

The nose knows: linking sensory cue use, settlement decisions, and post-settlement survival in a temperate reef fish

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Abstract Habitat selection by animals that migrate or disperse ultimately determines the biotic and abiotic environment they will experience in subsequent life stages. Intuitively, for habitat selection to be adaptive, animals should respond positively to cues produced by habitat characteristics that will enhance their fitness in the new environment. However, there are many examples of dispersing animals where individuals are attracted to cues produced by factors that reduce their fitness after arrival. In this study, we use a temperate reef fish to examine the relative importance of habitat-associated cues in habitat selection decisions, and assess whether use of these cues is adaptive across early life stages. We used a series of laboratory- and field-based manipulative experiments to test: (1) what habitat-associated cues are likely used to locate suitable habitat; (2) whether in situ settlement patterns reflect the cue response tested in the laboratory; and (3) whether the aspects of the habitat that stimulate settlement are the same as those that maximize survival. We observed a positive response to multiple habitat-associated cues, with conspecific cues eliciting the strongest behavioral response in laboratory choice experiments, and a strong inverse density-dependent relationship at settlement. Macroalgal cues also elicited a positive response at settlement, but were associated with higher

mortality after settlement, suggesting that habitat selection decisions are not always adaptive. We argue that this non-intuitive behavior may still be adaptive if it improves fitness at an earlier life stage, as habitat selection behavior is the result of tradeoffs in fitness costs across multiple stages.

Keywords Habitat choice · Settlement cues · Conspecific attraction · Adaptive behavior · *Trachinops caudimaculatus*

Introduction

Many animal and plant species occur in a few distinct habitat types within a local heterogeneous landscape, and individuals may experience different rates of development, fecundity, and survival among habitats (Pulliam and Danielson 1991). As a result of this demographic heterogeneity, habitat selection by animals that migrate or disperse can have profound effects on population dynamics at both local (Pulliam and Danielson 1991), and regional or metapopulation scales (Doherty and Williams 1988; Greene 2003). This is particularly true in the marine environment, where habitat selection occurs for many fish and invertebrates during the transition from the pelagic larval dispersal phase to a benthic or demersal lifestyle, known as settlement. The settlement stage is often a critical bottleneck in the life history of marine organisms, as behavioral decisions during this vulnerable transitional stage can have direct and fundamental implications for future fitness and survival (Connell and Jones 1991; Tupper and Boutilier 1997; Shima and Osenberg 2003).

In the dispersal phase, marine larvae must navigate through a heterogeneous environment, where there is inherent variation in the quality of habitat patches. At the end of the dispersal period, larvae must evaluate the relative

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quality of the prospective habitats they encounter and select a habitat for settlement (Stamps 2001). For species that are benthic or demersal as adults, decisions at settlement ultimately determine the benthic environment an individual will experience and the community they interact with in subsequent life stages [e.g., conspecific and competitive interactions (Jones 1988; Bonin et al. 2009; Ford and Swearer 2013a), food and shelter availability (Behrens 1987; Andrews and Anderson 2004), and predator abundance and behavior (Beukers and Jones 1998; Almany and Webster 2005; McCormick and Hoey 2006)]. Therefore, poor or misinformed habitat selection decisions at settlement can be fatal (Beukers and Jones 1998; McCormick and Hoey 2006), and the ability to discriminate between habitats of varying quality can be critical for individual survival.

Recently, there has been significant advancement in our understanding of the role of sensory abilities and behaviors in locating and selecting habitat at settlement by reef fish larvae, and it is now commonly accepted that most larval fishes have highly developed sensory organs (Wright et al. 2005) and likely use a combination of senses [auditory, olfactory, visual (Tolimieri et al. 2000; Lecchini et al. 2005; Simpson et al. 2010)], and habitat associated [e.g., coral (Bonin et al. 2009; Ben-Tzvi et al. 2010), conspecific (e.g., Sweatman 1983, 1985; Lecchini et al. 2005; Coppock et al. 2013), and/or predator (McCormick and Manassa 2008; Dixon et al. 2010)] cues at different spatial and temporal scales to locate and evaluate reef habitat from the pelagic environment (see Kingsford et al. 2002 and Leis et al. 2011 for a review of larval sensory abilities). Intuitively, for a habitat cue response to be adaptive, dispersing larvae should respond positively to cues produced by habitat characteristics that will enhance their fitness in the post-settlement environment (Stamps and Krishnan 2005). However, there are many examples of dispersing animals in both terrestrial and marine environments where individuals are attracted to cues produced by factors that reduce their fitness after arrival (e.g., Mönkkönen et al. 1990; Danchin et al. 2004; Stamps and Krishnan 2005). For example, several studies have found sites preferentially selected by coral reef fishes were also sites where predators were more abundant and/or survival was reduced (Beukers and Jones 1998; McCormick and Hoey 2004, 2006), suggesting that characteristics that stimulate settlement are not necessarily the same as those that maximize survival.

The aims of this study were to examine the relative importance of habitat-associated cues in habitat selection, and to determine if use of these cues is an adaptive behavior. We used the southern hulafish, *Trachinops caudimaculatus*, to investigate these questions, a highly abundant shoaling fish found on temperate rocky reefs throughout Southern Australia. We used a series of

laboratory and field experiments to test: (1) what habitat-associated cues settlement stage *T. caudimaculatus* respond to; (2) whether in situ settlement patterns reflect the behavioral response to the sensory cues tested; and (3) whether the aspects of the habitat that stimulate settlement are the same as those that maximize survival. We predicted that habitat selection decisions would be adaptive and, therefore, *T. caudimaculatus* should respond to habitat cues and settle to reefs with characteristics that increase post-settlement survival.

Methods

Study species and location

Trachinops caudimaculatus is a small-bodied (<150 mm), short-lived (1–5 years) zooplanktivorous fish found in high abundance on reefs throughout Victoria, Tasmania, and extending west to the Great Australian Bight in South Australia (Kuitert 2004; Ford and Swearer 2013a). It is a shoaling species, forming large shoals often in the thousands, at high densities (>100 fish m⁻²; Hunt et al. 2011). In the shallow rocky reef systems of Port Phillip Bay (PPB), a semi-enclosed embayment on the southeast coast of Australia, reefs are macroalgal dominated and have high biological complexity, species diversity and productivity (Edmunds et al. 2006; Jung et al. 2011). In PPB, *T. caudimaculatus* inhabit discrete patches of rocky reef surrounded by soft sediment; adults and recruits are positively associated with high structural complexity (Hunt et al. 2011), and recruits have been found to be negatively associated with canopy forming macroalgae on a reef (Fobert 2016). These associations are likely driven by predatory–prey interactions. Mortality rates of juvenile *T. caudimaculatus* are strongly influenced by both conspecific density and reef quality (Ford et al. 2016). As both pelagic and benthic predator guilds influence survival (Ford and Swearer 2013a), we hypothesized that high-density macroalgal beds are avoided as the canopy creates a barrier between the shoaling species and its refuge within the reef as well as providing camouflage for reef-based predators, thus increasing predation risk. *T. caudimaculatus* are highly site-attached after settlement; no movement of *T. caudimaculatus* has been recorded across expanses of open water greater than 20 m (Ford and Swearer 2013a), and previous experiments with calcein tagging have found no movement of fish to neighboring reefs (M. Le Feuvre and J. Ford, unpublished data); however, movement within a reef (i.e., ontogenetic microhabitat shifts) is common (Fobert 2016).

Experiment 1: response to habitat-associated cues

To assess how *T. caudimaculatus* respond to various habitat-associated chemosensory (i.e., olfactory, gustatory) cues, behavioral choice experiments were conducted using a two-chamber choice tank. Recently, settled *T. caudimaculatus* recruits were exposed to pairwise combinations of odor treatments thought to be proxy indicators of habitat quality (both positive and negative): (1) ambient seawater (control), (2) reef odor, (3) conspecific odor, and (4) reef and conspecific odor (see Online Resource 1 for choice tank design and creation of odor treatments). The use of pre-settlement stage larvae that have not previously been exposed to habitat-associated cues would have been ideal for this experiment; collection of pre-settlement stage *T. caudimaculatus* was not successful. Additionally, Dixson et al. (2008) found that laboratory reared-juvenile clownfish *Amphiprion percula* exhibited the same positive response to habitat-associated cues as pre-settlement larvae tested in the field, suggesting that cue responses are innate rather than learned. Therefore, we used newly settled *T. caudimaculatus* recruits to test cue response. Schnapper Point reef (38°12'S, 145°01'E) was surveyed every 1–2 days during *T. caudimaculatus* settlement period, and recruits were collected immediately (<48 h) following a settlement pulse to minimize potential post-settlement learned behavior. Fish were then acclimated for 24 h prior to experimental use, and were tested within 48 h following collection to minimize stress and holding tank effects.

All odor treatments were tested against each other, resulting in six treatment combinations. At the beginning of each trial, two of the four odor treatments were randomly assigned to one of the two choice chambers at the upstream end of the choice tank. For each test, a single *T. caudimaculatus* recruit was held in the downstream holding compartment of the choice tank to acclimate for 5 min. After 4 min, flow was established and treatment water added. The trial was completed when the fish remained in one of the choice chambers for >2 min, or after a 5-min period in which the fish made no choice (i.e., remained in the downstream compartment or continuously moved between chambers). The trial duration was determined following preliminary behavioral observations, which suggested that this was sufficient for *T. caudimaculatus* to respond to cues (i.e., all fish that made a 'choice' did so within the first two minutes). At the end of a trial, fish were removed from the choice tank, and measured for total length (TL) to the nearest millimetre. Individual fish were only used in one trial, regardless of treatment combination. Twenty individual fish were exposed to each treatment combination, and an additional 10 fish were used in control trials (ambient seawater vs. ambient seawater) to construct an expected distribution of directional movement in the absence of chemosensory cues

(a control for tank artifacts). The choice tank was flushed with ambient seawater after each trial, and wiped with 90% ethanol at the beginning of each day.

Statistical analysis

The behavioral response of recruits to chemosensory cues was evaluated using a Chi-square test, where the frequency of observed responses was compared against expected frequencies of a random choice for each combination of odor treatments. A Chi-square test was also used to test for a choice chamber bias independent of treatments (left vs. right). Two-tailed *t* tests were used to determine if there was a relationship between TL and response to the chemosensory cues, as TL can be indicative of age, which may influence an individual's response (e.g., Dixson et al. 2011).

Experiment 2: effects of adult conspecifics on settlement decisions

We used a set of artificial reefs constructed from milk crates and bricks to monitor settlement patterns of *T. caudimaculatus* in situ. This artificial reef design is very versatile, as the milk crate modules can be grouped and stacked in various configurations to adapt to the needs of each experiment (see Online Resource 2 for details). The gregarious settlement patterns of *T. caudimaculatus* were assessed in the field by manipulating the density of adult conspecifics on artificial reefs. Twelve artificial reefs were installed in a linear array at two locations within Port Phillip Bay: Altona in the north (37°54'S, 144°49'E) and Carrum in the east (38°05'S, 145°06'E). These two locations were selected due to their proximity to natural reefs that hosted *T. caudimaculatus* populations (<2 km), ensuring adequate larval supply to the reefs, and due to their accessibility by boat and divers (<10 m depth). Each reef was placed approximately 150 m apart, and at least 200 m from natural reef to discourage movement of *T. caudimaculatus* between reefs.

Adult *T. caudimaculatus* were transplanted onto the reefs to create three conspecific density treatments: control (0 adult fish), low density (10 adult fish), and high density (30 adult fish). Density treatments were randomly allocated to reefs and, at each location, four reefs were assigned to each treatment. Adult *T. caudimaculatus* were collected from nearby natural reefs [Wooley reef (38°09'S, 145°05'E) for Carrum; Sandringham Shoal (37°57'S, 144°59'E) for Altona]. Fish were transported and released onto reefs on the day of capture. Prior to release, visual surveys were conducted to ensure the absence of resident adult *T. caudimaculatus*. Divers then released the desired number of fish into the center of each reef. Fish were observed to readily seek out and find refuge within the reef structure.

Mesh nets, (4 mm) lined with 6 mm galvanized chain and pegged to the bottom to prevent fish entering or leaving the reef, were placed over each treatment reef for 24–48 h to reduce transient predator effects and allow the fish to adapt to the new reef environment. Reefs were initially stocked on 1 December 2010 (Carrum) and 13 December 2010 (Altona). Following experimental setup and stocking, visual surveys of the reefs were carried out by SCUBA divers at variable intervals (Carrum: 13, 43, and 77 days after stocking; Altona: 24, 50, and 86 days after stocking). During each survey, the number of recruits was recorded along with the number of adult *T. caudimaculatus* on each reef.

Statistical analysis

Data from the peak settlement period were used in the analysis, which was recorded in January at both sites. Due to variable loss of adult *T. caudimaculatus* on the artificial reefs, the initial density treatments of 0, 10 and 30 adult fish were not maintained throughout the duration of the experiment. Adult density was, therefore, treated as a continuous variable using the average density between the initial stocking and the recorded density from the January survey date, as the density on an individual reef at the time of settlement could have been any number between the initial and final recorded density. A single factor ANCOVA was conducted using location as a fixed factor and mean adult density as the covariate. Recruit density was log-transformed prior to analysis to meet model assumptions.

Experiment 3: effects of macroalgal cover and resident fishes on settlement decisions and post-settlement mortality

Settlement patterns of *T. caudimaculatus* in habitats with varying macroalgal densities were assessed using an additional set of artificial reefs on which the percent macroalgal cover was manipulated (see Online Resource 2 for details). Twelve artificial reefs were installed in September 2013 along a 600 m transect parallel to shore, approximately 300 m south of Schnapper Point. Each reef was placed approximately 50 m apart, and at least 50 m from the nearest natural reef to discourage movement of fish between reefs. A shorter distance between reefs was chosen in this location for logistical facility; however, any distance greater than 20 m is likely to be sufficient for limiting movement of *T. caudimaculatus* between reefs (Ford and Swearer 2013a).

A monospecific assemblage of *Ecklonia radiata*, a habitat-forming brown macroalgae endemic to southern Australia (Connell and Irving 2008), was transplanted onto the reefs to create the macroalgal habitat treatments. Similar sized *E. radiata* thalli were collected from Governor Reef

(38°9'S; 144°43'E) on the southwest side of the Bay, a location chosen for its abundance of healthy *E. radiata* plants. *E. radiata* were removed from natural reef by carefully detaching whole thalli including the holdfast. The stipes were then threaded through the braid of a rope, which was then attached onto the artificial reefs. The percentage cover of *E. radiata* was manipulated on each of the artificial reefs to conform to one of three treatments: 0% cover (no thalli), 50% cover (9 thalli), or 100% cover (18 thalli; which corresponds to a density of approximately 17 plants per m², nearing the maximum density observed in Port Phillip Bay; Johnson et al. 2015). The three treatments were assigned to reefs randomly within four blocks, to ensure treatments were evenly distributed along the 600-m reef array. All reef treatments were established five weeks prior to the beginning of the settlement surveys, and seven weeks prior to the first settlement pulse recorded on the artificial reefs.

From early November 2013 to late January 2014 (survey dates: 12, 18, 25, 30 Nov, 13, 16, 18, 31 Dec 2013, 9, and 16 Jan, 2014) between 0600 and 1300 h, the artificial reefs were surveyed for settlement of larval *T. caudimaculatus*—newly settled individuals were identified by their size and level of pigmentation. As differential mortality rates among treatments could mask the effects of preferential habitat selection at settlement, estimates of early post-settlement mortality were also recorded to account for this effect. Approximate age of recruits was recorded and estimates of mortality were inferred from the number of recruits remaining from each survey count. All losses from the reefs were assumed to be the result of mortality, as post-settlement movement across open water is highly unlikely (Ford and Swearer 2013a).

Prior to and during the settlement period, reefs were surveyed for fish residents and all fish species present were recorded. These fish community data were used to calculate total species abundance and benthic predator abundance on each reef, as we hypothesized that the fish community present at settlement could also be a factor influencing both settlement decisions and post-settlement mortality. The first settlement pulse was recorded on 25 November, and reefs were surveyed 5, 18, 21, 23, 36, 45, and 52 days after settlement commenced. Due to variable recruitment across reefs, reefs were stocked halfway through the settlement period to establish similar recruit densities across treatments. This was done to standardize any potential effect of resident conspecifics on settlement decisions. Recruits were collected from the neighboring natural reef at Schnapper Point, and released on to artificial reefs to establish a density of 25 recruits per reef (see Online Resource 3, Fig. S4 for a time series of *T. caudimaculatus* abundance). This resulted in two separate experiments: the first investigating the effects of canopy cover on *T. caudimaculatus* settlement with low abundance of juvenile conspecifics present

(pre-stocking), and the second investigating the effects of canopy cover on settlement with high abundance of juvenile conspecifics present (post-stocking).

Statistical analysis

To evaluate settlement patterns in varying macroalgal treatments on artificial reefs, we fit two separate zero-inflated generalized linear mixed models (GLMMs) to the low (pre-stocking) and high (post-stocking) juvenile conspecific abundance experiments. A negative binomial distribution was used to account for detected overdispersion. We included macroalgal treatment (0, 50 or 100%), resident conspecific abundance (the number of juvenile *T. caudimaculatus* present on the reef in the previous census), total fish abundance (excluding *T. caudimaculatus*), and benthic predator abundance as fixed factors, and reef as a random factor to account for non-independence among repeat observations from a site. To test the effects of the fixed factors on *T. caudimaculatus* settlement, we compared a series of increasingly complex models using Akaike Information Criterion for small sample sizes (AIC_c) for selection of the model of best fit. These values were rescaled as the difference between each model and the model with the lowest AIC_c (ΔAIC_c) to evaluate model performance. We inferred statistical significance of the main effects that were retained in the best-fit model.

The recorded mortality rates of settled *T. caudimaculatus* were calculated as proportions of the total abundance of juveniles present on each artificial reef. To evaluate differences in mortality in the different macroalgal treatments, we fit two separate GLMMs to the low and high juvenile conspecific abundance experiments. We used a binomial distribution with a logit-link function to account for proportional data (see Warton and Hui 2011), and we used AIC_c and ΔAIC_c again for model comparison and selection to test the effects of the fixed factors (macroalgal treatment, resident conspecific abundance, total fish abundance, and benthic predator abundance) on *T. caudimaculatus* mortality. For both settlement and mortality selected GLMM models, predictions and confidence intervals were calculated from model estimates, with covariates held at their mean values; however, predictions do not take the uncertainty of the random effect parameter into account.

Statistical software

All statistical analyses were completed using the statistical software R (R Core Team 2015). The package “glmmADMB” (Fournier et al. 2012) with function `glmmadmb` was used to conduct all GLMMs, and the package “AICcmodavg” (Mazerolle 2015) with function `AICctab` and “MuMIn” (Bartoń 2015) with function

`AICc` was used for model comparisons. The predict function (base R) was used to calculate GLMM model predictions and confidence intervals, and the package “ggplot2” (Wickham 2009) was used for all statistical figures.

Results

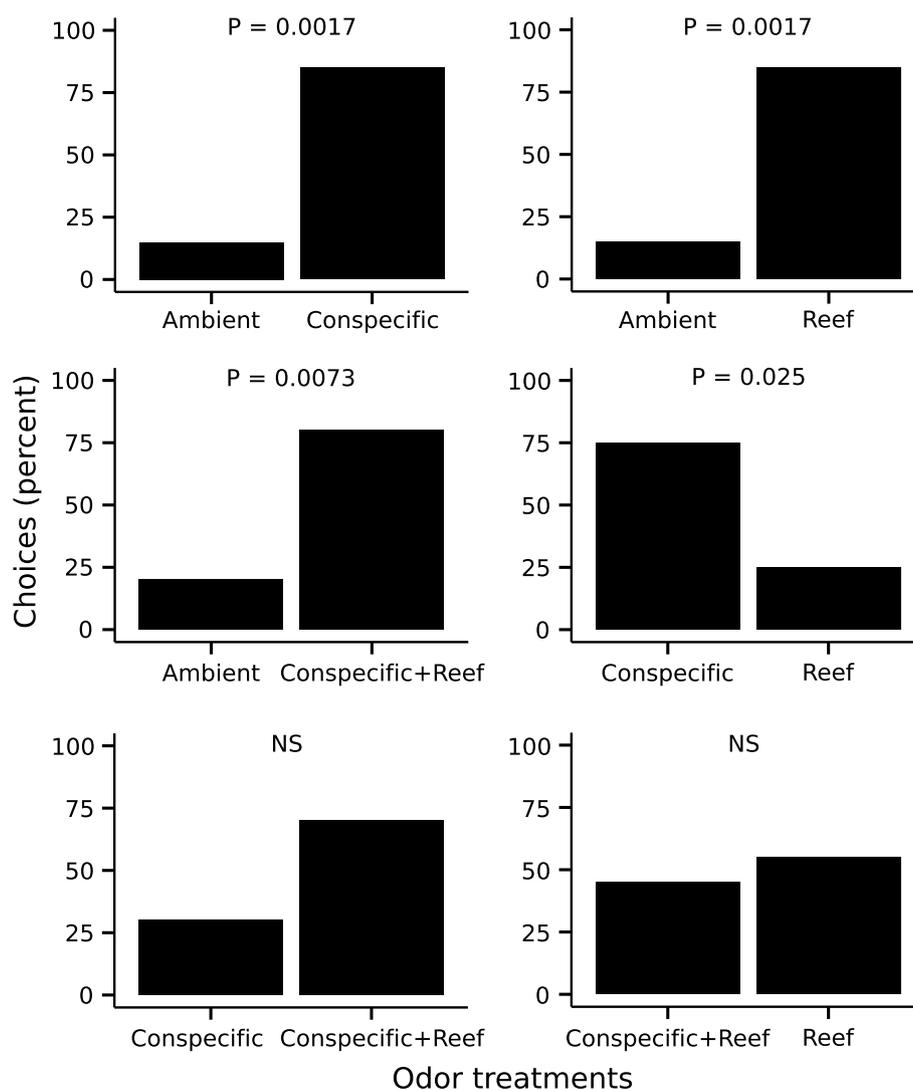
Behavioral response to chemosensory cues

In the control experiment where fish were exposed to ambient seawater in both the left and right chamber of the choice tank, none of the fish made a choice in the 5 min allocated ($n = 10$), meaning fish either did not leave the holding chamber, or moved continuously between choice plumes. All odor treatments were clearly preferred over ambient seawater: 85% of fish chose both the conspecific odor and the reef odor treatments over ambient seawater ($n = 20$; $\chi^2 = 9.8$, $df = 1$, $P = 0.0017$ in both cases; Fig. 1), and 80% of fish preferred the combined conspecific and reef odor treatment over ambient seawater ($n = 20$; $\chi^2 = 7.2$, $df = 1$, $P = 0.0073$). Fish also exhibited a strong preference for conspecific cues when given the choice between conspecific (75%) and reef odor (25%; $n = 20$; $\chi^2 = 5$, $df = 1$, $P = 0.025$). Although not significant, fish did exhibit a preference towards the combination conspecific + reef odor treatment when paired with conspecific odor alone (70%, $n = 20$; $\chi^2 = 3.2$, $df = 1$, $P = 0.074$); however, there was no preference observed between the combination odor treatment (45%) and the reef odor alone (55%, $n = 20$; $\chi^2 = 0.2$, $df = 1$, $P = 0.66$). There was no preference for one chamber in any of the pairwise experiments ($P > 0.05$), nor across all trials (across all trials: left = 52%, right = 48%, $n = 120$; $\chi^2 = 0.2$, $df = 1$, $P = 0.65$), and fish TL had no effect on the response behavior in any of the pairwise experiments ($P > 0.05$).

Effects of conspecifics on settlement decisions

At both sites, adult density had a significant effect on recruitment to the artificial reefs (ANCOVA: $R^2 = 0.76$; $df = 22$; $F = 20.42$; $P < 0.0001$; Fig. 2a), with the most densely populated reefs receiving 4 and 5.2 times as many recruits as those with no adult conspecifics present at Altona and Carrum, respectively. Site location had a strong effect on recruitment (ANCOVA: $F = 39.64$, $df = 1$, $P < 0.0001$), with an average recruit number of 129 fish per reef at Altona and only 26 fish per reef at Carrum.

Fig. 1 Proportion of *Trachinops caudimaculatus* recruits that chose each treatment odor in pairwise comparison trials in a two-chamber choice tank ($n = 20$ in each pairwise comparison). *NS* non-significant results based on Chi-square comparison with expected frequencies of a random choice



Effects of macroalgae and resident fishes on settlement decisions

Prior to stocking the artificial reefs, when juvenile conspecific abundance was low across reefs, none of the models for settlement performed better than the null model (Online Resource 4, Table S1). The model retaining conspecific abundance as an explanatory variable was assigned a ΔAIC_c value < 2 , suggesting similar support for this model; however, the relationship between settlement and resident conspecifics was not strong (Table 1; Fig. 2b).

Based on AICc criteria, the best-fit model for settlement after stocking retained only the macroalgal treatment term as an explanatory variable (Online Resource 4, Table S1). Therefore, when high abundances of juvenile conspecifics were present on the artificial reefs, the macroalgal canopy cover had a significant effect on *T. caudimaculatus* settlement patterns (Table 1), with nearly three times as many fish predicted to settle to reefs with 100% macroalgal cover

(GLMM model prediction = 8.35), than to reefs with 0% (GLMM model prediction = 3.17) or 50% (GLMM model prediction = 2.09) cover (Fig. 2c).

Effects of macroalgae and resident fishes on early post-settlement mortality

The best-fit model for juvenile mortality prior to stocking the reefs retained conspecific abundance as the only explanatory variable (Online Resource 4, Table S2). *T. caudimaculatus* mortality was negatively associated with the abundance of recruits that had previously settled on the reef, with lower mortality observed on reefs with higher conspecific abundance (Table 1; Fig. 3a). Although macroalgal cover was not retained in the best-fit model, it is worth noting that mortality was highest in the 100% cover treatment.

The model of best fit for mortality after stocking, when juvenile conspecific abundance was high, retained

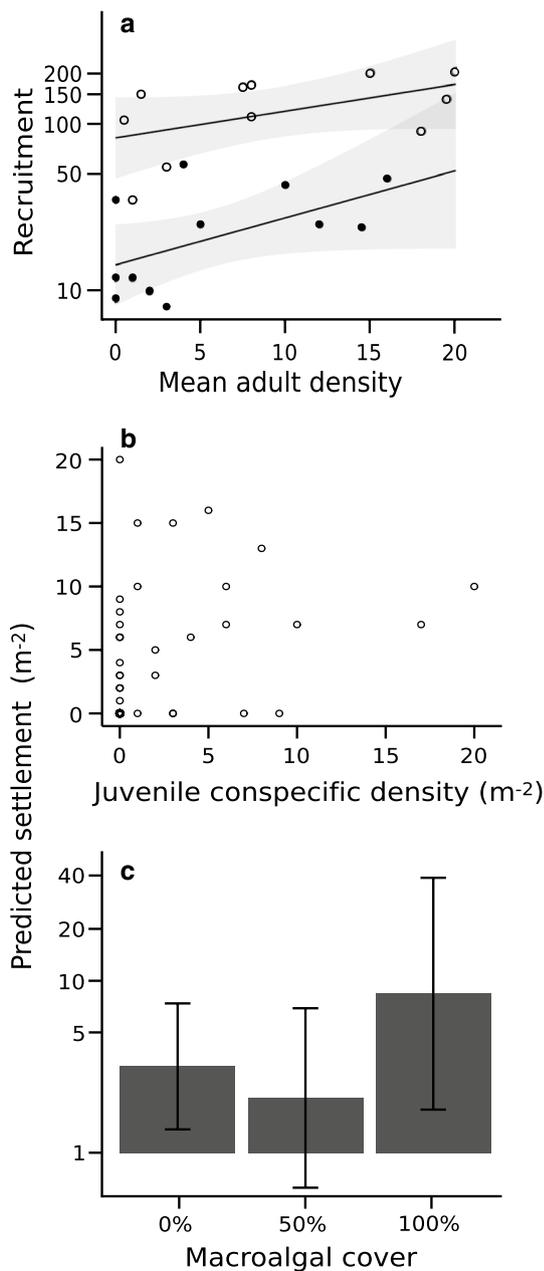


Fig. 2 Relationship ($\pm 95\%$ CI) between **a** recruitment of juvenile *Trachinops caudimaculatus* and mean adult density on artificial reefs at two locations—Altona (hollow circles; $R^2 = 0.256$) and Carrum (filled circles; $R^2 = 0.302$)—in Port Phillip Bay, **b** settlement of juvenile *T. caudimaculatus* and the density of previously settled juvenile conspecifics present on the Mornington patch reefs during the pre-stocking experiment (relationship not statistically significant), and **c** settlement of juvenile *T. caudimaculatus* in 0, 50, and 100% macroalgal canopy cover treatments on the Mornington patch reefs during the post-stocking experiment. Panels **b** and **c** are predictions based on ZINB GLMM model estimates for fixed effects only, back-transformed to the original scale, with other covariates held at their mean values. Predictions do not take the uncertainty of the random effect into account. Note the log scale used on the y-axis in panels **a** and **c**

macroalgal cover, conspecific abundance, and total fish abundance as explanatory variables (Online Resource 4, Table S2). Mortality rates were variable, but decreased significantly with increased juvenile abundance (Table 1; Fig. 3b). Juvenile *T. caudimaculatus* mortality was also lower on reefs with higher total fish abundance (Fig. 3c). In addition, mortality rates increased significantly with increased macroalgal cover, with the probability of mortality 20 and 4% higher in the 100% macroalgal cover treatment (GLMM model prediction = 0.68) compared to the 0% (GLMM model prediction = 0.47) and 50% (GLMM model prediction = 0.64) treatments, respectively (Fig. 3d).

Discussion

Multiple cue use at settlement

Results from both laboratory and field experiments suggest that *T. caudimaculatus* may use a hierarchy of chemosensory cues to aid in habitat selection at settlement; across all experiments, recruits showed positive responses to multiple cues; however, the strength of the response varied with the presence or absence of other cues. Both conspecific and reef cues elicited a strong positive response in the chemosensory choice experiment, however, when the two cues were tested against each other, conspecific cues were chosen more frequently, suggesting that *T. caudimaculatus* might rely primarily on conspecific cues for habitat selection decisions. Consistent with the choice experiments, we found conspecific cues to be an important driver of settlement decisions in the field. We observed a strong inverse density-dependent relationship at settlement, with significantly higher numbers of *T. caudimaculatus* settling to patch reefs with higher adult conspecific densities, and a non-significant trend of higher settlement with higher juvenile conspecific densities.

Preferentially selecting reefs with conspecifics is likely to be an adaptive strategy for *T. caudimaculatus*, as fish in the macroalgal manipulation experiment that settled to reefs with higher abundances of juvenile conspecifics, in both the pre- and post-stocking experiments, experienced significantly lower mortality in the weeks immediately following settlement. Conspecific attraction is an adaptive strategy exhibited by many terrestrial and marine organisms (colonial, solitary, and territorial species; Stamps 2001), including several coral reef fishes (Sweetman 1985; Lecchini et al. 2005; McCormick and Hoey 2006; Coppock et al. 2013). Such gregarious settlement behavior can stem from a number of processes; individuals may settle to habitat with conspecifics because (1) search costs are reduced

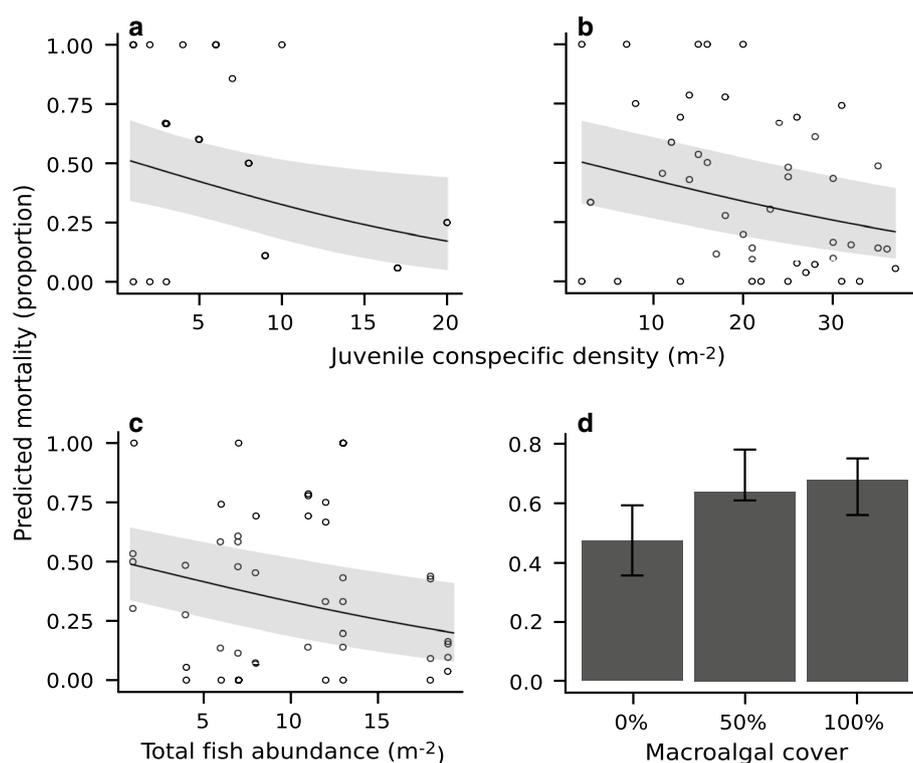
Table 1 Parameter estimates and test statistics for best models describing **a** settlement and **b** post-settlement mortality of *Trachinops caudimaculatus* prior to and post-stocking of artificial reefs (zero-inflated negative binomial GLMM fitted by glmmADMB)

Time	Parameter	Estimate (SE)	Z stat	P value	-CI	+CI
(a) Settlement						
Prior to stocking	Intercept	2.035 (0.134)	15.2	<0.001*	1.773	2.297
Post-stocking	Intercept (0%)	1.155 (0.428)	2.7	0.0069*	0.317	1.993
	Macroalgal cover (50%)	-0.42 (0.532)	-0.79	0.4294	-1.463	0.622
	Macroalgal cover (100%)	0.967 (0.499)	1.94	0.0524	-0.01	1.945
(b) Mortality						
Prior to stocking	Intercept	0.010 (0.352)	0.03	0.977	-0.679	0.7
	Conspecific abund.	-0.079 (0.035)	-2.27	0.023*	-0.147	-0.011
Post-stocking	Intercept (0%)	-0.105 (0.247)	-0.42	0.672	-0.589	0.38
	Macroalgal cover (50%)	0.678 (0.221)	3.07	<0.01*	0.449	1.278
	Macroalgal cover (100%)	0.863 (0.212)	4.08	<0.001*	0.245	1.111
	Conspecific abund.	-0.038 (0.009)	-4.38	<0.001*	-0.055	-0.021
	Total fish abund.	-0.066 (0.018)	-3.69	<0.001*	-0.101	-0.031

$\pm CI$ represents lower and upper confidence intervals

* Indicates a significant *P* value

Fig. 3 Relationship ($\pm 95\%$ CI) between mortality of juvenile *Trachinops caudimaculatus* **a** and density of previously settled juvenile conspecifics present on the Mornington artificial patch reefs during the pre-stocking experiment, and **b** density of previously settled juvenile conspecifics, **c** total fish abundance present, and **d** 0, 50, and 100% macroalgal canopy cover on patch reefs during the post-stocking experiment. Curves and means are predictions based on GLMM binomial model estimates for fixed effects only, back-transformed to the original scale, with other covariates held at their mean values. Note that predictions do not take the uncertainty of the random effect into account



if dispersers use conspecifics as an indirect cue of habitat quality, (2) settlement costs are reduced in the presence of conspecifics, and/or (3) fitness costs are reduced in the presence of conspecifics after settling (Alee effects; Stamps 2001). Our study suggests that the presence of resident *T. caudimaculatus* conspecifics both increases detectability of reef habitat at settlement, thus reducing dispersal costs, and also positively affects post-settlement survival. For a shoaling species such as *T. caudimaculatus*, recruiting to a reef

with resident conspecifics could increase individual fitness through greater predator detection and evasion (FitzGerald and Van Havre 1985; Roberts 1996), increased foraging success and feeding efficiency (Pitcher et al. 1982; Partridge et al. 1983; FitzGerald and Van Havre 1985), and thus enhanced post-settlement survival (White and Warner 2007). Although intraspecific competition can be high, the costs of the increased conspecific density can be outweighed by the benefits gained from group living strategies

(Shima 2001). It should be noted, however, that if shelter on a patch reef becomes saturated at high densities, refuge competition will increase and can reverse this positive density dependence. On similar sized patch reefs, Ford and Swearer (2013b) found this density-dependent relationship switched with densities of *T. caudimaculatus* ≥ 50 fish m^{-2} . In our study, the highest density of recruits observed on a patch reef was 37 fish m^{-2} . Therefore, at these lower densities, the fitness benefits gained from the presence of conspecifics outweighed the costs of increased competition.

Using habitat cues: is it always adaptive?

Interestingly, in our macroalgal manipulation experiment, *T. caudimaculatus* preferentially settled to the patch reefs with the highest macroalgal canopy cover. This result was not expected, as past studies have found no association between *T. caudimaculatus* adults, and a negative relationship between juveniles and macroalgal cover (Hunt et al. 2011; Fobert 2016). This settlement choice does not appear to be an intuitively adaptive behavior for *T. caudimaculatus*, as the highest macroalgal treatment, which received the highest number of recruits, also yielded the highest mortality rates (in both pre- and post-stocking experiments). Additionally, although the trend was consistent, the positive relationship between macroalgal cover and mortality was not significant in the pre-stocking experiment; however, this could be explained by the shoaling behavior of the study species. When *T. caudimaculatus* are found in small groups (<20 fish), shoaling does not occur and fish are more likely to forage as individuals close to the substrate (Fumei 2011; Ford and Swearer 2013a). The abundances of *T. caudimaculatus* on the reefs during the pre-stocking experiment (Online Resource 3, Fig. S4) were below the minimum threshold for shoaling above the canopy to be initiated and, therefore, the canopy effect on survival would not have manifested itself. Our results, therefore, suggest that cues used to locate and select habitat may not always deliver maximum fitness and survival in subsequent life stages. Animals might benefit from responding positively to cues associated with habitat characteristics that would intuitively reduce fitness for two reasons: (1) if a cue increases the detectability of the habitat in the search phase, and (2) if a cue is associated with other factors that increase individual fitness and, therefore, provide indirect information about habitat quality (Stamps and Krishnan 2005). As habitat features can have additive or interactive effects on fitness, and not all factors that might influence post-settlement fitness will be evident at the time of settlement (Stamps 2001), indirect cues are often used as proxy indicators of habitat quality to help animals make quick and efficient habitat selection decisions (Mönkönen et al. 1990, 1999; Danchin et al. 2004).

If macroalgal cues are used by *T. caudimaculatus* as a result of increased detectability, use of this cue to locate

habitat may result in decreased fitness in the post-settlement environment, but reduced costs of searching and, therefore, increased fitness in the searching and settlement stages. As habitat selection is a multi-stage process, a behavior that improves fitness in one stage does not necessarily lead to improved fitness at subsequent stages and, therefore, individuals may preferentially select a sub-optimal post-settlement habitat to reduce immediate fitness costs of dispersal. Because of this trade-off between immediate and delayed costs, the relative importance of a cue may shift over time, as larvae at varying stages of their pelagic larval dispersal period may be more or less selective about the suitability of settlement habitat (Burgess et al. 2012). Dispersers can be more selective at the beginning of the search phase, as individuals have more time and/or energy available for searching for high quality habitats; however, this selectivity declines with energy reserves and time spent in the plankton (Ward 1987; Marshall and Keough 2003). Larvae may, therefore, benefit from using cues that are not necessarily associated with high quality habitat, simply because they indicate habitat that is good enough, or there at all. Further research examining if habitat selection behavior in *T. caudimaculatus* is related to length of dispersal period or larval quality or condition at settlement would provide interesting insight into the mechanisms driving this seemingly maladaptive behavior.

The apparent maladaptive use of macroalgal cues for habitat selection at settlement could also be a by-product of the scale of the artificial patch reef system used to test the selection behavior. Although ecological experiments are most often performed in systems that are much smaller than the natural system of interest (e.g., Petersen et al. 1999), the relatively small size of these experimental systems may elicit different responses to experimental treatments than would be observed on their large-scale natural counterparts (Englund and Cooper 2003). For example, heterogeneity is often distorted in small-scale experiments; spatial heterogeneity of biotic and abiotic attributes generally increases with increasing size of the experimental arena (Englund and Cooper 2003). This is true for macroalgal cover on our artificial reefs compared to natural reefs in PPB. Although our 100% macroalgal treatment was based on the maximum densities of *E. radiata* recorded on natural reefs, even the most densely populated macroalgal canopies rarely reach contiguous 100% cover at the reef scale, but instead exhibit a mosaic of canopy forming algae, understory algae, and barren patches (E. Fobert, personal obs.). In the natural system, *T. caudimaculatus* could use macroalgal cues as a proxy indicator of reef quality to locate suitable habitat; however, once settled on natural reef, choose to move to patches devoid of macroalgae within that same reef, where recruits are less vulnerable to predation. This

hypothesis is supported by results from a concurrent study showing *T. caudimaculatus* recruits are primarily associated with microhabitat patches defined by an absence of macroalgal cover (Fobert 2016). On the small experimental patch reefs, particularly for individuals that settled to the 100% macroalgal cover treatment, canopy free patches were not available, resulting in higher juvenile mortality. However, on larger, natural reefs, use of macroalgal cues to locate settlement habitat may not be linked to high subsequent mortality and, therefore, may, in fact, be an adaptive behavior.

Conclusion

Animals use habitat-associated cues for multiple and mutually nonexclusive reasons while seeking habitat, and the use and function of these cues can shift with spatial and temporal scales. Our study on temperate rocky reefs found *T. caudimaculatus* to be attracted to multiple cues that were associated with both increased survival (con-specific cues) and increased mortality (macroalgal cues); however, the non-intuitive habitat selection behavior observed could be explained by fitness trade-offs across life stages, or by the distortion of spatial heterogeneity in small-scale experiments. This study has provided valuable insight into the importance of sensory information for habitat selection decisions at settlement as well as post-settlement survival and, thus, the recruitment patterns of a temperate reef fish. Further research into the mechanisms driving non-intuitive habitat selection behavior is needed to increase our understanding of the drivers of habitat selection and their consequences for recruitment dynamics in reef fishes.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest. All applicable institutional and national guidelines for the care and use of animals were followed in this study.

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