tris-NaCl buffer (0.5 M Tris, 0.1 M NaCl, 0.01M EDTA and 2% SDS adjusted to pH 8.0 with HCl) to a concentration of 1.25 µg RNase ml\(^{-1}\). DNase (3009 units mg\(^{-1}\)) was dissolved in Tris-NaCl buffer (to a concentration of 2500 units DNase ml\(^{-1}\)) and sufficient magnesium chloride hexahydrate added for a final concentration of 3 mM Mg\(^{2+}\) in the sample. EB was diluted with double distilled H\(_2\)O to a concentration of 0.033 µg/ml (working solution).

Analytical procedure — The methodology was adapted from Clemmesen (1993), which involves purification of tissue homogenates and subsequent fluorescence-photometric measurements using the specific nucleic acid dye EB. Individual larvae were homogenized in a glass Potter Elvhejem on ice (Clemmesen 1988) with 600 µl Tris-NaCl buffer. Homogenates were transferred into disposable Eppendorf vials (2 ml volume), 600 µl H\(_2\)O saturated phenol immediately added, and samples vortexed for 30 s. To purify the nucleic acids in the samples, two chloroform washes were done. First 600 µl chloroform were added and the sample vortexed for another 10 min, then centrifuged at 3800g for 10 min. Next, the aqueous phase was transferred to a new Eppendorf vial, another 600 µl of chloroform added and the sample vortexed and centrifuged again. The aqueous phase from the second wash was used for analysis of RNA+DNA and DNA-only. For the RNA+DNA sample, 200 µl of aqueous phase was diluted with 700 µl Tris-NaCl buffer. For the DNA-only sample, 690 µl Tris-NaCl buffer and 10 µl RNase working solution were added to the 200 µl of aqueous phase and the sample incubated at 37°C for 30 min to enable complete digestion of all RNA by the RNase. To determine the fluorescence of RNA+DNA, 450 µl of sample was pipetted into a microcuvette containing 150 µl EB working solution (adding the bigger volume of sample to the smaller volume of dye effectively mixed the two). The same procedure was used for the DNA-only sample. Fluorescence was read on a Perkin Elmer 650-10s spectrofluorometer at excitation and emission wavelengths of 365 and 590 nm,
respectively, with a bandwidth of 5 nm. Fluorescence of RNA was calculated as the difference between the fluorescence of RNA+DNA and DNA-only. Two replicate readings were made on RNA+DNA and DNA-only samples.

Standards— Standard curves for RNA and DNA (dissolved in Tris-NaCl buffer) were made for concentrations ranging from 2 - 20.2 µg ml⁻¹ for DNA and 5.8 - 58.5 µg ml⁻¹ for RNA. Two standard concentrations (DNA: 4.05 and 20.25 µg ml⁻¹ and RNA: 11.7 and 58.5 µg ml⁻¹) and blanks (Tris-NaCl buffer only) were read each day to check for reproducibility and sensor drift. To determine if the RNase treatment really destroyed all the RNA in the assay without affecting the DNA, and that the remaining fluorescence corresponded only to the DNA, fish standards were used as controls, following the procedure of Fara et al. (1996) for phytoplankton.

To determine the fluorescence range of fish samples and the amount of RNase necessary to digest the RNA in the sample, fish standards were made for various concentrations by diluting fish homogenates (pooled individuals) with Tris-NaCl buffer. The resulting so-called fish standard curve is shown in Fig. 6.2 B. A duplicate set of fish standards was treated with RNase. To ensure that the amount of RNase added was sufficient to digest all RNA present, standard RNA (17.55 µg ml⁻¹) was added to all the concentrations of fish standards used above. When the slopes for fish standards + RNase and fish standards + RNA + RNase were identical, we assumed that RNase digested all the RNA. To test that DNA was unaffected by RNase, the same concentrations of fish standards were treated with RNase after adding standard DNA (4.05 µg ml⁻¹). After RNase digestion the slopes of the fish standards + DNA and the slopes from fish standards were parallel, but differed by the amount of standard DNA added. To determine background fluorescence, different concentrations of RNA+DNA standards and fish standards were digested with both RNase and DNase. To calculate recovery of nucleic acids in the purification steps, the same concentrations of RNA and DNA standards as used for standard curve, were treated as fish samples, using the analytical procedure for nucleic acid purification, then measuring the amount of RNA and DNA left in the final aqueous phase.

Statistics

Partial correlations and descriptive statistics were done using STATISTICA for the Macintosh, Version 4.1 and procedures from Zar (1984).
RESULTS

Settlement and survival

Time series of daily settlement and weekly survival are reported elsewhere (Chapter 5). In the beginning of the 1997 settlement season, per capita survival rates were the lowest of all three years and increased to their seasonal maximum by day 200 (Fig. 6.1). The maximum survival rates in 1997 and 1996 were comparable. Later in the settlement season, survival rates in 1996 and 1997 showed a similar decrease. The highest survival rates of all three settlement seasons occurred at the beginning of the 1998 season and decreased over time to a level close to the maximum of the other two settlement seasons.

![Graph showing per capita post-settlement survival rates](image)

Fig. 6.1. Time series of weekly post-settlement, per capita survival rates (d⁻¹) for the settlement seasons of 1996, 1997, and 1998. Days of year begin from January 1.

Analytical results

Standard curves for RNA and DNA, as well as for RNA+DNA from fish homogenates were highly linear (Fig. 6.2 A, B). Losses resulting from handling and centrifuging were high with only 60% of the RNA and DNA standards recovered after the purification steps. However, the resulting two curves were also highly linear ($r^2 = 0.9028$ for DNA and $r^2 = 0.9633$ for RNA). Despite the low recoveries, RNA-DNA ratios of fish, calculated based on regressions of recovered standards, did not differ from ratios calculated from the regressions of untreated standards since losses of RNA and DNA were proportional. Reproducibility was good (< 5% error) and background fluorescence negligible.
Fig. 6.2. Standard curves for A) DNA and RNA and B) fish homogenates. Note that x-axes vary.

**Characteristics of settlers**

**RNA-DNA ratios and total length** — Settlers arriving during the night or day did not differ in nutritional status or total lengths ($t = 1.6, p = 0.11$ for RNA/DNA and $t = -1.87, p = 0.64$ for total length). For further analyses, samples collected at sunrise and sunset were pooled. RNA-DNA ratio and total length of settlers were highly variable over time (Fig. 6.3 A, B). Mean contents (± standard deviations) of nucleic acids per settler were $51.1 (± 23.2) \mu g$ RNA and $25.5 (± 8.9) \mu g$ DNA. The higher variability observed for the RNA is expected since the RNA content is dependent on the physiological status of the fish. Nutritional status of settling larvae varied about 10 fold within seasons (0.75 - 7.69) and within the same day (0.75 - 7.55) and no pattern was observed over time. Total lengths were also highly variable for the same settlement days (body lengths doubled) and within seasons. Mean RNA-DNA ratios and mean total lengths did not differ significantly between years (Table 6.1) and no relationship existed between size and nutritional status of settlers (Fig. 6.3 C).
Fig. 6.3. Morphological and biochemical characteristics. A) RNA-DNA ratio of individual settlers over time, B) total length of settlers over time, and C) RNA-DNA ratio versus total length (mm). For time series, days of year begin from January 1.
Table 6.1. Mean ratios of RNA/DNA and total length (mm) of settlers for the settlement seasons of 1996, 1997, and 1998. N represents number of fish analysed or measured.

<table>
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<th>Variable</th>
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<th>Std. Deviation</th>
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<td>2.55</td>
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<td>58</td>
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<td></td>
<td>1998</td>
<td>85</td>
<td>2.17</td>
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</tr>
<tr>
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<td>19.05</td>
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</tbody>
</table>

Over the span of the development and settlement season, surface waters experienced their most rapid warming. From spring to late summer, the temperature increased from 14 to 26 °C. While no relationship was found for mean water temperature (weekly) and RNA/DNA, the variability between ratios of RNA-DNA was higher than temperature variability for the same time period (Fig. 6.4).

Fig. 6.4. Mean weekly RNA-DNA ratios versus mean weekly coastal water temperatures for the settlement seasons of 1996, 1997, and 1998. Error bars show standard deviations.
**Stomach contents** — Of the 149 stomachs analysed, 39% were empty, 49% had food contents, and 12% were full. Stomachs were empty in 59.6% of the larvae settling during the night and in 22% settling during the day. Diets consisted mainly of copepods (Table 6.2), which were present in 87.3% of the stomachs containing food.

**Table 6.2.** Stomach contents found in settled larvae and their percentage of occurrence. A total of 149 stomachs was analysed.

<table>
<thead>
<tr>
<th>Stomach contents</th>
<th>% occurrence</th>
</tr>
</thead>
<tbody>
<tr>
<td>Copepods</td>
<td></td>
</tr>
<tr>
<td><em>Cyclops</em> spp.</td>
<td>35.2</td>
</tr>
<tr>
<td>other</td>
<td>63.3</td>
</tr>
<tr>
<td>Ostracods (<em>Cypridina mediterranea</em>)</td>
<td>12.1</td>
</tr>
<tr>
<td>Other crustaceans</td>
<td>1.0</td>
</tr>
<tr>
<td>Algae</td>
<td>11.0</td>
</tr>
</tbody>
</table>

In full stomachs, 89% were filled with copepods, and the most common species of copepods were *Cyclops*. In addition to copepods, we found smaller amounts of ostracods (*Cypridina mediterranea*), other crustaceans (Grasse et al. 1976), and algae. No relationship was observed between the amount of food in stomachs and the nutritional status of settlers. The mean RNA-DNA ratio (± standard deviations) of fish with empty stomachs (*N* = 58) was 2.24 (± 1.12), of fish with some food contents in stomachs (*N* = 73) was 2.03 (± 0.92), and of fish with full stomachs (*N* = 18) was 1.66 (± 0.43). Unfortunately, not enough data on stomach contents were available to determine seasonal cycles in food availability.

**Characteristics influencing post-settlement survival**

Neither RNA-DNA ratios, total length, nor numbers of settlers showed any clear relationship with short-term post-settlement survival (Fig. 6.5 A-C). Since there were no differences between years in mean lengths and RNA-DNA ratios, partial cross correlations were carried out on pooled data. Size of settlers seems to be more important for survival (partial correlation coefficient, p.c.c. = 0.19) than the numbers of settlers (p.c.c = 0.15) or nutritional status (p.c.c. = 0.07). The combination of the three factors only explained 26% (multiple-\( r = 0.26 \)) of the variance on survival.
Fig. 6.5. Comparison of settle characteristics with weekly survival rate (standardized per day) for the settlement seasons of 1996, 1997, and 1998. A) mean RNA-DNA ratio, B) mean length of settlers for the week of survivor censuses (error bars represent standard deviations), and C) the quantity parameter expressed as numbers of settlers (summed over weekly survivor censuses and standardized per day).
DISCUSSION

Pelagic characteristics: nutrition and morphology of settlers

The characteristics chosen to represent pelagic condition of newly settled larvae were total length, nutritional status (RNA/DNA), and stomach contents. Length occurs on the longest time scale and represents seasonal growth during the pelagic phase. The ratio between RNA and DNA is directly correlated to protein synthesis, representing intermediate time scales, while stomach content, representing feeding and digestion, occurs on the smallest time scale of hours (e.g. Clemmesen 1994, 1996, Theilacker et al. 1996, Suthers 1998).

Not only did stomach contents of recently settled fish indicate food was available nearshore but the diurnal differences show feeding was primarily during the day. The lack of diel cycles in ratios of RNA to DNA implies the ratio is a conservative measurement and probably not affected by short term feeding and stressors (Clemmesen 1996). Integrated over the longer time scales, prey availability affects length of larvae through its effect on growth and the nutritional status (Ferron and Leggett 1994, Buckley et al. in press). Diurnal changes in RNA/DNA were less pronounced for partly fed to starved individuals than for well fed larvae in the laboratory and field samples (Clemmesen 1996). Buckley et al. (in press) suggested the absence of a strong diel pattern in RNA/DNA may be a result of lower metabolic rates for some cold water species. Larvae of the temperate reef fish *Aidablennius sphynx* develop in cooler, lower salinity waters offshore (Sabatés and Olivar 1996). Despite a nearly linear trend in warming of surface waters from 14 to 26 °C during the settlement season, no significant seasonal differences were observed in either total length or nutritional status. Relatively small changes in water temperature greatly influenced the patterns in variability in age and size at metamorphosis for settlement of tropical reef fishes, where metamorphosis occurred earlier in warmer waters resulting in settlement of smaller fish (McCormick and Molony 1995). Anomalies in temperature might also influence the timing of settlement for our temperate reef fish. One problem with the temperature data in our study is measurements were taken nearshore at the time of capture, and might not be comparable to temperatures in the offshore water masses where these larvae develop. This could explain the lack of a relationship between temperature and RNA/DNA, and between RNA/DNA and length of settled larvae (based on the age at metamorphosis). To sample in situ temperatures in which pelagic larvae develop requires detailed measurements of the larval distributions offshore, as well as in situ temperature measurements in these coastal water masses. While these offshore measurements were beyond the scope of this study, satellite images of sea surface temperature were available and showed a complex
spatial distribution of temperature associated with mesoscale structures and fronts (Chapter 3).

It is unlikely that the lack of a relationship between RNA/DNA and total length is explainable by differences in time scales of these indices. Indeed, we would expect well fed fish to grow faster, as shown for laboratory reared larvae, where RNA-DNA ratios increased with length as did the variability within the ratios (Clemmesen 1994). In the same study, RNA/DNA of field caught larvae, within a small size range (5 mm), was highly variable and deviated from well fed laboratory animals, leading Clemmesen (1994) to conclude that 41.2% of the field caught larvae were starved. However, environmental factors, such as temperature, were not taken into consideration. Using the model of Buckley (1984), the critical RNA-DNA ratio (at zero growth) decreases with increasing temperature. Thus, if Clemmesen’s larvae developed in warmer waters than those reared in the laboratory, they may not have been starving. The high variability of RNA-DNA ratios for A. sphynx probably reflected the high variability or patchiness of the food supply in the pelagic environment. Unfortunately, this could not be substantiated by the stomach contents, which ranged from full to empty for fish collected on the same day, since fish may have digested food before collection. Theilacker et al. (1996) found the nutritional status improved with growth of fish larvae, regardless of prey densities, and only a few older larvae were malnourished. For our study, settlers represent the end of the larval stage, i.e. older larvae. However, just because these older larvae survived up to settlement does not mean they were not starved since starvation may not cause death directly, but indirectly as a result of increased loss by predation through smaller size and reduced swimming abilities (Olla et al. 1996). The lack of correlation between larval size and RNA/DNA has also been observed in other field studies (Lough et al. 1996, Chicharo et al. 1998). We suggest either RNA-DNA ratios do not integrate over time scales sufficiently long to resolve the whole growth history in the pelagic phase, or other environmental factors besides food supply, e.g. temperature, are responsible for the high variability in the nutritional condition within a size class.

Pelagic characteristics versus post-settlement survival

Of all the parameters we compared to survival (RNA-DNA ratios, total length, and numbers of settler), post-settlement survival was more strongly related to the size of settlers than the nutritional status or number of settlers. These observations are consistent with other studies (e.g. Tupper and Boutilier 1995b, Sogard 1997). Like survival, mean total length of the population declined over the three settlement seasons, though not statistically significant. The majority of larvae, and therefore also the majority of large larvae, settled at the beginning of the settlement seasons when survival
was usually highest. Numbers of settlers were weakly related to survival, and probably only reflect the higher probability of survival when more fish settled during episodic peaks at the beginning of the settlement seasons (Chapter 5). The large variability in the measured characteristics of larvae surviving the pelagic phase did not sufficiently explain survival after settlement. Since factors from the pelagic phase did not explain post-settlement survival, factors in the benthic environment must be responsible. Therefore, our data indicate that processes occurring in the benthic phase are decoupled from pelagic processes.

**Beyond pelagic characteristics of settlers**

Based on the data presented here and additional investigations at the same study site (Chapter 5), we suggest onshore processes are the most important for determining post-settlement survival. Habitat selection and habitat suitability strongly influenced settlement and recruitment on small spatial scales (Chapter 4). A carrying capacity of approximately 2 per m² suitable habitat was reached before the end of all seasons (Chapter 5) and the numbers of settlers determined how fast this carrying capacity was attained. At the beginning of the seasons, when habitat was not limited, the majority of settlers arrived, most of which were large larvae. Once the carrying capacity was reached, survival was decoupled from settlement and per capita survival declined, regardless of numbers settling or the size of fish. It is difficult to state if larger fish really have higher survival probabilities or if habitat availability determines survival, since larval size and habitat availability covary over the settlement season. For other temperate species, habitat-specific growth and mortality at post-settlement did influence population structure (Tupper and Boutilier 1995a).

Other habitat factors important for survival of settlers, recruits, and juveniles are competition (Tupper and Boutilier 1995b, Steele 1998) and predation (Carr and Hixon 1995, Beets 1997, Steele 1997b, 1998, Connell 1998). Competition seems to have a minor effect on settlers of *Aidablennius sphynx*, since per capita, post-settlement loss rates were not dependent on the density of conspecifics (Chapter 5). Steele (1998) found predation was more important than competition in determining abundances of reef fish. Unfortunately, little information on predation is available for our species though we did observed that adults and juveniles of *A. sphynx* were preyed upon by other fish species (e.g. *Serranus cabrilla, Oblada melanura*). Further studies to separate the interconnection of size and habitat quality, including predation (Gibson 1994), are necessary to determine the factors effecting post-settlement survival.
CONCLUSIONS

The high variability in size and nutritional status of larvae signify conditions in the pelagic phase were patchy, though food was available close to shore. Size or nutritional status were not associated with nearshore temperature increases over the duration of the settlement season. RNA/DNA was not reflected by the stomach contents, probably because of the disparity in time scales. While larval characteristics during the pelagic phase (i.e. nutritional status, size and numbers of larvae settling) explained 26% of the variance in survival, we suspect other factors associated with benthic phase (i.e. habitat availability, competition, predation) accounted for most of the variability.

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7. 'Recruitment limitation' or 'competition regulation'? The case of a temperate, rocky shore fish

For most benthic invertebrates and fishes, the local production of offspring has no direct role for local population size because larvae have a dispersal life-stage offshore and do not return to spawning grounds. Therefore, recruitment or more clearly settlement of larvae from the pelagic to the benthic habitat (see Appendix) is the only input to local populations. One of the crucial questions in reef fish ecology is if settlement (or recruitment) patterns are represented in long-term (generation time) patterns of reef fish populations (e.g. Mapstone and Fowler 1988). Different models have been proposed, based on recruitment limitation and competition regulation, and will be discussed below.

Recruitment limitation

Recent studies in reef fish ecology followed the idea of recruitment limitation, proposed by Doherty (e.g. 1983). Littoral or reef habitats of fish are believed to be undersaturated and for this reason, local fish populations can not reach their possible maximum density. Consequently, populations are thought to be 'non-equilibrial' and limited by larval input or settlement (recruitment) (see Appendix). This implies processes occurring in the plankton should be the major factor limiting numbers of larvae settling (e.g. review of Doherty 1991). The recruitment limitation hypothesis predicts: 1) the variation in larval supply should be reflected in subsequent variation in local population densities; and 2) mortality occurring after settlement should be density-independent.

Competition regulation

An alternative idea is that reef fish populations are saturated with larvae. This implies populations are at their maximum densities and are regulated (see Appendix) by processes occurring after settlement, i.e. by post-settlement processes. The maximum density or level of local reef fish population represents a stable equilibrium where input equals output, and the level represents the carrying capacity (Begon et al. 1990, see Appendix). Consequently, regulation of a population only occurs as a result of one or more density-dependent processes (e.g. predation and competition) acting on the demographic processes of settlement (input), migrations (in- and output), and mortality (output). Recruitment, however, may also be dependent on density when already settled individuals have either positive or negative effects on settling larvae (e.g. Sweatman 1985). Competition is an interaction between individuals by a shared requirement for a resource in limited supply. Intraspecific competition occurs between individuals of the
same species and interspecific competition between species. Interspecific competition can be interpreted in two ways (Begon et al. 1990). The first is 'current competition' where different species restrict each other to narrow niches, but the ability to expand remains. In this case, the composition of reef fish communities would be defined by individuals of different species settling to vacant sites first, resulting in a composition 'lottery' (Mapstone and Fowler 1988). The amount of common resources individuals are competing for would limit the total number of fish at a site. The second interpretation is 'evolutionary avoidance of competition', where natural selection favours individuals able to adapt to a fundamental niche not shared by competitors. This niche differentiation would therefore not be a result of recent competition but of evolutionary avoidance of past competition. The avoidance mechanism would lead to a stable co-existence of species where the number of species at a site would be dependent on habitat heterogeneity and the abundance of individuals of each species would vary with the amount of suitable habitat available. Because of niche differentiation, competition would be mainly intraspecific and the population would be in a 'single species equilibrium', where the number of species and number of individuals within a species would remain constant as long as resources remain constant (Mapstone and Fowler 1988).

CASE STUDY

The study species, Aidablennius sphynx (family Blenniidae), is a temperate, rocky shore fish with a dispersal larval stage where larvae develop < 50 km offshore (Sabatés 1994). It is one of the most common species along the Mediterranean coast (Corbera et al. 1996) and has a settlement season during summer (June–September), making it a typical representative of temperate species (Chapter 2). To investigate if larval input is the limiting factor for local populations of A. sphynx and if variation in larval supply is reflected by subsequent variation in juvenile densities, factors affecting the settlement process were studied. To investigate if processes onshore regulate juvenile densities, factors affecting post-settlement processes were determined. By combining these observations, the impact of settlement and post-settlement processes on populations of Aidablennius sphynx will be compared in order to answer if recruitment limitation or competition regulation occurs.

Settlement

The variability in settlement was a result of spatial, temporal, and physiological differences in the pelagic environment. On large spatial scales (100 km) variability was low since no differences in settler densities were found in several locations along the
Variability on the largest temporal scale resulted from seasonal settlement and the different durations of the seasons. Differences in the onset of settlement seasons were directly related to the development of stratified waters and mesoscale activity along the entire coast (Chapter 2). The low variability on the largest spatial scale is consistent with the extent of the physical structure of water masses, encompassing the whole coastline. These mesoscale processes determine seasonal duration of settlement and probably regulate settlement on geographic scales as well.

On intermediate spatial scales of 100 m, no differences in settler densities were found in open bays (Chapter 3). In contrast, variability was highest on intermediate temporal scales within seasons, changing on a weekly to daily basis (Chapter 4). This variability was manifest in episodic settlement and was highly correlated to wave and storm events. These wave processes dominate spatial scales < 100 km (Horikawa 1988), smoothing the variability over spatial scales, including the intermediate scales of bays. The links between spatial and temporal settlement are the physical transport mechanisms acting on large to intermediate spatial scales but highly variable in time. The hypothesis is wave processes aided the shoreward transport of settlers and probably passively transported plankton. The high concentrations of zooplankton contained in stomachs of pelagic larvae (Chapter 5) reflect the association of ichthyo- and zooplankton patches. Slicks generated by internal waves may concentrate pelagic larvae (Kingsford and Choat 1986), especially surface dwelling species such as Aidablennius sphynx, and transport them onshore on the scale of days to hours (Shanks 1983, Kingsford and Choat 1986), corresponding to the time scales resolved by the analysis of stomach contents.

The physiological variability in growth and nutritional status, acting on large and intermediate temporal scales, respectively, is high and reflects patchiness of food and physical properties in the pelagic environment (Chapter 5). Near surface temperatures are highly variable in the mesoscale structures despite the general seasonal warming. These temperature can have two effects: 1) a direct effect on the physiology of the developing larvae: and 2) an indirect effect on food availability, where gradients create patches. Larvae of A. sphynx may not be passively transported but actively following high food densities in patches since they have highly developed fins (Sabatés 1994) and are adapted to swimming in the pelagic environment (A. Sabatés pers. comm.). However, swimming extracts metabolic costs on growth and nutritional status, which in addition to temperature determines the physiological age (McCormick and Molony 1995). Unfortunately, the calendar age of settled larvae could not be determined since no continuous increments in otoliths were seen. In the transition from the pelagic to the benthic stage, there were no differences in the numbers settling during the day or night.
or in the settlement patterns over 10 m scales (i.e. transects) (Chapter 4). Feeding, however, took place mainly during the day (Chapter 5), which implies visual feeding and encounter probabilities that are affected by turbulence and flows on the scale of centimeters (e.g. Kiorboe 1997).

Settlers reaching the shoreline were highly selective in their habitat, preferring bare rock substrates with small encrusting algae in the surface (Chapter 3). Other species, with similar life-histories and habitat, occupied separate niches. Parablennius incognitus preferred high densities of algal cover and Tripterygion tripteronotus intermediate densities of algal covers in the subsurface zones. After removal of individuals, no extension of habitat use was observed for any of the three species, suggesting settlers are adapted to a fundamental niche, not shared by competitors of other species. Intraspecific competition, however, may still occur.

**Post-settlement**

Settlement patterns reflect the variability of the pelagic stage. Short term (i.e. weekly) post-settlement losses were very high and altered these initial settlement patterns to such a degree that survival patterns no longer reflected the variability of the pelagic stage, thus, post-settlement losses decoupled patterns in the pelagic and benthic phases (Chapter 4). Another indication for decoupling of the pelagic and benthic life stage is the lack of dependence of post-settlement survival on physiological characteristics acquired in the pelagic stage. Losses were not dependent on densities of already settled individuals, but varied with the number of settlers arriving over time, and were highest during episodic peaks in settlement. Since the total number of survivors at the end of the settlement seasons fluctuated around the same mean density for 5 consecutive years, it is assumed a carrying capacity is reached. Densities of Aidablennius sphynx only depended on the total amount of suitable habitat available (Chapter 3). In locations with more suitable habitat, densities increased, indicating resource limitation and intraspecific competition. Given this, the low variability in settler densities on large spatial scales along the coast may be interpreted as fluctuations of survivors around the carrying capacity and not settlement driven by mesoscale processes (as was proposed above), since high, short-term losses were included in weekly observations. Unlike the unaliased settlement time series from a single site sampled by high frequency collections (Chapter 4), a sampling frequency higher than weekly along the entire coast is necessary to determine large spatial differences in settlement. The differences in survivor densities between locations at the end of settlement seasons may reflect the heterogeneity within the suitable habitat. For one location, where the substrate surface provided more cover (e.g. crevices, holes), survivor densities were
highest (Chapter 3), probably a consequence of increased visual separation between individuals and thus, decreased intraspecific competition. Intraspecific competition and predation are connected in two ways. First, whenever densities are high enough for intraspecific competition to occur, predation can reduce competition by decreasing population density. Second, intraspecific competition favors predation when the weakest individuals are chased out of the suitable habitat and preyed upon (Begon et al. 1990). Losses of *A. sphynx* were not a function of settler densities in the first part of the settlement season, however, after carrying capacity was reached, losses increased proportionally with increasing settlement (Fig. 7.1). Lastly, it is doubtful settlement was dependent on density of residents since adults had no consequence on habitat choice of settlers (Chapter 3) as shown for other species (Sweatman 1985).

**Final conclusions**

The combined findings of factors influencing settlement and post-settlement processes of *Aidablennius sphynx* lead to the conclusion that littoral population densities are not limited by settlement (i.e. recruitment) but by intraspecific competition. This results in a carrying capacity and habitat saturation when populations reach their maximum densities. Since the number of individuals increased with increasing amounts of suitable habitat but the number of species remained constant, populations of *A. sphynx* are in a 'single species equilibrium'.

![Graph showing cumulative settlement and post-settlement survival over the season.](image)

**Fig. 7.1.** Time series of cumulative, daily settlement (settlers) and weekly observations of post-settlement survival (survivors) over the season. Curves are smoothed from three years of data. Losses are the difference of the two curves, where the density-dependent losses (hatched bars) occur when the curves are linearly increasing, while density-independent losses (shading) happen once the carrying capacity of the survivors is reached.
TOWARDS ROCKY SHORE MANAGEMENT

For reef fish management, the whole spectrum of temporal and spatial scales over the life-cycle needs to be considered (e.g. P.F. Sale personal communication). Very few studies have been carried out in temperate reefs and particularly on the Mediterranean rocky shore. If Aidablennius sphynx is representative of rocky shore fish in general, more emphasis should be placed on post-settlement, rather than pre-settlement processes. Since other Mediterranean species apply strategies other than episodic settlement, i.e. periodic shoaling (Macpherson 1998, Vigliola et al. 1998), and need a wider array of habitats, more work needs to be done to determine if habitat saturation is linked to the temperate system or to single species. Nevertheless, availability of suitable habitat along the shore could be a key management parameter easily integrated into protection programs of coastal zones. If suitable habitat is lost, intraspecific competition will increase and the composition of reef fish communities will change, which may have larger ecological consequences. Lastly, future studies on both temperate and coral reefs need to sample more frequently to capture unaliased settlement time series to determine if recruitment limitation or competition regulates population dynamics.

Appendix of definitions

**Settlement.** Arrival of a new individual from the pelagic to the benthic habitat and its transition from a planktonic larva into a benthic oriented juvenile (Chapter 2).

**Recruitment.** Juvenile fish surviving to the end of the settlement season. For the recruitment limitation model it is defined as larvae that have ended their dispersive stage and begun their reef-associated stage.

**Habitat.** Place where a microorganism, plant or animal lives (Begon et al. 1990), however, with many scales, boundaries, and environmental conditions involved.

**Limitation.** When processes add to or subtract individuals from a population (in Caley et al. 1996)

**Regulation.** The tendency of a population to decrease in size when it is above a particular level, but to increase in size when below that level (Begon et al. 1990). Regulation occurs when at least one of the demographic processes is density-dependent and a population never goes extinct or increases to infinity (in Caley et al. 1996).

**Carrying capacity.** The maximum population size supported indefinitely by a given environment, after intraspecific competition has reduced the 'per capita net rate of increase' to zero. An idealized concept not to be taken literally in practice (Begon et al. 1990)
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