Understanding patterns of habitat use in reef fish:

Implications of ontogenetic shifts in habitat-use for population demography

by

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Figure 1 – *Forsterygion lapillum* (the common triplefin) perched on a cobble covered in encrusting coralline algae ("pink paint").
Abstract

Quantitative surveys of habitat associations of New Zealand’s common triplefin fish, *Forsterygion lapillum*, show that a small-scale ontogenetic shift in habitat use occurs shortly after settlement. Availability of habitat over-used by settler aged *F. lapillum* (*Cystophora*) explains ~55% of the variation in settler abundance, while juvenile and adult abundance patterns are not well explained by their respective over-used habitat (encrusting coralline algae). Predation is identified as a possible mechanism underlying the habitat use of settlers.

Methodologically similar surveys of a tropical species of labrid (*Thalassoma amblycephalum*) and a large body of published literature suggest that ontogenetic shifts in habitat use may be taxonomically and geographically widespread. Young *T. amblycephalum* disproportionately associate with small patch reefs comprised of living coral. In contrast, adults of this species show no clear patterns of association with measured habitat features within the lagoon, and are found higher in the water column. Findings suggest that juvenile *T. amblycephalum* may seek refuge from the high energy environments occupied by stronger swimming adults, in specific benthic microhabitats.

The mechanisms underlying ontogenetic shifts in habitat use and the ecological consequences of these shifts are not well understood. I chose New Zealand’s common triplefin (*Forsterygion lapillum*) as a model species to examine the underlying mechanisms and consequences of age-specific shifts in habitat use. Behavioural “choice” experiments, suggest that newly settled *F. lapillum* exhibit a preference for the habitat which they over-use. Results of a field experiment that manipulated *Cystophora* cover at two sites showed that *Cystophora* abundance can
positively affect settler densities, and may limit *F. lapillum* recruitment if in low abundance.

Taken together, these results suggest that: 1) ontogenetic shifts in habitat use may be widespread among fish taxa within both temperate and tropical reef systems; 2) patterns of habitat use may be a result of behavioural preferences; and 3) habitats which are preferred by early stages have the potential to cause population bottlenecks.
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Chapter 1: General Introduction

Most demersal and benthic marine species are characterised by a complex bipartite life cycle in which bottom dwelling, relatively site attached adults give rise to dispersive pelagic larvae (Thorson 1950, Leis 1991, Caley et al. 1996). Consequently, patterns of distribution and abundance of these species can be affected by a complex array of interacting processes acting at various stages during their life-cycle (Jones 1991). Variation in the supply of pelagic larvae, the behaviour of larvae as they settle, and post-settlement processes affecting growth and mortality, may all act to varying extents to create observed patterns of distribution and abundance. Processes affecting each of these stages may in turn be influenced by available habitat. For example large pulses of larvae delivered to the Florida keys have been directly associated with specific meso-scale oceanographic processes within their pelagic habitat (sub-mesoscale frontal eddies; Sponaugle et al. 2005). Active swimming behaviour of competent larvae (Leis & Carson-Ewart 2000) and active orientation of larvae toward habitat characteristics of specific sites (Montgomery et al. 2001), may influence patterns of settlement. Finally, habitat complexity may provide predation refuges for post-settlement stages, reducing mortality (Tupper & Boutilier 1997) or increasing growth in specific microhabitats (Levin et al. 1997).

Habitat use often changes throughout the ontogeny of benthic and demersal marine organisms at a range of spatial scales. At the largest spatial scale a drastic shift in habitat use is undertaken by propagules that are ejected into a pelagic environment by benthic or demersal adults, and again when fully developed pelagic larvae settle back to the juvenile/adult benthic habitat (Thorson 1950, Caley et al. 1996). These transitions in habitat use are often accompanied by a large spatial
displacement, and may have short term benefits for organisms, such as reducing mortality by moving vulnerable larvae away from predator rich inshore adult habitats (Bonhomme & Planes 2000). Large scale spatial displacement of larvae (i.e. dispersal) may also have longer term benefits for a species by allowing it to persist through small scale extinction events (Bonhomme & Planes 2000).

At an intermediate scale, the post-settlement stages of many tropical reef dwelling species appear to disproportionately use non-reef inshore habitats, such as mangroves and seagrass beds as juveniles, and subsequently shift to offshore coral reef habitat as adults (de la Moriniere et al. 2002, Gillanders et al. 2003, Halpern 2004). This spatial partitioning in age classes has led to the development of the ‘nursery’ concept; i.e., that certain habitats facilitate enhanced growth and survival of juvenile stages (Rooker et al. 2004), and thus contribute disproportionately to overall recruitment into adult populations (Beck et al. 2001).

Finally, ontogenetic shifts may occur at scales of metres to 10’s of metres, after pelagic larvae settle to adult benthic habitats. Small-scale ontogenetic shifts in habitat use may occur at numerous stages after settlement and have been described for tropical reef fish (Lirman 1994, Light & Jones 1997, Vagelli 2004, Lecchini & Galzin 2005) temperate reef fish (Carr 1989, Anderson 1994), flatfishes (Ryer et al. 2004), and sea urchins (Williamson et al. 2004). The explanations that are most often invoked for such shifts are similar to those argued for the role of nursery habitats, and include: relief of intra-specific competition (density dependence) through resource partitioning (Lirman 1994), reduced predation rates (Carr 1989, Ryer et al. 2004), increased feeding efficiency, or a combination of factors (Dahlgren & Eggleston 2000). All of the above explanations implicitly suggest potentially strong effects of microhabitats on demographic rates (e.g., growth and/or survival, which
eventuate into recruitment) within post-settlement stages of marine organisms. At one extreme, stage specific use of habitat could result in limitation of a population by imposition of a bottleneck to recruitment to later stages. Natural fluctuations in the abundance of specific algal habitat required by settlers could, in poor years, have limiting effects on the numbers of new settlers introduced to a population. Reduced settlement may then limit recruitment to later stages of the species creating a population bottleneck.

Many studies identifying ontogenetic shifts in habitat use are motivated by a need to identify key conservation areas for management programmes such as marine reserves. This has been the primary driving force behind studies of nursery habitats (Beck et al. 2001). To apply knowledge of stage specific habitat use in effective management and conservation programmes, we must first identify the specific processes that drive such shifts, and then quantify the demographic consequences of these shifts. A common (and usually untested) assumption of studies of habitat use is that “habitat association” is a result of some preference for the habitat by the occupying individual (Crowe & Underwood 1998). Such a conclusion could hamper conservation efforts for a species which was not associated with a particular habitat through any preference on its part, but rather as a result of extrinsic processes, such as competitive exclusion from habitats that would otherwise be preferred (Underwood et al. 2004).

Mechanisms underlying patterns of habitat use may be divided into two categories: (1) those that are extrinsic, and (2) those that are intrinsic or “behavioural” on the organisms’ part. Non-random patterns of habitat use could result from extrinsic mechanisms such as differential settlement driven by oceanographic processes (e.g. Sponaugle et al. 2005), or random patterns of
settlement that are subsequently modified by post-settlement processes (Jones 1991) such as differential predation rates between different habitats (Underwood et al. 2004). Conversely, non-random patterns of habitat use may occur as a result of an intrinsic, behavioural preference of an organism for specific habitat types (Olabarria et al. 2002), preferences which may alter with growth and development. These behavioural preferences may develop in response to increased growth, decreased mortality (as a result of predation refuges or resource partitioning), or a combination of the two whereby an organism may choose the habitat that minimises the ratio of mortality risk to growth rate (e.g. the 'minimize μ/g hypothesis'; Werner & Gilliam 1984). It is likely that a combination of extrinsic and intrinsic processes may act to drive observed ontogenetic shifts in habitat use.

Identifying shifts in resource use, determining the underlying cause of the shift, and finally determining the potential for limitation or facilitation of abundance at various life stages, is therefore essential to a full understanding of how resources affect population dynamics. The primary goals of this study are to: 1) evaluate habitat use patterns of a temperate and a tropical reef fish, with specific attention to understanding the nature of ontogenetic shifts in habitat use; 2) to experimentally assess a mechanism that may underlie habitat shifts, and; 3) to experimentally assess the ecological consequences of an ontogenetic shift for a species of reef fish.

I use a preference index and a quantitative sampling method to statistically evaluate habitat associations of an endemic New Zealand temperate reef fish (*Forsterygion lapillum*) at three stages through its ontogeny: (1) as new settlers (< ~2 week's post-settlement age), (2) as recruited juveniles (~ 2 weeks to ~6 months post-settlement) and (3) as reproductive adults (age > ~6 months). I evaluate patterns of abundance of each age class as a function of the availability of “critical” (over-used)
habitat, and as a function of the abundance of a potential predator and competitor (*F. varium*).

Secondly, I use the same preference index and a similar quantitative sampling method to evaluate habitat associations of a tropical reef fish (*Thalassoma amblycephalum*) in Moorea, French Polynesia. I grouped observed individuals into two size categories to evaluate patterns and consequences of habitat use between young (settlers and juveniles) and adults of this species.

Finally, I use a laboratory experiment to test a potential mechanism (behavioural preference) that may underlie the habitat association of newly settled *F. lapillum* with *Cystophora* (see Chapter 2). I also manipulate percent cover of the habitat preferred by settlers in a field experiment, to estimate the effects of habitat limitation and facilitation on recruitment of *F. lapillum*.

The following three chapters have been written as scientific papers intended for publication. Consequently, there is some repetition of material presented within subsequent chapters and this general introduction.
Chapter 2: A small scale ontogenetic shift in habitat use of a temperate reef fish

2.1 ABSTRACT

Quantitative surveys of habitat associations of New Zealand’s common triplefin fish, *Forsterygion lapillum*, suggest that young settlers disproportionately occur within the fronds of two structurally similar species of large brown algae (*Cystophora retroflexa* and *C. torulosa* hereafter collectively referred to as *Cystophora*). This apparent preference is specific to *Cystophora* (i.e., fish do not exhibit strong patterns of association with other structurally similar macroalgal species), and older juvenile or adult *F. lapillum* do not exhibit the same patterns of habitat use. Taken together, these observations suggest that young *F. lapillum* undergo an ontogenetic shift in habitat use sometime after settlement. Spatial variation in abundance of *Cystophora* explained ~55% of the variation in density of recently settled *F. lapillum* (*p* = 0.002). The densities of older stages of *F. lapillum* were not strongly predicted by key habitat features. Local densities of recently settled *F. lapillum* were negatively correlated with local densities of the congener *F. varium*, a known predator (*R* = -0.510, *p* = 0.052), though this was marginally significant at the 5% level. Overall, these results suggest that *Cystophora* habitat may: 1) provide a refuge from predation for recently settled *F. lapillum*; 2) limit recruitment; and 3) result in a population bottleneck to subsequent juvenile and/or adult stages.

2.2 INTRODUCTION

Many marine organisms use different habitats as they progress through their ontogeny (Werner & Gilliam 1984). Most benthic or demersal marine organisms
undergo a series of prominent habitat shifts, first when propagules are ejected into a pelagic environment and again when fully developed pelagic larvae settle back to the juvenile/adult benthic habitat (Thorson 1950, Caley et al. 1996). These transitions in habitat use are often accompanied by a large spatial displacement, and may have short term benefits for organisms, for example by moving vulnerable larvae away from predator rich inshore adult habitats, (Bonhomme & Planes 2000). Large scale spatial displacement of larvae (i.e. dispersal) may also have longer term benefits for a species by allowing it to persist through small scale extinction events (Bonhomme & Planes 2000).

In tropical reef systems, many reef dwelling species appear to disproportionately use non-reef inshore habitats, such as mangroves and seagrass beds as juveniles, and subsequently shift to offshore coral reef habitat as adults (de la Moriniere et al. 2002, Gillanders et al. 2003, Halpern 2004). Such organisms represent an example of an “intermediate” spatial scale at which habitat shifts may occur. This spatial partitioning in age classes has led to the development of the ‘nursery’ concept; i.e., that certain habitats facilitate enhanced growth and survival of juveniles (Rooker et al. 2004), and thus contribute disproportionately to overall recruitment into adult populations (Becket al. 2001). Despite the intuitive appeal of the nursery habitat concept, relatively few studies have demonstrated movement between “nursery” and adult habitats (but see Halpern 2004).

Even less well understood are the demographic consequences of apparent habitat shifts that often occur between various age classes, such as settlers and juveniles, or juveniles and adults, at much finer spatial scales. Shifts in microhabitat use over spatial scales of meters to 10’s of meters appear relatively common across a wide range of taxa, and have been described for tropical reef fish (Lirman 1994,
Light & Jones 1997, Vagelli 2004, Lechini & Galzin 2005) temperate reef fish (Carr 1989, Anderson 1994), flatfishes (Ryer et al. 2004), and sea urchins (Williamson et al. 2004). The explanations that are most often invoked for such shifts are similar to those argued for the role of nursery habitats, and include: relief of intra-specific competition (density dependence) through resource partitioning (Lirman 1994), reduced predation rates (Carr 1989, Ryer et al. 2004), increased feeding efficiency, or a combination of factors (Dahlgren & Eggleston 2000). All of the above explanations implicitly suggest potentially strong effects of microhabitats on demographic rates (e.g., growth and/or survival, which eventuate into recruitment). At one extreme, stage specific use of habitat could result in limitation of a population by imposition of a bottleneck to recruitment to later stages.

Here I use a preference index to statistically evaluate habitat associations of a temperate reef fish (*Forsterygion lapillum*) at three stages through its ontogeny: (1) as new settlers (< ~2 week’s post-settlement age), (2) as recruited juveniles (~ 2 weeks to ~6 months post-settlement), and (3) as reproductive adults (age > ~6 months). I define “critical habitat” for each ontogenetic stage as any habitat that is disproportionately over-used (electivity value > 0, see methods), and then evaluate patterns of abundance of each age class as a function of availability of critical habitat. Finally, I evaluate potential effects of a common congeneric species (*F. varium*), which may prey upon recently settled *F. lapillum* (personal observations) and possibly compete with juvenile and adult *F. lapillum* for space and/or food resources.
2.3 METHODS

2.3.1 Study Site and Species

I conducted surveys at multiple rocky reef sites along the Miramar Peninsula, which adjoins Wellington Harbour with the more wave-exposed Wellington South Coast (Fig. 1). Rocky reef habitat in this area is spatially discrete and relatively shallow (generally offshore of coastal headlands, comprised of cobbles, boulders, and/or rock outcrops persisting to a depth of up to ~12m), and is often separated by sandy embayments (personal observations). The focal study species, Forsterygion lapillum (the “common triplefin”) is endemic to New Zealand and is one of the most abundant reef fishes in the Wellington region (personal observations). Adults spawn benthic egg masses on smooth rock or cobbles (often encrusted with coralline algae) between June and January (Francis 2001). All New Zealand triplefins appear to be site-attached, spending their adult lives within a few square metres of reef (Clements 2003). Pelagic larvae emerge from benthic eggs after ~20 days (Francis 2001), and young F. lapillum generally settle back to rocky reef habitats in the Wellington region between November and March, at an average size of 27.82mm TL (SD = 4.10mm; J. Shima unpublished data). Three ontogenetic stages of F. lapillum were defined based on size classes (15-29mm, 30-49mm, and 50mm+). These size classes were chosen to correspond roughly to age classes of “new settlers” (15-29mm, average settlement size 27.82mm), “juveniles” (30-49mm) and “adults” (>50mm, approximate size that juveniles become sexually mature adults; Francis 2001). F. lapillum become sexually mature at ~5cm after ~6 months (Francis 2001), and fish usually do not survive more than 2 breeding seasons (Doak 2003).
2.3.2 Patterns of Abundance

At 5 sites around Miramar Peninsula (see Fig. 1) I established three permanent 20m transects parallel to shore. The first transect was placed at a 3m
depth contour and subsequent transects were placed parallel to this at a perpendicular distance of 10m and 20m respectively. Initial positions of transects within each site were randomly determined. Along each transect I sampled 1m$^2$ quadrats at 5m intervals (n= 4 quadrats per transect; 12 quadrats per site). Within each quadrat I visually estimated the number of *Forsterygion lapillum* classifying individuals into one of three size categories representing new settlers, juveniles and adults as defined above. All quadrats were sampled on two separate occasions 1 month apart in December 2003 and January 2004.

Average densities of *F. lapillum* for each size class (see above) were evaluated separately for the two sampling dates using the three transects as replicate measures for each site. I used a Generalized Linear Model (GLM) to conduct an ANODEV using a Poisson distribution, in the statistical package R (version 1.9.0). This analysis uses a parametric model that makes the assumption that the response has a Poisson distribution (where the mean equals the variance; commonly seen in count data), rather than a normal distribution (as used in ANOVA). Using such a test mitigates problems associated with modelling count data as normal. In biological data the variance is often greater than the mean (termed overdispersion) which has the effect of inflating Type 1 error (Quinn & Keough 2004). To correct for overdispersion in any tests which showed this I used a quasi-likelihood model where the dispersion parameter is estimated from the actual data. For significant tests, I conducted all possible pairwise comparisons of means, using a sequential Bonferroni correction to allow for multiple testing.
2.3.3 Role of Habitat

Spatial variation in *F. lapillum* densities around Miramar Peninsula may arise from underlying variation in habitat characteristics. To examine the potential role of habitat variability on fish density, I quantitatively explored patterns of habitat use (using an “electivity index”) and then evaluated how well critical habitats (i.e., those habitat types that were disproportionately over-used by fish) explained spatial variation in *F. lapillum* densities.

Within each quadrat that was surveyed for *F. lapillum* densities (n=4 for each transect), I visually estimated percent cover of the following species/microhabitat categories: *Cystophora* (abbreviated Cy), *Carpophyllum maschalocarpum* (Ca), *Ecklonia radiata* (E), *Macrocystis pyrifera* (M), *Undaria pinnatifida* (U), empty water (W), geniculate coralline algae (GC), encrusting coralline algae (EC), rock and cobble (R), sand and broken shell (SS), bare sand (S), small stones and pebbles (<5cm diameter; St), live mussels (Mu), dead mussel shells (MH), and other encrusting invertebrates (Sp). Percent covers for the benthos and for canopy forming species (where percent cover of canopies was estimated approximately 30cm from bottom) were estimated separately. This gave a total possible cover of 200% per quadrat; this value was subsequently standardised to 100% cover.

In addition to estimating densities of *Forsterygion lapillum* stratified among three size categories (described above), I recorded the microhabitat type (see above list) directly below each individual at the time of observation.

I evaluated habitat use by new settlers, juveniles and adults separately using Manly’s Alpha (Manly et al. 1972, Chesson 1978, Shima 2001). This measure is based on the proportion of fish within a given quadrat on a given habitat type,
relative to the probability of the fish associating with that habitat type under conditions of random assortment and is calculated as:

\[
\alpha_i = \frac{F_i}{H_i} \sum_{j=1}^{n} \frac{F_j}{H_j} \quad i = 1, \ldots, n
\]

where habitat use (\( \alpha \)) is evaluated separately for each habitat type (1 through \( n \)) in each replicate sampling unit (quadrat), \( H \) is the proportion of surveyed habitat of a given type, and \( F \) is the proportion of censused fish on a given habitat type. I converted \( \alpha_i \) values to electivities (\( \epsilon_i \)) to represent habitat use as an index ranging from -1 (never used) to +1 (exclusively used) with 0 representing neutral association, using the equation:

\[
\epsilon_i = \frac{n \alpha_i - 1}{(n-2)\alpha_i + 1} \quad i = 1, \ldots, n
\]

where \( n \) is the number of habitat types (Chesson 1983). Manly's alpha and electivity values were calculated separately for each fish size class within each quadrat. Mean electivity values (+/- 95% confidence intervals = CI) were calculated for each microhabitat type using quadrats as replicates.

I classified “critical habitat” as the unweighted aggregate of all habitats with an electivity value significantly greater than zero (i.e. 95% CI don’t overlap 0). Percent cover of critical habitat was averaged for each transect over the two sample dates. Densities (no. fish/4m\(^2\)), for each size class of \( F. lapillum \) were averaged for each transect over the two sample dates. I used linear regression (SPSS version 11.5 for Windows) to explore the relationship between over-used habitat and fish densities separately for recently settled \( F. lapillum \), juveniles, and adults. In addition, I incorporated these same habitat metrics as covariates in GLM models (described above) used to explore spatial variation in abundance of \( F. lapillum \).
2.3.4 Role of congener

Forsterygion varium is a common congener and known predator of small *F. lapillum* (personal observations) and therefore may have a negative affect on densities of settler and juvenile aged *F. lapillum*. Additionally, *F. varium* may compete with larger *F. lapillum* for food or habitat resources and thus may have additional negative effects on the abundance of adult aged *F. lapillum*. To evaluate the potential effects of *F. varium* on *F. lapillum* densities I used the following approach: 1) I calculated electivity values for juvenile and adult *F. varium*; 2) I explored the effects of *F. varium* densities on each age class of *F. lapillum* using regression analyses; 3) I incorporated densities of *F. varium* as a co-variate in the GLM analysis (described above) to explore spatial variation in abundance of *F. lapillum*.

Methods used to estimate *F. varium* densities and electivities were identical to those used for *F. lapillum* (described above), with the exception that the size class for *F. varium* categorised as “juveniles” ranged from 30-69mm; individuals 70mm and larger were categorised as “adults” in keeping with available life-history information (Francis 2001).

2.4 RESULTS

2.4.1 Patterns of Abundance

Densities of *Forsterygion lapillum* settlers varied significantly among sites for both sample dates (Fig 2A,D; Table 1). Densities of juveniles varied significantly among sites in January 2004 only (Fig 2E, Table 1). Although adult densities appeared heterogeneous among sites (Fig 2), overall variation was not statistically significant. Pairwise comparisons of means using sequential Bonferroni corrections
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were conducted on the three significant results. However, these tests failed to detect differences between specific pairs of sites. A visual inspection of results (Fig 2A,D) strongly suggests that densities of recently settled *F. lapillum* may be greater at Shelly Bay than at other sites. Similarly, densities of juveniles appear to be greatest at Shelly Bay for both sampling dates (Fig 2B,E), and seem particularly low at Worser Bay on the second sample date (Fig 2E).

Table 1 – Spatial variation in densities of recently settled, juvenile, and adult *Forsterygion lapillum* on two sample dates. Given are statistics from a Generalized Linear Model (ANODEV, using a poisson distribution) Significance levels indicated by * (P < 0.05) or ** (P < 0.01) or *** (P < 0.001).

<table>
<thead>
<tr>
<th>I. December 2003</th>
<th>Source</th>
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<th>Deviance</th>
<th>Residual Df</th>
<th>Residual Deviance</th>
<th>P(&gt;Chi)</th>
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<tbody>
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<td>10</td>
<td>11.6515</td>
<td>0.0033**</td>
</tr>
<tr>
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<tr>
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<table>
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<th>Deviance</th>
<th>Residual Df</th>
<th>Residual Deviance</th>
<th>P(&gt;Chi)</th>
</tr>
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<td>47.462</td>
<td>0.014*</td>
</tr>
<tr>
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<td>10</td>
<td>22.379</td>
<td>0.019*</td>
</tr>
<tr>
<td>C. Adults</td>
<td>Site</td>
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<td>21.438</td>
<td>10</td>
<td>34.245</td>
<td>0.121</td>
</tr>
</tbody>
</table>
Figure 3 - Spatial variation in densities of *Forsterygion lapillum* at five sites along Miramar Peninsula (see Fig 1 for geographic locations). Panels A-C represent densities stratified by age classes surveyed in December 2003; panels D-F represent densities stratified by age classes surveyed in January 2004. Supporting statistics are given in Table 1.

### 2.4.2 Role of Habitat Availability

Patterns of habitat use by new settlers (Fig 3A) differed greatly from those of juveniles (Fig 3B) and adults (Fig 3C), and suggest a possible ontogenetic shift in habitat use sometime after settlement. Settler electivities for *Cystophora* (CY) were strong, and although variable (likely a function of among-site variation in fish abundance relative to habitat percent cover), 95% CI does not overlap zero,
indicating a significant “over-use” of this microhabitat type. Juvenile and adult electivities for encrusting corallines (EC; Fig 3B,C), were both positive, with 95% CI’s not overlapping zero, suggesting a statistically significant over-use of this microhabitat type.

Spatial variation in density of recently settled *F. lapillum* were plotted against the abundance of critical habitat (electivity significantly >0) and analysed using regression (Fig 4). Densities of recently settled *F. lapillum* were explained by the proportionate cover of *Cystophora* habitat ($r^2 = 0.5475$, $p = 0.002$). Sites with more *Cystophora* generally had more young *F. lapillum*. Both juvenile and adult *F. lapillum* show no significant relationship with their over-used habitat (juveniles $r^2 = 0.1376$, $p = 0.174$; adults $r^2 = 0.0648$, $p = 0.360$).

A GLM used to explore the effects of spatial variation in habitat cover within- and among sites (including a site X habitat interaction; Table 2) suggests that (1) *Cystophora* as a covariate explains a significant amount of additional variation in the densities of recently settled *F. lapillum* sampled in January 2004, and (2) encrusting corallines explain a significant amount of additional variation in the densities of adults sampled in January 2004. Over-used habitats failed to account for any additional variance beyond the effects of “sites” for any of the other analyses conducted, and in no cases were interactions between site and habitat found to be significant.
Figure 4 - Patterns of habitat use by A) recently settled *F. lapillum*, B) juveniles, and C) adults. Given are electivity values calculated for each microhabitat category (Mean +/- 95% CI). Habitat categories are: Cy – *Cystophora*, Ca – *Carpophyllum maschalocarpum*, E – *Ecklonia radiata*, M – *Macrocystis pyrifera*, U – *Undaria pinnatifida*, O – other foliose macroalgae, W – mid-water above bottom, GC – geniculate coralline algae, EC – encrusting coralline algae, R – rock and cobbles, SS – sand and broken shell, S – bare sand, St – small stones and pebbles, Mu – live mussels, MH – mussel half shells (dead), and Sp – other encrusting invertebrates (e.g. sponges and bryozoans). “ND” represents habitat categories that never co-occurred with that age class of *F. lapillum* in sample quadrats.
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Figure 5 – Spatial variation in densities of *Forsterygion lapillum* explained by habitat for A) settlers, B) juveniles and C) adults. Each point represents the density of *F. lapillum* at one transect averaged over the two sample dates. Relevant habitats were determined from electivity analyses (see Fig 3) and are comprised of habitats with electivity values significantly > 0, specific to each age class. For settlers, over-used habitat is *Cystophora*; for juveniles and adults, over-used habitat is encrusting coralline algae. Linear regression summary statistics are given within each panel.
Table 2 – Additional effects of habitat attributes to account for spatial variation in density of *F. lapillum*. (c.f., Table 1). Given are results of GLM analyses (ANODEV) used to evaluate effects of “site”, “habitat”, and their interaction, separately for settlers, juveniles, and adults for two sample dates. “Habitat” for recently settled *F. lapillum* is the proportion of *Cystophora* (CY) cover; for older juveniles and adults, habitat is the proportion of encrusting coralline (EC) cover (see Fig 3). Significance levels indicated by * (P < 0.05) or ** (P < 0.01) or *** (P < 0.001).

| Source   | Df | Deviance | Residual Df | Residual Deviance | P(>|Chil|) |
|----------|----|----------|-------------|-------------------|--------|
|          |    |          |             |                   |        |
| **I. December 2003** |        |          |             |                   |        |
| A. Settlers | Site | 4 | 15.7763 | 10 | 11.6515 | 0.0033** |
|           | CY  | 1 | 0.0213  | 9  | 11.6302 | 0.884  |
|           | Site x CY | 2 | 1.7934  | 7  | 9.8368  | 0.4079 |
| B. Juveniles | Site | 4 | 29.268  | 10 | 36.88   | 0.103  |
|            | EC  | 1 | 9.578   | 9  | 27.302  | 0.112  |
|            | Site x EC | 4 | 4.455   | 5  | 22.847  | 0.883  |
| C. Adults  | Site | 4 | 3.565   | 10 | 40.847  | 0.782  |
|           | EC  | 1 | 1.876   | 9  | 38.971  | 0.338  |
|           | Site x EC | 4 | 26.594  | 5  | 12.377  | 0.011* |
| **II. January 2004** |        |          |             |                   |        |
| A. Settlers | Site | 4 | 45.623  | 10 | 47.462  | 0.01*  |
|            | CY  | 1 | 17.265  | 9  | 30.197  | 0.024* |
|            | Site x CY | 1 | 0.011   | 8  | 30.187  | 0.955  |
| B. Juveniles | Site | 4 | 24.479  | 10 | 22.379  | 0.095  |
|            | EC  | 1 | 0.111   | 9  | 22.269  | 0.85   |
|            | Site x EC | 4 | 6.08    | 5  | 16.189  | 0.742  |
| C. Adults  | Site | 4 | 21.438  | 10 | 34.245  | 0.043* |
|           | EC  | 1 | 8.379   | 9  | 25.866  | 0.05   |
|           | Site x EC | 4 | 10.595  | 5  | 15.271  | 0.302  |

2.4.3 Role of congener

No newly settled *F. varium* were observed during my sampling. Hence, subsequent analyses for this species are restricted to patterns observed for juveniles and adults. Patterns of habitat use by juvenile (Fig 5A) and adult (Fig 5B), *F. varium*, appear similar to those exhibited by juvenile and adult *F. lapillum* (c.f.,
Figure 3B & C). Adult *F. varium* had a positive electivity value for encrusting corallines (Fig 5B), and 95% CI’s did not overlap zero, suggesting a statistically significant over-use of this microhabitat type.

Densities of recently settled *F. lapillum* were negatively correlated with densities of *F. varium* though this was not significant at the 5% level (Fig 6A, $r^2 = 0.26$, $p = 0.052$). Regression analyses suggest no significant relationship between densities of juvenile *F. lapillum* and *F. varium* (Fig 6B, $r^2 = 0.0195$, $p= 0.620$). Densities of adult *F. lapillum* were positively correlated with densities of *F. varium* (Fig 6C, $r^2 = 0.3412$, $p=0.022$).

A GLM used to explore the effects of spatial variation in *Forstergyion lapillum* densities within- and among sites (including a site X *F. varium* interaction; Table 3) suggests that *F. varium* as a covariate explains a significant amount of additional variation in the densities of juvenile *F. lapillum* sampled in December 2003 and a significant interaction in this test suggests that the effect of *F. varium* densities varied with site. Densities of *F. varium* failed to account for any additional variance beyond the effects of “sites” for any of the other analyses conducted.
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Figure 6 - Patterns of habitat use by A) juvenile *F. varium*, and B) adults. Given are electivity values calculated for each microhabitat category (Mean +/- 95% CI). Habitat categories are: Cy - *Cystophora*, Ca - *Carpophyllum maschalocarpum*, E - *Ecklonia radiata*, M - *Macrocystis pyrifera*, V - *Undaria pinnatifida*, O - other foliose macroalgae, W - mid-water above bottom, GC - geniculate coralline algae, EC - encrusting coralline algae, R - rock and cobbles, SS - sand and broken shell, S - bare sand, St - small stones and pebbles, Mu - live mussels, MH - mussel half shells (dead), and Sp - other encrusting invertebrates (e.g. sponges and bryozoans).
Figure 7 - Spatial variation in densities of *Forsterygion lapillum* explained by densities of *F. varium* for A) settlers, B) juveniles and C) adults. Each point represents the density of *F. lapillum* and *F. varium* at one transect averaged over the two sample dates. Linear regression summary statistics are given within each panel.
Table 3 – Additional effects of *Forsterygion varium* densities to account for spatial variation in density of *F. lapillum*. (c.f., Table 1). Given are results of GLM analyses (ANODEV) used to evaluate effects of "site", "*F. varium*", and their interaction, separately for settlers, juveniles, and adults for two sample dates. Significance levels indicated by * (P < 0.05) or ** (P < 0.01) or *** (P < 0.001).

### I. December 2003

| Source          | Df | Deviance | Residual Df | Residual Deviance | P(>|Chi|) |
|-----------------|----|----------|-------------|------------------|--------|
| **A. Settlers** |    |          |             |                  |        |
| Site            | 4  | 15.7763  | 10          | 11.6515          | 0.0033** |
| *F. varium*     | 1  | 0.3086   | 9           | 11.3429          | 0.5785 |
| Site x *F. varium* | 4  | 4.4807   | 5           | 6.8622           | 0.3448 |
| **B. Juveniles** |    |          |             |                  |        |
| Site            | 4  | 29.268   | 10          | 36.88            | <0.0001*** |
| *F. varium*     | 1  | 17.436   | 9           | 19.444           | <0.0001*** |
| Site x *F. varium* | 4  | 17.009   | 5           | 2.435            | <0.0001*** |
| **C. Adults**   |    |          |             |                  |        |
| Site            | 4  | 3.565    | 10          | 40.847           | 0.869  |
| *F. varium*     | 1  | 8.312    | 9           | 32.536           | 0.087  |
| Site x *F. varium* | 4  | 12.433   | 5           | 20.103           | 0.357  |

### II. January 2004

| Source          | Df | Deviance | Residual Df | Residual Deviance | P(>|Chi|) |
|-----------------|----|----------|-------------|------------------|--------|
| **A. Settlers** |    |          |             |                  |        |
| Site            | 4  | 45.623   | 10          | 47.462           | 0.055  |
| *F. varium*     | 1  | 2.348    | 9           | 45.114           | 0.49   |
| Site x *F. varium* | 4  | 11.049   | 5           | 34.065           | 0.691  |
| **B. Juveniles** |    |          |             |                  |        |
| Site            | 4  | 24.479   | 10          | 22.379           | 0.045* |
| *F. varium*     | 1  | 0.164    | 9           | 22.215           | 0.798  |
| Site x *F. varium* | 4  | 8.886    | 5           | 13.329           | 0.471  |
| **C. Adults**   |    |          |             |                  |        |
| Site            | 4  | 21.438   | 10          | 34.245           | 0.121  |
| *F. varium*     | 1  | 10.141   | 9           | 24.104           | 0.063  |
| Site x *F. varium* | 4  | 3.877    | 5           | 20.227           | 0.858  |

### 2.5 DISCUSSION

Statistical analyses of habitat associations exhibited by settler, juvenile and adult *Forsterygion lapillum*, suggest an ontogenetic shift in habitat use occurs sometime after settlement. Newly settled *F. lapillum* over-used *Cystophora* (CY), while later age classes over-used encrusting coralline algae (EC). A large proportion (55%) of the spatial variation in densities of recently settled *F. lapillum* is explained...
by the proportion of reef covered by *Cystophora* while over-used habitat was a poorer predictor of spatial variation in densities of juvenile and adult *F. lapillum*.

The explanations most often invoked for apparent ontogenetic shifts in habitat use are primarily related to fitness maximising strategies such as: relief of intra-specific competition (density dependence) through resource partitioning (Lirman 1994), or reduced predation rates (Ryer et al. 2004). These explanations implicitly suggest that overused habitats may have strong effects on the patterns of abundance of the stages using them. Further to this, the occurrence of shifts in the patterns of habitat use with ontogeny suggests that these effects may vary both in cause and strength at different life-history stages. Consequently, early ontogenetic stages may be limited by the habitat that they use, and in extreme cases this limitation could create a bottleneck to recruitment to later stages.

The data I have presented for *Forsterygion lapillum* suggests a shift in microhabitat use sometime after settlement and also suggests that for the earliest benthic stage of this species, the availability of over-used microhabitat has a significant effect on patterns of abundance. This apparent preference of settlers for *Cystophora* may be related to an increased foraging success within the fine, densely branching fronds of *Cystophora*. Taylor (1998) found that production of small mobile invertebrates (the primary food source of triplefins) was highest in finely-structured vegetated habitats. Taylor & Cole (1994) found that *Cystophora* spp. supported very high densities of small mobile invertebrates relative to most other brown seaweeds sampled. In contrast, habitat which was shown to be over-used by juveniles had only a very small effect on juvenile abundance and for adults had no effect on abundance. A possible explanation for this is that some level of limitation may be imposed at the settler stage by habitat and that the population may have gone
through a bottleneck caused by this limitation. This may have resulted in densities of adults and juveniles that are at or below some threshold value at which their habitat may become limiting. In support of this, patterns of juvenile abundance seem to reflect patterns of settler abundance among sites (see Fig 2). The absolute densities of settlers are much lower than those of juveniles; however continual settlement and fast growth rates of settlers due to abundant food resources may be responsible for this apparent discrepancy. Patterns of adult abundance however, do not reflect patterns of settlers. Such a pattern contrasts with other results for reef fish in which densities of adults reflect juvenile recruitment (e.g. Jones 1984b). This may be a result of changes in settlement patterns between years, perhaps due to changes in Cystophora abundance, or a result of some migration of adults from areas with high settlement, to avoid competition. A longer term observational study may be able to address some of these points by tracking a settlement pulse through to adulthood.

Analysis of the association of settler aged Forsterygion lapillum with the densities of a congener (F. varium) show a negative pattern of association. This pattern is not quite statistically significant at the 5% level, but may still be biologically meaningful. Analyses of habitat associations of F. varium suggest that both juveniles and adults of this species over-use the same microhabitat as juvenile and adult F. lapillum (i.e. encrusting corallines). Active predation by adult F. varium of settler sized F. lapillum was observed a number of times during this study, and has been recorded photographically (in Montgomery 2003). In addition, Thompson & Jones (1983) showed that F. varium is capable of altering habitat use by another species of fish that is much larger than F. lapillum settlers. This suggests that predation pressures from F. varium may be partly responsible for the observed habitat use patterns in settler aged F. lapillum. Juveniles of a congener, F. capito,
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have been shown to have a similar habitat association with Cystophora (Duffy 1989). Duffy (1989) hypothesised that this pattern was a result of these fish seeking shelter in complex Cystophora, having noticed that the approach of a diver often triggered the fish to dart into the surrounding macroalgae. Complex habitats such as those provided by densely branching macroalgae (such as Cystophora) have been shown in a number of other studies to act as refuges from predation induced mortality (e.g. Tupper & Boutilier 1997), and in this case small scale habitat partitioning between settler F. lapillum (using Cystophora) and a predator (adult F. varium, using encrusting corallines), may reduce negative encounters between adult F. varium and newly settled F. lapillum. Juvenile F. lapillum densities show no association with densities of F. varium, and adult F. lapillum densities show a positive association with densities of F. varium. Together with the observation that juvenile and adult F. varium use the same microhabitat type as juvenile and adult F. lapillum, this suggests that there is strong potential for competition between the older stages of these two species for resources, and such competition may affect the patterns of abundance and distribution of the juvenile and adult stages of these two species. Testing such hypotheses would require further study, preferably with careful experiments.

Studies that investigate the variability of habitat use, or indeed variable patterns of any resource use, are targeted at developing a better understanding of the mechanisms responsible for producing observed ecological patterns. This understanding is important in the application of conservation and management programs for marine systems. The presence and apparent widespread nature of ontogenetic shifts in habitat use has potential implications for conservation and management actions and decisions. Habitat restoration and protection are common conservation tools, which if applied without a full understanding of the potential for
shifts in habitat use with ontogeny, and of the effects of these shifts, could have poor results. This research illustrates that the careful selection of target habitats may be crucial to the success of such programmes, and that the selection of target habitats will require careful study of habitat use patterns at all ontogenetic stages.
Chapter 3: An ontogenetic shift in habitat use of a tropical reef fish; *Thalassoma amblycephalum*

3.1 ABSTRACT

Quantitative surveys of the tropical Labrid, *Thalassoma amblycephalum*, at Moorea, French Polynesia, suggest that young juveniles disproportionately associate with small patch reefs comprised of living coral. In contrast, adults of this species show no clear patterns of association with measured habitat features within the lagoon. One interpretation of this pattern is that young *T. amblycephalum* may have specific microhabitat requirements, while older stages may be habitat generalists. These findings are consistent with other research into the swimming ability of this species, which suggests that swimming ability increases with age, and that relative position in the water column changes in response to ontogenetic development of swimming ability. My research suggests that juvenile *T. amblycephalum* may seek refuge from the high energy environments (occupied by stronger swimming adults) in living coral patch reefs. Potential implications of age-specific habitat specialisation (e.g. population bottlenecks and maintenance of community diversity) are discussed.

3.2 INTRODUCTION

Small-scale age related shifts in micro-habitat use are relatively common across a wide range of taxa, and may have strong effects on vital demographic rates of populations. The potential effects of ontogenetic habitat shifts on patterns of abundance, and the apparent widespread nature of these shifts, has specific implications for the design and application of conservation and management...
programs *(reviewed in Ch 1).* My previous work on the temperate reef fish *Forsterygion lapillum* suggests an apparent ontogenetic shift in habitat use sometime after settlement. To evaluate the generality of such age-related habitat shifts early in the ontogeny of reef fishes, I employed similar quantitative methods to conduct a comparable study on a tropical Labrid, *Thalassoma amblycephalum* in Moorea, French Polynesia.

Coral reef systems are well known for the high fish diversity they often support in comparison with temperate reef systems (Mora et al. 2003). Moorea supports a total of 50 species of Labrid (Randall 1985). The maintenance of such diversity may require specific niche partitioning to alleviate inter-, and intra-specific competition for resources, as well as to afford age or size specific refuges from a diverse array of predators. In such a system, ontogenetic shifts in habitat use may become particularly important as a mechanism by which tropical fish may partition niches to avoid competition (Lirman 1994), or afford young stages with refuges from predators until some size refuge is reached (Ryer et al. 2004).

The temperate reef fish *Forsterygion lapillum* is sedentary and relatively site-attached throughout the post-settlement part of its life-cycle *(see Chapter 2).* In contrast, while juvenile *Thalassoma amblycephalum* are relatively site attached, adults are more mobile, actively swimming in the water column during daytime foraging and mating (Fulton 2001). Microhabitat characteristics may be particularly important for the juvenile stages of this species. Specific characteristics of the microhabitat may convey some refuge from predation, or increased growth through improved foraging. In contrast the more mobile adults of this species may respond to different habitat parameters.
Here I use comparable methods to those employed in chapter 2, to statistically evaluate microhabitat associations of a tropical reef fish (*Thalassoma amblycephalum*). I sampled individuals from two size classes (designed to correspond roughly to "settlers/juveniles" and "older adults"), and defined critical habitat for each size class as any habitat that is disproportionately over-used (electivity value > 0). Lastly, I evaluate patterns of abundance of each size category as a function of the availability of critical habitat.

### 3.3 METHODS

#### 3.3.1 Study Site and Species

This study was conducted on the island of Moorea, French Polynesia (17°30′ S, 149°50′W, Fig 7) during March 2004. Moorea is surrounded by a shallow lagoon which is flanked by a fringing reef along the shore and barrier reef (reef crest) approximately 1km offshore; much of the lagoon bottom is comprised of sand or rubble bottom, with patch reefs of variable size and isolation. Lagoon depth is approximately 3m, although the north shore of the island has two deep bays (Cook’s Bay and Opunohu Bay) that are ~ 30m deep. My surveys were conducted within the lagoons located east and west of Baie de Cook. This area is dominated by small patch reefs, comprised predominately of the mounding coral *Porites* spp. often with small colonies of branching corals (*Acropora* spp., *Pocillopora* spp.). Patch reefs in this area are generally separated from each other by low lying reef flat, consisting of sand and fine coral rubble or pavement (cemented coral rubble). Patch reefs become larger, flatter and shallower closer to the reef crest.

The two tone wrasse (sometimes known as the bluntheaded wrasse, *Thalassoma amblycephalum*) is moderately common in the lagoon of Moorea. Adults
form aggregations over shallow reef. Juveniles are generally found nearby in small groups of 3 to 5 individuals (*personal observations*). *T. amblycephalum* feed on zooplankton within the water column (Randall et al. 1990), and the mating system is thought to be promiscuous for initial phase group spawners and lek-like for terminal phase males (Donaldson 1995).

### 3.3.2 Patterns of Abundance

I surveyed abundance of *Thalassoma amblycephalum* at 6 sites; two sites were located east of Baie de Cook (E1 & E2, Fig 7), the remaining four were west of Baie de Cook (W1, W2, W3 & VOE, Fig 7). At all but one site (VOE, Fig 7) I surveyed an “outer” zone, which was close to the reef crest, and an “inner” zone which was 100 metres further inshore (South) in a line perpendicular with the reef crest. Three permanent 25m x 4m transects were set up in each zone running perpendicular to the reef spaced 10m apart. Within each transect I recorded visual counts of *T. amblycephalum*, giving a total abundance of fish per 100m² for each transect. Fish were classified into two size categories (10-29mm, and 30mm+). In the absence of any preliminary information on sizes at settlement and/or sexual maturity, these size categories were chosen somewhat arbitrarily; my intent was to disentangle patterns of abundance and habitat use for young stages (e.g., recent settlers and juveniles) and older *T. amblycephalum*. Hereafter I refer to the general size categories as “juveniles” and “adults”. All transects were sampled within a single day on each of three dates (15/3/04, 25/3/04, 30/3/04); the order that sites were sampled in was randomised among sampling dates.
Figure 8 – Map showing study sites. Black stars indicate locations of 6 sites surveyed for patterns of abundance and habitat use of Thalassoma amblycephalum. Inset is a map of Moorea Island. The following GPS co-ordinates were recorded for each of the sites using a Garmin hand held GPS unit: VOE - 17°28.648'S, 149°50.379'W. W3 - 17°28.691'S, 149°50.042'W. W2 - 17°28.698'S, 149°49.968'W. W1 - 17°28.697'S, 149°49.916'W. E1 - 17°28.565'S, 149°48.992'W. E2 - 17°28.490'S, 149°48.967'W. Map adapted from Adjeroud et al (2002).

Average densities of *T. amblycephalum* for each size class (see above) were evaluated separately for the three sampling dates using the three transects as replicate measures for each zone (inner and outer) nested within each site. I used a Generalized Linear Model (GLM) to conduct an ANODEV using a Poisson distribution in the statistical package R (version 1.9.0). This analysis uses a parametric model that makes the assumption that the response has a Poisson distribution (where the mean equals the variance; commonly seen in count data) rather than a normal distribution (used in ANOVA). Using such a test negates
problems associated with modelling count data as normal. In biological data the variance is often greater than the mean, termed overdispersion, which has the effect of inflating Type 1 error (Quinn & Keough 2004). To correct for overdispersion in any tests which showed this, I used a quasi-likelihood model where the dispersion parameter is estimated from the actual data. For significant tests, I conducted all possible pairwise comparisons of means, using a sequential Bonferroni correction to allow for multiple testing.

### 3.3.3 Role of Habitat

Spatial variation in *T. amblycephalum* densities across the lagoon may arise from underlying variation in habitat characteristics. To test this hypothesis I quantitatively explored patterns of habitat use (using an “electivity index”) and then evaluated how well critical habitats (i.e. habitat types that were disproportionately over-used by fish) explained observed variation in *T. amblycephalum* densities.

Habitat composition was determined for each of the 33 transects using a standard point contact technique. At every 1 metre interval along each transect I identified the habitat under 5 points; one was located on the transect line, and two points were located either side of the transect line, 0.5 and 1 metre away respectively. This gave a total grid of 130 habitat points per transect. The following microhabitat categories were recorded: live coral patch reef (coral mound surrounded by reef flat) (CB), dead coral patch reef with macroalgal cover (AB), pavement (cemented dead coral) on reef flat (PF), dead coral rubble on reef flat (RF), sand on reef flat (SF), and live coral on reef flat (CF). Percent cover of each micro-habitat type was estimated from the point contact data.
In addition to estimating densities of juvenile and adult Thalassoma amblycephalum, I recorded the microhabitat type (described above) directly below each observed individual.

I evaluated habitat use by juveniles and adults separately using Manly’s Alpha to evaluate the proportion of fish within any given transect that occurred on each habitat type, relative to the probability of a fish associating with that habitat type under conditions of random assortment. These values were converted to habitat electivities ($e$) to represent habitat use as an index ranging from -1 (never used) to +1 (exclusively used) with 0 representing neutral association (for full methods including equations see section 2.3.3). Manly’s Alpha and electivity values were calculated separately for each fish size class within each transect. Mean electivity values (+/- 95% confidence intervals = CI) were calculated for each microhabitat type using transects as replicates for all sample dates combined.

I classified “critical habitat” as the unweighted aggregate of all habitats with an electivity value significantly greater than 0 (i.e. 95% CI don’t overlap 0). Percent cover of critical habitat was averaged for each transect over the three sample dates. Densities (no. fish/100m$^2$), for each size class of T. amblycephalum were averaged for each transect over the two sample dates. I used linear regression (SPSS version 11.5 for Windows) to explore the relationship between critical habitat and fish densities, separately for juvenile and adult T. amblycephalum. In addition, I incorporated these same habitat metrics as covariates in GLM models (described above) used to explore spatial variation in densities of T. amblycephalum among sites.
3.4 RESULTS

3.4.1 Patterns of Abundance

Densities of *Thalassoma amblycephalum* juveniles varied significantly among sites for the first two sample dates and among zones for the first sample date (Fig 8A,B; Table 4). During the second sampling date there was also an effect of zone nested within site, suggesting that for juveniles in this sample, the effect of zone varied among sites. Densities of *Thalassoma amblycephalum* adults varied significantly among sites and zones for all sample dates (Fig 8D-F, Table 4). Additionally, the effect of zones on densities of adults was shown to vary with site during the second sample date. A visual inspection of results (Fig 8A-F) suggests that densities of both juvenile and adult *T. amblycephalum* may be greater at outer zones, than inner zones (i.e. closer to the reef crest). However, given the variation between dates and sites, and nested effects of zone (distance from reef) within sites for juveniles and adults during the second sample (Table 4), this pattern may be variable.
Table 4 – Spatial variation in densities of juvenile and adult *Thalassoma amblycephalum* among Sites, Zones, and among Zones nested within Sites, on; A) 15/3/2004, B) 25/3/2004 and C) 30/3/2004. Given are statistics from a Generalized Linear Model (ANODEV, using a Poisson distribution). Significance levels indicated by * (P < 0.05) or ** (P < 0.01) or *** (P < 0.001).

| I. Juveniles | Source   | Df | Deviance | Residual Df | Residual Deviance | P(>|Chi|) |
|--------------|----------|----|----------|-------------|------------------|--------|
|              | A) Site  | 5  | 40.704   | 27          | 80.416           | 0.002**|
|              | Zone     | 1  | 18.593   | 26          | 61.823           | 0.003**|
|              | Site: Zone| 4  | 9.276    | 22          | 52.547           | 0.36   |
|              | B) Site  | 5  | 20.699   | 27          | 46.466           | 0.001**|
|              | Zone     | 1  | 0.2      | 26          | 46.266           | 0.654  |
|              | Site: Zone| 4  | 19.011   | 22          | 27.255           | 0.001**|
|              | C) Site  | 5  | 8.125    | 27          | 45.906           | 0.349  |
|              | Zone     | 1  | 0.699    | 26          | 45.208           | 0.488  |
|              | Site: Zone| 4  | 10.052   | 22          | 35.156           | 0.141  |

| II. Adults | Source   | Df | Deviance | Residual Df | Residual Deviance | P(>|Chi|) |
|------------|----------|----|----------|-------------|------------------|--------|
|            | A) Site  | 5  | 376.62   | 27          | 590.53           | 0.000348***|
|            | Zone     | 1  | 167.05   | 26          | 423.48           | 0.001426**|
|            | Site: Zone| 4  | 37.76    | 22          | 385.72           | 0.68   |
|            | B) Site  | 5  | 60.279   | 27          | 98.115           | < 0.0001***|
|            | Zone     | 1  | 15.468   | 26          | 82.647           | 0.006**|
|            | Site: Zone| 4  | 30.95    | 22          | 51.697           | 0.004**|
|            | C) Site  | 5  | 360.65   | 27          | 600.88           | 0.000435***|
|            | Zone     | 1  | 193.82   | 26          | 407.07           | 0.000518***|
|            | Site: Zone| 4  | 8.11     | 22          | 398.96           | 0.97   |
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Figure 9 – Spatial variation in densities of *Thalassoma amblycephalum* at “outer” and “inner” zones within the 6 sites in the Northern Moorea Lagoon (see Fig 7 for geographic locations). Note there is no “inner” zone for site VOE. Panels A-C represent densities of juveniles sampled on; A) 15/3/2004, B) 25/3/2004 and C) 30/3/2004. Panels D-F represent densities of adults sampled on these same three dates. Supporting statistics are given in Table 4.

3.4.2 Role of Habitat

Patterns of habitat use by juvenile *Thalassoma amblycephalum* (Fig 9A) differ greatly from those of adults (Fig 9B), and suggest a possible ontogenetic shift in habitat use between juveniles and adults. Juvenile electivities for live coral patch reefs (CB) were strong and while variable, the 95% CI does not overlap zero
(indicating a significant “over-use” of this microhabitat type). Adult electivities were not greater than zero for any of the recorded habitat types, indicating no pattern of overuse for any specific recorded microhabitat type.

Spatial variation in density of juvenile *Thalassoma amblycephalum* were plotted against the abundance of critical habitat (electivity significantly $>0$) and analysed using regression (Fig 10). Densities of juvenile *T. amblycephalum* were not explained by the proportion of live coral patch reef habitat ($r^2 = 0.0305, p = 0.331$). Adult *T. amblycephalum* showed no patterns of specific microhabitat use.

A GLM used to explore the effects of spatial variation in over-used habitat cover within and among sites and zones (including site X habitat and site X zone interactions; Table 5) suggests that (1) live coral patch reef as a covariate explains a significant amount of additional variation in the densities of juveniles sampled on 25/3/2004 and (2) during the first sample date (15/3/2004), there was a significant interaction between habitat (live coral patch reef) and site, suggesting that the effects of over-used habitat on juvenile densities may be variable among sites.
Figure 10 – Patterns of habitat use by A) juvenile and B) adult _Thalassoma amblycephalum_. Given are electivity values calculated for each microhabitat category (Mean +/- 95% CI). Microhabitat categories are: CB – live coral patch reef, AB – macroalgae on dead coral patch reef, PF – pavement (cemented dead coral) on reef flat, RF – dead coral rubble on reef flat, SF – sand on reef flat, and CF – live coral on reef flat.
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Figure 11 – Spatial variation in densities of juvenile *Thalassoma amblycephalum* explained by “critical” habitat. Each point represents one average values for one transect. Relevant habitats were determined from electivity analyses (see Fig #) and are comprised of habitats with electivity values >0. Over-used habitat for juvenile *T. amblycephalum* is live coral patch reef (CB). Linear regression summary statistics are given within the panel.

Table 5 – Additional effects of habitat attributes to account for spatial variation in density of juvenile *Thalassoma amblycephalum* (c.f., Table 4). Given are results of GLM analyses (ANODEV) used to evaluate effects of “Site”, “Zone”, “Habitat” and the interaction of these three factors for three sample dates. “Habitat” is the proportion of live coral patch reef cover (CB) (see fig 9). Significance indicated by * (P < 0.05) and ** (P < 0.001).

| Source | Df | Deviance | Residual Df | Residual Deviance | P(>|Chi|) |
|--------|----|----------|-------------|------------------|---------|
| A) 15/03/2004 | Site | 5 | 40.704 | 27 | 80.416 | <0.001** |
| | Zone | 1 | 18.593 | 26 | 61.823 | <0.001** |
| | CB | 1 | 1.19 | 25 | 60.633 | 0.185 |
| | Site x Zone | 4 | 8.158 | 21 | 52.475 | 0.017* |
| | Site x CB | 5 | 38.596 | 16 | 13.879 | <0.001** |
| B) 25/3/2004 | Site | 5 | 20.699 | 27 | 46.466 | <0.001** |
| | Zone | 1 | 0.2 | 26 | 46.266 | 0.629 |
| | CB | 1 | 5.124 | 25 | 41.142 | 0.014* |
| | Site x Zone | 4 | 14.285 | 21 | 26.857 | 0.002** |
| | Site x CB | 5 | 8.094 | 16 | 18.763 | 0.093 |
| C) 30/3/2004 | Site | 5 | 8.125 | 27 | 45.906 | 0.147 |
| | Zone | 1 | 0.699 | 26 | 45.208 | 0.402 |
| | CB | 1 | 3.389 | 25 | 41.819 | 0.065 |
| | Site x Zone | 4 | 13.719 | 21 | 28.1 | 0.008** |
| | Site x CB | 5 | 9.899 | 16 | 18.201 | 0.077 |
3.5 DISCUSSION

Analyses of patterns of habitat use of a tropical reef fish (*Thalassoma amblycephalum*) suggest an ontogenetic shift in habitat use occurs between "juveniles" (10-29mm) and "adults" (30mm+). Young *T. amblycephalum* appear to over-use live coral patch reef habitat while later age classes of this species show no patterns of association with any of the habitat types that were characterised in this study. Adults and juveniles of this species show similar patterns of distribution across the lagoon, appearing to favour sites close to the reef crest, though there is a large amount of variability in the distribution patterns between sampling dates. This variability is likely a result of the aggregating behaviour of adults. These aggregations are dense and fairly diffuse in their distribution throughout the lagoon (*Personal observations*). Movements of the aggregations of adults can therefore create substantial day to day variation in the densities of fish within a fixed transect. The availability of "over-used" habitat explains a significant amount of the spatial variation in densities of young *T. amblycephalum* on one sampling occasion.

One hypothesis for this ontogenetic shift in habitat use is that juveniles of this species may have specific bottom microhabitat requirements, whereas adults may respond to different habitat characteristics such as water movement. Juvenile *T. amblycephalum* are relatively sedentary, occurring close to the substrate, while adults are found free swimming, on average ~1m above the bottom, in high wave energy environments (Fulton 2001). Observed patterns of microhabitat use by juveniles may be a mechanism to avoid predation, intra- or inter-specific competition, or to increase foraging success. Habitat requirements may change with age as fish reach size refuges from predation, or develop different ecological requirements.
These findings are particularly interesting within the context of a study carried out on *Thalassoma amblycephalum*, among several other Labrids, on Australia’s Great Barrier Reef. Fulton and Bellwood (2002) looked at the effect of wave energy on the distribution patterns of adult and juvenile wrasses. Fin morphologies were used to estimate swimming ability at different ontogenetic stages and were hypothesised to predict ontogenetic shifts in distribution patterns. For several Labrid species, fin morphology (specifically, aspect ratio) changed with ontogeny, and in all but one of these species there was a subsequent age specific, vertical shift within the water column. As the swimming ability of these wrasses developed they moved away from the substratum further up into the water column. *Thalassoma amblycephalum* displayed this pattern, and Fulton and Bellwood (2002) hypothesised that bottom topography may provide a refuge for the young ontogenetic stages of this species from the high wave energy of the adult environment, without requiring any associated spatial migration.

In addition to these findings, my results suggest that not only are juvenile *Thalassoma amblycephalum* closely associated with bottom substrates, but there is also some evidence that they over-use of specific bottom microhabitat (live coral patch reefs; CB). This pattern was apparent from electivity calculations which showed juveniles to disproportionately over-use live coral patch reefs. However the importance of live coral patch reef cover to juvenile distribution patterns was not clear. Further study and more intensive sampling will be required to better understand the importance of this apparently over-used habitat. Patch reef structures may create substantial refuges from flow by providing lee-side shelter for juveniles. In addition live coral cover of the patch reef (as opposed to dead and damaged coral patch reefs that generally have few or no branching corals; *personal observations*)
may provide added complexity in the form of branching coral heads (e.g. *Pocillopora* spp. and *Acropora* spp.), or other benefits such as increased foraging efficiency within the interstices of branching corals. A full understanding of the mechanisms underlying the pattern of association with live coral patch reefs would require careful experimentation.

If small coral patch reefs provide a refuge from the high energy environment of adults for juvenile *Thalassoma amblycephalum*, the abundance of such microhabitat may have strong effects on the abundance and distribution patterns of juveniles. In a case where the abundance of this habitat type dropped below some threshold level, juvenile recruitment may become limited by availability of suitable habitat. Subsequent recruitment to adult stages may in turn be limited due to a population bottleneck at early stages in the absence of sufficient juvenile habitat. Major tropical cyclones have been recorded for Moorea as early as 1906, and more recently during 3 El Niño events: 1982 to 1983, 1991 and 1997 to 1998 (Adjeroud et al. 2002). Coral bleaching events are also known for French Polynesia and have been reported in 1983, 1984, 1987, 1991, 1994 and 1998 (Adjeroud et al. 2002). These natural disturbances may have a profound effect on the abundance of live coral on the reef, especially delicate branching corals, though smaller effects have been documented for small *Porites* patch reefs that dominate the inner barrier reef flat in Moorea (Adjeroud et al. 2002). In this study I did not differentiate between the species of coral that live coral patch reefs consisted of, though most patch reefs in the study area are predominantly *Porites* with small colonies of branching corals such as *Acropora* and *Pocillopora*. It would therefore be necessary to carry out more specific manipulative experiments to determine the exact relationship of juvenile *T. amblycephalum* with particular features of the coral patch reefs they are associated
with, in order to better understand the potential effect of natural disturbances on juvenile abundance, and the potential for any indirect effects on adult populations.

Latitudinal gradients in fish diversity have been well documented for the Pacific Ocean (Mora et al. 2003). Fish diversity in tropical coral reef systems has been shown to be substantially greater than in temperate reef systems and in the society islands of French Polynesia there are 50 recorded species of Labrid (Randall 1985). In these tropical systems, niche partitioning may play an important role in maintaining fish diversity, where different species may develop specialist resource usage to alleviate direct competition. Intra-specific niche partitioning, through ontogenetic shifts in resource use, may be an additional mechanism for avoiding intra-specific competition, or perhaps for allowing juveniles to persist in adult habitats which are unsuitable for immature fish. In this study, I have observed an apparent ontogenetic shift in habitat use between juvenile and adult *Thalassoma amblycephalum*, which has been hypothesised to be partially due to juveniles seeking refuges from high energy adult environments. Here, an ontogenetic shift may be an important mechanism allowing specialisation in resource use (niche) for this species. This lends support to the hypothesis that ontogenetic shifts may be an important mechanism by which fish diversity is maintained in coral reef systems. Interestingly, while overall fish diversity in temperate reef systems is lower than in coral systems, the diversity within the family Tripterygiidae around New Zealand, is high. 26 species of triplefin (Tripterygiidae) are known from New Zealand (Clements 2003); including my study species *Forsterygion lapillum* (see Chapter 2). Given that a similar ontogenetic shift in habitat use was observed for this species, widespread patterns of ontogenetic shifts in habitat use may be an important mechanism for maintaining fish diversity in many marine systems.
Chapter 4: Underlying mechanisms and consequences of an ontogenetic shift in habitat use

4.1 ABSTRACT

Quantitative surveys of habitat associations of New Zealand’s common triplefin fish, *Forsterygion lapillum*, have shown that a small-scale ontogenetic shift in habitat use occurs shortly after settlement, and suggest that this may act as a bottleneck to recruitment (see Chapter 2). Methodologically similar surveys of a tropical species of labrid (*Thalassoma amblycephalum*, see Chapter 3) and a large body of published literature, suggest that such patterns may be taxonomically and geographically widespread. To determine whether the over-use of *Cystophora* by newly settled *F. lapillum* in New Zealand could be attributed to a behavioural preference for this specific habitat, I conducted a lab-based, choice experiment. Using a purpose-built “choice chamber” that facilitated assessments of behavioural responses of focal individuals provided with a choice of four common habitat types, I determined that newly settled *F. lapillum* selected chambers containing *Cystophora* in greater frequencies than predicted by random assortment. To test the ecological consequences of this behavioural preference, I conducted a field experiment that manipulated *Cystophora* cover and examined subsequent patterns of recruitment by *F. lapillum*. At a site where *Cystophora* was naturally rare, experimental additions of *Cystophora* cover enhanced local recruitment of *F. lapillum*. Comparable experimental removals at a site where *Cystophora* was naturally abundant resulted in a decrease in recruitment by *F. lapillum*, though the magnitude of the effect was markedly reduced and not statistically significant. Together, these results suggest that
small-scale, age-specific shifts in micro-habitat preference may act as a demographic bottleneck that limits local populations.

4.2 INTRODUCTION

Small scale ontogenetic shifts in habitat use are relatively common across a wide range of taxa. In chapters 2 and 3, I presented data for a species of temperate reef fish (Forsterygion lapillum) and a species of tropical reef fish (Thalassoma amblycephalum) that show distinct shifts in microhabitat use with ontogeny. While there have been numerous published descriptions of such patterns, our understanding of the mechanisms and the demographic consequences of these shifts is incomplete.

Many studies identifying ontogenetic shifts in habitat use are motivated at least in part, by a need to identify key conservation areas for management programmes such as marine reserves. This has been the primary driving force behind studies of nursery habitats (Beck et al. 2001). To apply knowledge of stage specific habitat use in effective management and conservation programmes, we must first identify the specific processes that drive such shifts, and then quantify the demographic consequences of these shifts. A common (and usually untested) assumption of studies of habitat use is that “habitat association” is a result of some preference for the habitat by the occupying individual (Crowe & Underwood 1998). Such a conclusion could hamper conservation efforts for a species which was not associated with a particular habitat through any preference on its part, but rather as a result of external processes, such as competitive exclusion from habitats that would otherwise be preferred (Underwood et al. 2004).

Mechanisms underlying patterns of habitat use may be divided into two categories: (1) those that are “external”, and (2) those that are behavioural on the
organisms' part. Non-random patterns of habitat use could result from external mechanisms such as differential settlement driven by oceanographic processes or random patterns of settlement that are subsequently modified by post-settlement processes (Jones 1991) such as differential predation rates between different habitats (Underwood et al. 2004). Conversely, non-random patterns of habitat use may occur as a result of a behavioural preference of an organism for specific habitat types (e.g. Olabarria et al. 2002), preferences which may alter with growth and development. These behaviours may develop in response to increased growth, decreased mortality (as a result of predation refuges or resource partitioning), or a combination of the two whereby an organism may choose the habitat that minimises the ratio of mortality risk to growth rate (e.g. the 'minimize $\mu/g$ hypothesis'; Werner & Gilliam 1984). It is likely that a combination of external and behavioural processes may act to drive observed ontogenetic shifts in habitat use.

Resource shifts of any kind can have important consequences for species interactions and community dynamics (Werner & Gilliam 1984). Preferred resources may have a limiting effect or a positive effect on an organisms abundance. If a shift in preferred resources also occurs with ontogeny, then resources which are preferred by young stages could have indirect positive or negative effects on adult stages. Such effects may be a result of a bottleneck in supply of young individuals, or an overabundance of young individuals for the next ontogenetic stage due to fluctuations in the resource (e.g. habitat) availability. Therefore identifying shifts in resource use, determining the underlying cause of the shift, and finally determining the potential for limitation or facilitation of abundance at various life stages, is essential to a full understanding of how resources affect population dynamics.
Here, I use a laboratory experiment to test a potential mechanism (behavioural preference) that may underlie the habitat association of newly settled *F. lapillum* with *Cystophora*. I also manipulate percent cover of the habitat preferred by settlers in a field experiment, to estimate the effects of habitat limitation and facilitation on recruitment of *F. lapillum*.

### 4.3 METHODS

#### 4.3.1 Mechanism underlying habitat association: A behavioural preference?

To test whether the observed pattern of over-use of *Cystophora* by newly settled *Forsterygion lapillum* (see Chapter 2) could be attributed to a behavioural preference for *Cystophora*, I constructed a “choice-chamber” (modified from Lecchini et al. 2005; Fig 11)

A total of 102 newly settled *Forsterygion lapillum* were collected from three sites around the Wellington south coast and harbour using clove-oil and hand nets. These were kept over-night, without food, in a bare glass aquarium devoid of substrate. Individuals were tested separately the day after collection to evaluate their preference (inferred from movement patterns) for one of four microhabitats: *Cystophora* (Cy), *Carpophyllum maschalocarpum* (Ca), geniculate (erect) corallines on small rocks (GC), and encrusting corallines on small rocks (EC). Samples of microhabitat (sufficient to create 100% cover of a compartment) were distributed randomly among compartments 1-4 of the choice chamber. *Carpophyllum maschalocarpum* was chosen because it is a canopy forming macroalgae common to our study area, and is structurally similar to *Cystophora*. The two forms of coralline algae on rock were chosen as they are representative of much of the rocky reef
substrate in the study area, and are known to provide settlement cues for some other species (e.g. abalone; Morse & Morse 1984). The latter category was also the habitat that was disproportionately used by juvenile and adult *F. lapillum* (see Chapter 2).

Each individual was introduced to the central compartment of the choice chamber by means of a clear plastic release compartment (Fig 11, compartment A). Following introduction to the release compartment, the focal fish was allowed to acclimatise for 1 minute before the release compartment was lifted by a remote-operated pulley system to minimise disruption to the fish. Following release into the choice chamber, the movements of the focal fish were observed for 2 minutes (preliminary data suggested this duration was sufficient for a fish to make a “choice”; see Results). The first movement into one of the four adjoining compartments (Fig 11, compartments 1-4) was scored as the choice for the focal fish.

At the end of each 2-minute run, the fish was removed, fresh seawater was allowed to flow into the tank for 20 seconds, and the water in the tank was briskly stirred with a plastic spatula. After a batch of 7 fish had been tested in this manner, microhabitat units were repositioned randomly among the four compartments. Following testing of 15 fish, the tank was drained so that seawater and microhabitat units could be completely replaced. These measures were taken to control for potential non-independence in the responses of individuals tested sequentially (e.g., arising from scent trails that might influence subsequent choices).

A chi-square analysis was used to test the null hypothesis that the four microhabitats were chosen in an equal frequency, and more specifically, to determine whether newly settled *F. lapillum* exhibit a behavioural preference for *Cystophora*. 
Figure 12 – Choice chamber design. Construction was of 3mm clear perpex with all outside walls covered with white waterproof paper. The four “choices” presented to a focal individual were located in chambers 1-4. Chamber A is a moveable clear plastic ring with holes around the bottom edge. This was used to acclimatise the focal individual to the chamber and allow it to sense (visually and olefactorily) its four choices. Chamber A could then be lifted via the pulley system leaving the fish in the central arena of the choice chamber and free to move into any of the four chambers 1-4.

4.3.2 Field manipulations of preferred habitat: Consequences for recruitment?

I manipulated Cystophora abundance (the microhabitat preferred by newly settled F. lapillum; see Results) to evaluate the effect of this behavioural preference on local recruitment. Using 2.25m² quadrats as the unit of replication, I established the following four treatments (n=4 quadrats/treatment): 100% Cystophora canopy cover, 25% Cystophora canopy cover, 0% Cystophora, and a disturbed control (with
ambient *Cystophora* density). I duplicated this design at two sites (see Fig. 1, Shelly Bay and Kau Bay): at Shelly Bay, *Cystophora* was naturally abundant, while at Kau Bay (approximately 1.5km north-east) *Cystophora* was naturally rare. Consequently, construction of my experimental treatments involved removals and/or additions of *Cystophora* (using collected "plants" with holdfast naturally attached to small cobbles) at Shelly Bay, and mainly additions of *Cystophora* at Kau Bay (using "plants" collected from Shelly Bay). At each site, quadrats were arranged along a 3m depth contour (parallel to shore), spaced 5m apart, with treatments randomly assigned to quadrats.

Abundance of newly settled *F. lapillum* (15-30mm TL, see section 2.3.2) in the quadrats was censused visually 1 and 2 months after the establishment of the treatments. Due to marking failures and/or disturbance, a number of replicate quadrats were unable to be accurately identified for sampling. Consequently, statistical analyses were based upon an unbalanced design; however, all treatments/observations had sample sizes ≥2. I tested the effect of *Cystophora* cover on recruitment of *F. lapillum* using RM-ANOVA. Analyses were conducted using the GLM procedure of SPSS (version 11.5 for Windows), and all analyses met ANOVA assumptions.

4.4 RESULTS

4.4.1 Mechanism underlying habitat association

The habitat preferences of 102 newly settled *F. lapillum* (measuring 26.15mm +/- 0.21SE, TL) were evaluated in the choice chamber. The average time taken to make a "choice" was 26.56s +/- 3.46 (Mean +/- SE) and only 8 fish failed to
make a choice in less than 2 minutes. Of the 94 fish that made a choice within 2 minutes: 36 chose *Cystophora* first, 27 chose *Carpophyllum maschalocarpum* first, 16 chose geniculate corallines first, and 15 chose encrusting corallines first. This distribution is significantly different from the null distribution 25:25:25:25 ($\chi^2 = 12.64$, df = 3, $P < 0.01$). Figure 12 shows the variation from the expected distribution for each habitat type; *Cystophora* was chosen substantially more than the expected frequency, *Carpophyllum maschalocarpum* was chosen slightly more than the expected frequency, while geniculate and encrusting corallines were chosen far less than expected. A second Chi$^2$ analysis was conducted to test whether *Cystophora* was chosen significantly more than the other three habitat types (i.e. $H_0$: $P_{Cy} = (P_{Ca} + P_{GC} + P_{EC})/3$). This test (a functional equivalent of a post-hoc test) suggests that *Cystophora* was chosen significantly more than would be expected under conditions of random assortment ($\chi^2 = 8.87$, df = 1, $P < 0.005$).

![Figure 13 - Variation in observed number of fish that chose each habitat from the expected null distribution of 25:25:25:25. Cy = Cystophora, Ca = Carpophyllum maschalocarpum, GC = geniculate coralline algae on cobbles, and EC = encrusting coralline algae on cobbles.](image-url)
4.4.2 Manipulations of preferred habitat: Consequences for recruitment

Repeated surveys of *F. lapillum* recruits within experimental plots indicate significant among-site variation and an effect of experimentally imposed *Cystophora* cover (Fig 13A,B; Table 6). Overall recruitment was greater at Kau Bay (where *Cystophora* was relatively rare), and within each site, recruitment was enhanced with increasing densities of *Cystophora*; although a post-hoc Tukey test suggests control plots (with ambient densities of *Cystophora*) and 0% *Cystophora* had similar low levels of recruitment relative to 25% *Cystophora* and 100% *Cystophora* plots with similarly higher levels of recruitment. There was also a significant interaction between site and treatment effects, suggesting that the effect of treatments differed between sites.

Table 6 - Spatial variation in densities of settler aged *Forsterygion lapillum* within experimental plots. Given are statistics from a RM-ANOVA. Data are from 2 repeat survey dates (2/3/2005 and 12/4/2005), 2 sites and 4 treatments (see ‘Materials and methods’). Significance levels indicated by * (P < 0.05) or ** (P < 0.01) or *** (P < 0.001)

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<th>I. Multivariate test (Wilk's Λ)</th>
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<table>
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<tr>
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<th>Source</th>
<th>SS</th>
<th>df</th>
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Figure 14 - Average settler abundance as a function of experimentally imposed Cystophora cover at Shelly Bay (unshaded) and Kau Bay (shaded) for the March survey (A), and the April survey (B) (Mean +/- 1SE). Horizontal lines above graphs represent homogeneous subsets from post hoc Tukey test.
4.5 DISCUSSION

Studies describing non-random associations of species with particular habitat often conclude that there is a preference exhibited by the species for that habitat. As reviewed by Underwood et al. (2004), the application of such interpretations within the fields of conservation and management may be detrimental to goals. While non-random patterns of association between an organism and a habitat may be a result of a behavioural preference for that habitat, these patterns may also be driven through negative interactions between species. Inter- or intra-specific competition may act to force a species (or a specific age class of a species) out of preferred habitats into habitats which convey poorer or no fitness advantages. Predation may have a similar effect, driving species out of habitats which would otherwise convey greater growth or reproductive advantages. In such cases, making the assumption that over-used habitat is preferred by the focal species (or specific age class of the species) may lead to inefficient or ineffective management targeted at habitat. At the very least there is likely to be a poor result of such conservation or management; results which may be improved through programmes targeted at removal or control of competitors or predators (Underwood et al. 2004).

In the case of a habitat association which cannot be shown to be behaviourally mediated, abundance of the over-used habitat might have a range of possible effects on abundance of the focal species. If patterns were driven by competitive exclusion of some form, then occupied habitats may have little or no effect on abundance of the focal species. If patterns were driven by differential predation of the focal species in different habitats, then abundance patterns of over-used habitat may have a positive effect on abundance of the focal species due to reduced mortality within that habitat type. However, in this case there may also be a
cost associated with habitats which convey a refuge from predation but reduce foraging efficiency, for example.

Habitat associations which are a result of a behavioural preference, should have fairly strong effects on the species abundance (i.e. habitat availability may limit or facilitate population size). Organisms may choose preferred resources (such as habitat) because the resource increases growth or decreases mortality or decreases the ratio of mortality to growth (Werner & Gilliam 1984), thus gaining fitness advantages. The level of the effect of such preferred habitats on the species using them would depend on the specific processes underlying the preference. A preference that was an adaptation to increased growth and decreased mortality should have a very strong effect on the abundance of that organism. On the other hand, a preference which was an adaptation to some trade off between growth and mortality may not have such a strong effect on the species abundance.

In this study, I have shown that the non-random pattern of habitat use displayed by newly settled Forsterygion lapillum is partially a result of a behavioural preference for the over-used habitat (Cystophora). Interestingly, this habitat appears to be preferred over all other macro-algal habitats, including the structurally similar Carpophyllum maschalocarpum, though the later was chosen more than expected by chance, it was only marginally so. Given this, and the above discussion, I would hypothesise that this preference may be an ecological response to: (1) decreased mortality through shelter from predation and or resource partitioning alleviating inter- or intra-specific competition; (2) increased growth perhaps due to improved foraging success in Cystophora, or (3) a trade off response favouring a decreased ratio of mortality to growth. Findings in chapter 2 identify predation by a con-generic (F. varium), to potentially be alleviated by spatial separation of settlers from F.
varium, which use a different microhabitat type. I would therefore hypothesise that the abundance of Cystophora could have strong effects on the population demographics of F. lapillum. Further research into the specific sensory mechanisms utilised by settlers in choosing habitat, and of the feeding behaviour of settlers may further elucidate the specific mechanisms behind this behaviour.

To test the actual effects of preferred settlement habitat (Cystophora) on abundance of settlers, I experimentally manipulated Cystophora density at a site with naturally occurring Cystophora and a site from which Cystophora was naturally rare. Results from this experiment show that at both sites, increasing the density of Cystophora in experimental plots, facilitated recruitment. Notably though, the relationship between recruitment and Cystophora density is not linear, suggesting that there is still some limiting affect to recruitment levels (such as settler availability). This result suggests that for species which show some behavioural preference for over-used habitats, supplementing the habitat may be an effective conservation and management tool. In addition, I found some evidence for limitation of settlers through eliminating over-used habitat (Cystophora) at a site where Cystophora was common (Shelly Bay), as evidenced by a difference in settler abundance between control plots and 0% Cystophora plots at this site. This pattern was not statistically significant perhaps due to the over-all lower abundances of settlers at this site being below levels at which limitation may occur. This lower level of settlement may have been a result of stochastic settlement processes, or a result of diffusion of available settlers at the site which had naturally high densities of Cystophora (i.e. due to high ambient densities of Cystophora at Shelly Bay - compared with almost no natural Cystophora at Kau Bay - available settlers would be more dispersed within the site, reducing concentrations in treatment plots).
Chapter 4 – Mechanisms and Consequences of a habitat shift

Analogous experiments run by Jones (1984a) on juvenile *Notolabrus celidotus* indicated that recruitment of this species increased following seaweed addition and decreased following seaweed removals suggesting that macroalgal habitat may be an important habitat for other New Zealand reef fishes.

In conclusion, my results show that patterns of non-random micro-habitat use can be driven by behavioural preferences for specific micro-habitats. Such habitat preferences are likely to be driven by fitness maximising strategies and therefore availability of preferred habitat(s) may have strong effects on the abundance patterns of local populations of a species. I found that experimentally increasing the abundance of preferred habitat of settler aged *Forsterygion lapillum* resulted in significant facilitation of recruitment. In species which undergo ontogenetic shifts in habitat use, the mechanisms underlying the patterns of habitat use, and the resulting effects of habitat abundance could potentially be different among ontogenetic stages. At early stages, specific habitat preferences may result in limitation of that stage if habitat is scarce, which may in turn create a bottleneck to recruitment to later stages thereby indirectly affecting later stages of the population.
Chapter 5: General Conclusions

5.1 SUMMARY OF FINDINGS

Quantitative surveys of habitat associations of the temperate reef fish *Forsterygion lapillum*, suggested that an ontogenetic shift in habitat use occurs sometime soon after settlement. Such shifts in habitat use are often explained with fitness maximising strategies. These hypotheses generally assume that shifts in association are a result of changes in preference, and imply that over-used habitats should have strong effects on the abundance patterns of the stages using them. In keeping with this, habitat used by newly settled *F. lapillum* (*Cystophora*; CY) explains about 55% of the spatial variation in densities of new settlers. In comparison, the habitats which were over-used by juvenile and adult *F. lapillum* did not explain any of the spatial variation in densities of these age classes. One explanation for this is that low levels of settler habitat has already limited settlement, and that resulting recruitment into the juvenile and adult population is lower than some level at which the habitat used by these stages may become limiting. Through such a process, availability of habitats used by early stages could have strong indirect effects on populations of later ontogenetic stages.

Similar quantitative surveys of a tropical reef fish *Thalassoma amblycephalum* suggested that an ontogenetic shift in habitat use may take place between juvenile and adult stages. This shift seems to be related to not only microhabitat characteristics, but also to water column characteristics. It is hypothesised that for this species, the bottom topography of live coral patch reefs provides a shelter refuge from the high wave energy environment near the reef crest where adults occur. Specific microhabitat use by juveniles may allow them to settle
and persist in the same zones that adults use, even though flow characteristics of such areas may be unsuitable for poorer swimming juveniles. Ontogenetic shifts in habitat use may be an important mechanism by which tropical fish diversity is maintained.

Behavioural “choice” experiments carried out to evaluate the apparent preference of newly settled *Forsterygion lapillum*, suggested that this pattern of association was partially driven by a significant preference for *Cystophora*. Manipulations of *Cystophora* cover in a field experiment suggested that the availability of this habitat did affect settlement of *F. lapillum*. Settler abundance increased with *Cystophora* abundance suggesting that this habitat may limit or facilitate settlement. Due to the site attached nature of this species, it follows that changes in the availability of settler habitat (*Cystophora*) could have potentially strong indirect effects on later stages through either facilitation or limitation of recruitment to juvenile and adult stages.

Together these results suggest that small scale ontogenetic shifts in habitat use may be common among reef fish. These shifts can be a result of behavioural preferences driven by fitness maximising strategies, and preferred habitats can have strong direct effects on the stages using them, potentially indirectly affecting later stages.

### 5.2 FUTURE DIRECTIONS

The choice chamber I used to test habitat preferences of settler *F. lapillum* (Fig 11) was based on a two way chamber used by Lecchini *et al* (2005) designed to test mechanisms of habitat selection. The original design allowed isolation of visual, olfactory and tactile stimuli to test the specific sensory mechanisms used in selection of habitat. The chamber which I built for this project has these same features and
thus the potential to be used to further test the specific sensory mechanisms used by *F. lapillum* settlers to choose *Cystophora* habitat.

Findings of this research suggest that habitats preferred by young ontogenetic stages can have strong effects on that stage and that they may also have the potential to indirectly affect abundances of older stages. Due to constraints on time, the experiment carried out to test the effects of preferred settler habitat could not quantify indirect effects on juveniles and adults within the population. A longer term study utilising similar methods could be used to build a more complete picture of the potential implications of settler habitat availability for juvenile and adult *F. lapillum*.

This study presents one of the first attempts to not only identify an ontogenetic shift in habitat use, but to experimentally evaluate a potential mechanism behind the shift and some of the ecological consequences of the shift. Given the apparent widespread nature of small scale ontogenetic shifts in habitat use, and the potentially varied ecological effects of these shifts, the application of specific experiments to test the mechanisms and consequences of shifts in other species is needed to further our understanding of the effects of habitat use on the population demographics of reef fish.
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