Site fidelity and homing behaviour of intertidal sculpins revisited

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To assess the repeatability of an ecological study, this study both partially replicates and extends a previous study on the site fidelity and homing ability of two abundant and ecologically important species of rocky intertidal sculpin fishes, *Oligocottus maculosus* and *Oligocottus snyderi*. A traditional mark and recapture approach was utilized and found that both of these species display high site fidelity to a home range of tidepools and homing ability to these pools, confirming the findings of previous work. Unlike the previous study, however, there was no effect of body size on homing ability and a modelling approach that incorporates encounter probability provided evidence for a sex effect on homing ability. In addition, this study extends the maximum homing ability of *O. snyderi* to 179 m and *O. maculosus* to 218 m, which were the maximum displacement distances for each species in this study, suggesting they may be capable of even greater homing distances. This work, however, finds that homing success was negatively related to displacement distance. These findings suggest adult sculpin populations are likely to be highly sub-structured geographically, possibly contributing to the exceptionally high species richness of the group.

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Key words: animal navigation; dispersal; experimental replication; Pacific coast; tidepool.

INTRODUCTION

Ecological studies are rarely replicated, hindering the perceived rigour of the discipline in relation to other lines of scientific inquiry such as physics or chemistry (Fisher, 1974; Kelly, 2006). Ecological studies often focus on replication of treatments within experiments (Gotelli & Ellison, 2004), but it is much less common for entire experiments to be replicated, diminishing the confidence of the scientific understanding of the natural world. As a step towards ameliorating this problem, this study takes advantage of a previous study conducted on the site fidelity and homing ability in intertidal sculpin fishes (Yoshiyama *et al.,* 1992) to investigate how robust previous results are to over two decades of intervening time.

The ability of many animals to accurately navigate over complex landscapes has been observed in disparate phylogenetic clades (Lohmann *et al.,* 2008) and has fascinated biologists and the general public alike for centuries (Darwin, 1873). One important

type of animal navigation is homing ability, which allows an individual to return to a specific home or home range after displacement (Hasler, 1966; Matthews, 1990). In addition, many animals exhibit site fidelity, or a preference for a specific home range (Gerking, 1959; Larson, 1980*a*, *b*, *c*; Hixon, 1981). These issues have received considerable attention from fish ecologists and the home range and site fidelity of some fish species have been found to be dependent on various life-history characteristics, such as size (Larson, 1980*c*; Nanami & Yamada, 2008) and sex (Kerwath *et al.,* 2007), but it is yet unclear how general these factors may be as predictors of fish homing ability and site fidelity.

Sculpins are intertidal and subtidal benthic fishes that are highly abundant in tidepools and rocky reefs in northern temperate and boreal marine habitats (Miller & Lea, 1972; Yoshiyama, 1981; Ramon & Knope, 2008). A number of species of sculpins have been reported to display strong site fidelity over extended periods of time (Williams, 1957; Green, 1971*a*, *b*; Khoo, 1974; Mireles *et al.,* 2011), but comparatively less is known about their homing ability. Yoshiyama *et al.* (1992), however, studied site fidelity and homing behaviour in the intertidal sculpins, *Oligocottus maculosus* Girard 1856 and *Oligocottus snyderi* Greeley 1898, and found evidence for both site fidelity and the ability to return to home tidepools after displacement (homing).

This study both partially replicates and extends the Yoshiyama *et al.* (1992) study using traditional mark and recapture field techniques. The specific objectives of this study were to (1) determine if the site fidelity of individual intertidal sculpins is related to size, sex and species identity; (2) determine if homing ability after displacement from a home tidepool is related to distance, size, sex and species identity and (3) evaluate if the findings support the previous findings of Yoshiyama *et al.* (1992) and assess the repeatability of the findings of an ecological field experiment.

MATERIALS AND METHODS

STUDY AREA

This study was conducted from June to August 2012 on the southern Oregon coast at Sunset Cove State Park (43° 20' 04·06" N, 124° 22' 28·59" W), one of the two study localities of Yoshiyama *et al.* (1992); see Fig. 1 for a satellite map of location and the spatial distribution of habitat types and study pools.

CAPTURE, MARKING AND TRANSLOCATION

The tidepools utilized in this study were known from preliminary investigation to have moderate to high abundance of sculpins and were amenable to sampling (*e.g.* pools that were too large or had large boulders or crevices where fishes could easily hide and avoid capture were excluded). The experimental design followed Yoshiyama *et al.* (1992) except it was impossible to know the exact tidepools used in their previous study and only the Sunset Cove locality (and not South Cove at Cape Arago State Park) was used due to logistical constraints. Additionally, another intertidal sculpin species [*Clinocottus globiceps* (Girard 1858)] that was included in their study was not present in sufficient abundance during the present study. The experimental design included both a relocation group to test for the possible presence of homing behaviour and a control group to determine if the fishes were localized to a home range (site fidelity). The experimental design included five home pools (labelled A−E in Fig. 1 and Table I) and three relocation pools (labelled R1−R3 in Fig. 1 and Table I). Home pools were pools where the sculpins were originally found, and where fishes in the control group were returned after
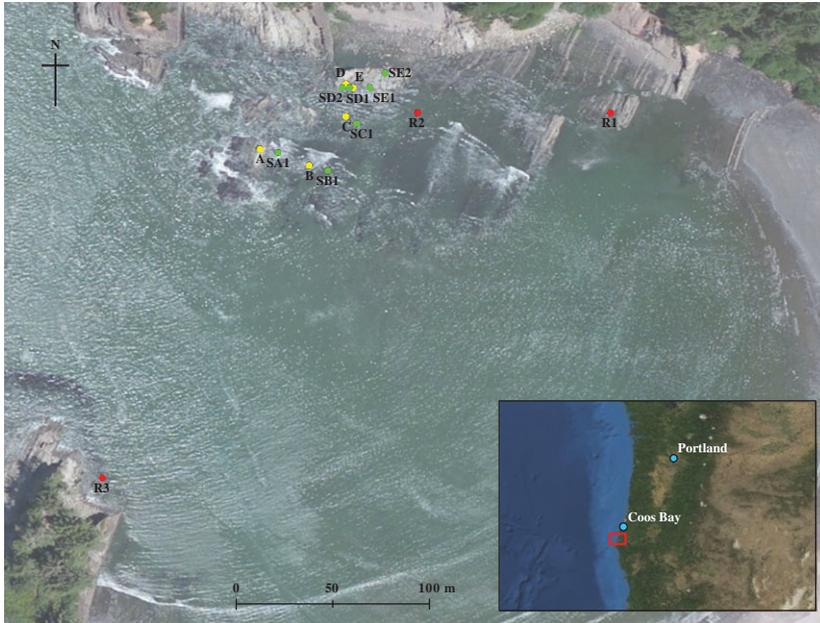
FIG. 1. Location of study pools. Pools A–E (○) were home pools of original capture. Pools R1–R3 (●) were relocation pools where fishes were displaced. Pools SA1–SE2 (●) were search pools in the immediate vicinity of the home pools.

tagging. Fishes in the relocation group were released in one of the relocation pools after being originally caught in one of the home pools and tagged. Two of these relocation pools (R1 and R2) were on the same side (north end) of Sunset Cove as the home pools and were connected by largely contiguous rocky intertidal habitat to one another and the home pools (Fig. 1). The third relocation pool (R3) was on the south side of Sunset Cove and separated by *c.* 150 m of open sandy habitat from all other study pools (Fig. 1). In addition, seven other pools in the vicinity of the home pools were designated as search pools (Table SI, Supporting Information) to identify sculpins that may have homed to the immediate vicinity of their original pool of capture. All sculpins in the relocation group that returned to their home pool or one of the search pools in the immediate vicinity of their home pool were interpreted as demonstrating successful homing behaviour. All tidepool locations were recorded with hand-held GPS units in the field (Table I) and mapped using ArcGIS v. 10.2 (Fig. 1).

In total, 92 sculpins (43 *O. maculosus* and 49 *O. snyderi*) were captured, marked and released. All captures were done by dip-net on low tides, without bailing water from pools to minimize disturbance. Each individual was sexed and measured for total length (L_T) in mm. Sex is easily distinguishable in these species, as males have external genitalia (Miller & Lea, 1972). For *O. maculosus*, of the 43 individuals, 23 were males and 20 were females and for *O. snyderi*, of the 49 individuals, 17 were males and 32 were females. The *O. maculosus* males ranged in size from 36 to 69 mm L_T and the *O. maculosus* females ranged from 25 to 86 mm L_T. The *O. snyderi* males ranged in size from 28 to 64 mm L_T and the *O. snyderi* females ranged from 27 to 67 mm L_T. Of the 92 total fishes, 71 (32 *O. maculosus* and 39 *O. snyderi*) were displaced from their home pool to one of the three relocation pools at varied distances from the home pools (pools R1–R3; Fig. 1). The remaining 21 sculpins (11 *O. maculosus* and 10 *O. snyderi*) were returned to their pool of capture (home pool) to test for site fidelity over the duration of the experiment. The home pool and the seven search pools in the immediately adjacent area (Table I) were then exhaustively searched on five subsequent low tide days over the next 30 days. Visible implant elastomer tags (VIE tags; Northwest Marine Technology, Inc.; www.nmt.us) were used

TABLE I. Distance between home pools (pool #1) and relocation pools (pool #2), number of individuals displaced, total length (L_T) range and sex ratio of those individuals

Pool #1	Pool #2	GPS distance (m)	# Individuals	L_T (mm)	Sex ratio
A	R1	129	11	25–66	5M:6F
A	R2	59	11	29–62	4M:7F
A	R3	179	9	43–64	4M:6F
A	B	17	NA	NA	NA
A	C	33	NA	NA	NA
A	D	44	NA	NA	NA
A	E	45	NA	NA	NA
B	R1	119	6	27–61	3M:3F
B	R2	55	3	32–40	1M:2F
B	R3	172	2	42,47	2F
B	C	35	NA	NA	NA
B	D	50	NA	NA	NA
B	E	49	NA	NA	NA
C	R1	102	3	37–45	1M:2F
C	R2	29	3	30–49	1M:2F
C	R3	206	3	25–49	1M:2F
C	D	17	NA	NA	NA
C	E	15	NA	NA	NA
D	R1	100	3	36–51	2M:1F
D	R2	29	3	39–55	2M:1F
D	R3	218	4	42–53	3M:1F
D	E	4	NA	NA	NA
E	R1	98	3	36–57	2M:1F
E	R2	27	2	42,86	1M:1F
E	R3	219	2	44,69	2M

M, male; NA, not applicable; F, female.

to uniquely identify each individual. A VIE tag consists of a two-part silicone-based coloured compound that is injected subcutaneously. Marked sculpins have been shown to have minimal to no adverse effects on fish health or behaviour for >2 years in the laboratory and 1 year in the field after marking (Halverson, 1982), although disturbance due to handling may reduce site fidelity of the woolly sculpin *Clinocottus analis* (Girard 1858) (Williams, 1957). Two small injections of differing colour (red, blue, orange or pink) were placed in each of four predefined quadrants on the ventral surface of each fish, posterior to the vent along the sides of the anal fin. The combinations of colours, locations of injections, species identity, size (in mm L_T) and sex were recorded to allow for unique identification of each fish.

STATISTICAL APPROACHES

In this study, data were analysed with two statistical approaches. A similar statistical approach to Yoshiyama *et al.* (1992) was implemented and, in addition, a statistical modelling approach that specifically incorporates encounter probability was implemented (White & Burnham, 1999). The most general model includes sex and species effects on encounter probability (P), defined as the probability of observing an individual if it is present in the tidepool sampled (some individuals will be alive and in the tidepool, but will not be recaptured due to sampling error). To determine the probability of an individual successfully homing (returning to its original pool), the probability of encountering a displaced sculpin was divided by the probability of encountering a sculpin that was not removed from its home pool ($P_{displaced} P_{control}^{-1}$). Using

both statistical approaches allows not only for comparison with the results of Yoshiyama *et al.* (1992), but also makes it possible to assess the sensitivity of the results to the incorporation of encounter probability.

MARK–RECAPTURE MODELLING

Initially, a set of 64 models was constructed *a priori* to test the hypotheses concerning the effect of sex and species on apparent survival and encounter probability and these were fitted to the live encounter data using the programme MARK (White & Burnham, 1999). The general linear model for apparent survival and encounter probability of the control group (those not displaced from their original tidepool) was:

$$\Phi_{\text{control}} \left(\text{or } P_{\text{control}} \right) = \beta_1 + \beta_2 \, (\text{sex}) + \beta_3 \, (\text{species}) + \beta_4 \, (\text{body size}) + \varepsilon$$

in which apparent survival of the control group (Φ_{control}) and encounter probability (P_{control}) are functions of an intercept (β_1) plus a slope (β_2) times a sex term, a slope (β_3) times a species term, body size as an individual covariate with a linear effect (β_4 as the slope) and an error term (ε). The β parameters for apparent survival and encounter probability were estimated separately. The general linear model for the apparent survival and encounter probability for the displaced group was similar to that for the control group, but also included the distance individuals were displaced from their home pool as an individual covariate with a linear effect (β_5 as the slope):

$$\Phi_{\text{displaced}} \left(\text{or } P_{\text{displaced}} \right) = \beta_1 + \beta_2 \, (\text{sex}) + \beta_3 \, (\text{species}) + \beta_4 \, (\text{body size}) + \beta_5 \, (\text{distance}) + \varepsilon$$

Apparent survival and encounter probability were assumed to be constant over time due to the short time intervals between sampling. Thus, the model set consisted of a series of nested, reduced parameter models, which were symmetrical for all main effects, resulting in 64 models total for the control (site fidelity) model set and 128 models in the model set for displaced sculpins (there were twice as many models in the set for the displaced sculpins compared with the non-displaced individuals because distance displaced from home pool was only included as an individual covariate for the displaced group). An interaction term for sex and species was not included because of small sample size for male *O. snyderi*. Instead, only an additive effect of sex and species was considered.

Apparent survival (Φ) was close to 100% in all cases. For subsequent analyses, the effects of apparent survival were removed (set $\Phi = 1$), reducing the control (site fidelity) model set to eight models investigating only the effects of sex and species on encounter probability. For displaced sculpins, distance from home pool was also included as an individual covariate, resulting in a set of 16 models. Relative support for each model was ranked using Akaike information criterion (AIC) weights, which indicate the relative goodness of fit of each model in a nested group. Models with AIC values which differed by <2 were deemed equivalent (Burnham & Anderson, 2002). The overdispersion parameter $\hat{c}$ could not be estimated because of the inclusion of individual covariates, so AIC_c values were not adjusted. The relative importance of individual predictor variables in the models was assessed by summing the normalized AIC weights of the candidate models (up to 95% to avoid trivial factor weight additions); importance of a variable can be defined by making inference from all the models in the candidate set. AIC weights were summed for all models containing each predictor variable (*i.e.* factor) x_j, $j = 1, \ldots, R$. If these sums are denoted as $w_+(j)$, the variable with the highest sum is estimated to be the most important, while the variable with the smallest sum is estimated to be the least important predictor. Proportional support can be assessed by scaling individual variable sums, relative to the largest sum, among variables in the sub-set of models being considered. This approach can be extended to sub-sets of variables, conditional that the candidate model set is symmetrical, or nearly so, with respect to model terms (Burnham & Anderson, 2002).

The probability of observing a sculpin that homed was a combination of the probability that the sculpin successfully returned to its home pool and the probability that the sculpin was detected.

The encounter probability for the displaced sculpins ($P_{displaced}$) combined both the probability that the individual successfully returned to its home pool and that it was recaptured (encountered) after it returned ($P_{displaced} = P_{homing} \, P_{control}$). To separate these two events, the detection probability was assumed to be the same for non-displaced sculpins and those that returned to their home pools (equal to $P_{control}$). Therefore, to find only the probability of homing (P_{homing}), the probability of encountering a displaced sculpin ($P_{displaced}$) was divided by the probability of encountering a control (non-displaced) sculpin ($P_{control}$). S.E. for homing probability was calculated using the delta method (Cramér, 1946) and statistically significant differences between these estimates were determined using a Monte-Carlo permutation test (Fisher, 1935) implemented using the R package RMark (Laake, 2013; www.R-project.org). Four permutation tests were conducted to create distributions under the null hypothesis that there were no differences in homing probability based on distance, size, sex or species. For the test, the predictor of interest (distance, size, sex or species) was randomly shuffled for all control individuals and all displaced individuals, respectively, assigning them to the observed capture histories and individual traits in the experimental data. The homing probability for each shuffled dataset was calculated by implementing the same methods as described above for the experimental data. This shuffling and homing probability calculation was repeated 5000 times for each predictor and used to create a distribution of the difference in homing probability between sexes and between species. Homing probability differences based on sex and species from the experimental data were then compared with these distributions of reshuffled data to determine if experimental homing probabilities fell within the 95% C.I. To determine the effect of distance and size, the slope and intercept for a linear regression by sex and species were calculated and these four values were compared with the slope and intercept of a linear regression based on that individual covariate fit to the observed experimental data. Due to the low sample size of *O. snyderi* males, only differences in *O. maculosus* males and females and only differences in females of *O. maculosus* and *O. snyderi* were considered for all analyses of sex and species effects, respectively.

RESULTS

SITE FIDELITY

Of the 21 sculpins that were released back into their home pool, 57% (12 individuals) were recaptured in that home pool or an immediately adjacent pool on a subsequent sampling date (although only one individual was recovered in an adjacent pool and all others were recovered in their original pool of capture). Of the 11 *O. maculosus* released into their home pool after initial capture and marking, seven (64%) were recaptured in that pool or an immediately adjacent pool on a subsequent sampling date (Table I). Likewise, of the 10 *O. snyderi* released into their home pool after initial capture and marking, 50% (five individuals) were recaptured in that pool or an immediately adjacent pool on a subsequent sampling date (Table I). No significant difference was found in the likelihood of recapture in a home pool based on species identity (Fisher exact test, $P > 0.05$). Similarly, no difference was found between the sexes for *O. maculosus* (Fisher exact test, $P > 0.05$) that were recaptured in their home pool *v*. those that were released but not recaptured in their home pool. Of the 10 individuals of *O. snyderi*, only one male was originally captured in the study, preventing any assessment of sex differences for this species. Furthermore, no significant difference was found in the size of those individuals that were recaptured in their home pool *v*. those that were released but not recaptured in their home pool for *O. maculosus* (two-sided *t*-test: $t = 1.21$, d.f. $= 8$, $P > 0.05$), for *O. snyderi* (two-sided *t*-test: $t = 1.00$, d.f. $= 8$, $P > 0.05$) or for both species combined (two-sided *t*-test: $t = 1.13$, d.f. $= 19$, $P > 0.05$).

HOMING

Of the 71 sculpins that were displaced, 39% (28 individuals) returned to their home pool or an immediately adjacent pool. The number of *O. maculosus* individuals that successfully homed and were recaptured was 10 of 28 (36%), while for *O. snyderi* 18 of 35 (51%) successfully homed and were recaptured. No significant difference was found, however, in homing ability between the two species ($\chi^2 = 1.63$, d.f. = 1, $P > 0.05$). For *O. maculosus*, no difference in homing ability was found between the sexes (Table I; $\chi^2 = 0.82$, d.f. = 1, $P > 0.05$). In addition, no difference was found in either species for homing ability based on size (*O. maculosus*, two-sided t-test: $t = 1.06$, d.f. = 30, $P > 0.05$; *O. snyderi*, two-sided t-test: $t = 0.15$, d.f. = 36, $P > 0.05$). For both species combined, however ($\chi^2 = 16.67$, d.f. = 2, $P < 0.001$), and for *O. snyderi* alone ($\chi^2 = 15.43$, d.f. = 2, $P < 0.001$), a strongly significant negative effect of displacement distance on homing success was found. This effect was not found for *O. maculosus* alone ($\chi^2 = 3.47$, d.f. = 2, $P > 0.05$).

MARK–RECAPTURE MODEL

For the data of sculpins returned to their home pools, six models had equivalent support based on AIC values (ΔAIC < 2; Table SII, Supporting Information) indicating no conclusive evidence for effects of size, sex or species on site fidelity (when accounting for detection probability). This was supported by the fact that the total cumulative weight of each factor was similar, but there was marginally more support for a size effect compared with the other predictors (Table II). For the displaced sculpin data, a single model with distance and sex effects had a significantly lower AIC value (ΔAIC > 2; Table SII, Supporting Information) and had *c*. 54% of model weight (Table SII, Supporting Information). When the entire model set was considered, there was 72% model weight for sex and 96% for distance (Table II).

When comparing all individuals of *O. maculosus* to all individuals of *O. snyderi* for the group returned to their home pools, there was a somewhat higher encounter probability of *O. snyderi*, but this may be an artefact of estimating the parameter value based on a single male in *O. snyderi* [Fig. 2(a)]. There was a slightly higher probability, however, of encountering males across both species in the displaced group, where sample size was higher [Fig. 2(b)]. Furthermore, in the displaced group, there was no difference in encounter probability based on species, but there was a difference based on sex [Fig. 2(b)]. Fitting the data using a linear model, there was a significant decrease in homing probability for both males and females as displacement distance increased (Fig. 3). For homing probability (Fig. 4), there was a strong difference based on sex in *O. maculosus* (Table III; permutation test, $P < 0.05$), but not based on species (Table III; permutation test, $P > 0.05$). After fitting a linear regression to the shuffled data using size as the predictor variable, neither the estimated slope nor intercept were significant, except the intercept for *O. maculosus* males. The linear regression using distance as the predictor, however, had a highly significant slope and intercept ($P < 0.001$), for *O. maculosus* males and females ($P < 0.001$). There was also a significant slope for female *O. snyderi* ($P < 0.01$) and the intercept was not statistically significant ($P > 0.05$; *O. snyderi* males were not included in this analysis due to low sample size; Table IV).

TABLE II. Weight of group effects. Cumulative Akaike information criterion (AIC) weight of each factor used to predict encounter probability included in the models. Total model weights are included for each factor, with the contribution of individual model weights in the cumulative weight column. The cumulative weight column contains the AIC weight for individual models in the model set that included these factors (*e.g.* two models included sex + species as an additive effect, one with *c.* 14% of the support and the other with *c.* 9% of the support, for a total AIC weight of 23% for an additive sex and species effect). Only models within the top 95% of the normalized AIC weights of the candidate models were included to avoid trivial factor weight additions; weight of individual models outside of the top 95% of the summed normalized AIC weights are rounded down to 0 for display in the tables. Encounter probability weight contributions to factors are separated for (a) the control sculpin group and (b) the displaced sculpin group

Factor	Cumulative weight	Total
(a) Control encounter probability		
Sex + species	$0 \cdot 14002 + 0 \cdot 09086$	$0 \cdot 23088$
Sex	$0 \cdot 13896 + 0 \cdot 06749$	$0 \cdot 20645$
Species	$0 \cdot 11622 + 0 \cdot 06958$	$0 \cdot 18580$
L_T	$0 \cdot 13086 + 0 \cdot 09086 + 0 \cdot 06958 + 0 \cdot 06749$	$0 \cdot 35879$
No factor	$0 \cdot 24600 + 0 \cdot 13086$	$0 \cdot 37686$
(b) Displaced encounter probability		
Sex + species	$0 \cdot 18333 + 0 \cdot 06063 + 0 + 0$	$0 \cdot 24396$
Sex	$0 \cdot 53658 + 0 \cdot 18192 + 0 + 0$	$0 \cdot 71850$
Species	$0 + 0 + 0 + 0$	0
L_T	$0 \cdot 18192 + 0 \cdot 06063 + 0 + 0 + 0 + 0 + 0 + 0$	$0 \cdot 24255$
Distance	$0 \cdot 53658 + 0 \cdot 18333 + 0 \cdot 18192 + 0 \cdot 06063 + 0 + 0 + 0 + 0$	$0 \cdot 96246$
No factor	$0 + 0 + 0 + 0$	0

L_T, total length

DISCUSSION

SITE FIDELITY

The recapture numbers of marked sculpins in or near their original pool of capture support the results of previous studies (Gersbacher & Denson, 1930; Green, 1971*a*, *b*; Richkus, 1978; Craik, 1981; Yoshiyama *et al.,* 1992) and show that these species display strong site fidelity at widely varied localities and ecological settings across time, indicating site fidelity is not a local phenomenon or spurious result. *Oligocottus snyderi* and *O. maculosus* tend to be found in tidepools where the substratum and algal colour correlate with variation in fish skin colour (M. L. Knope, pers. obs.). This site fidelity may be a means to ensure adequate camouflage, as similarly found for freshwater stream sculpins matching their local substratum background (Whiteley *et al.*, 2009). In addition, for intertidal fishes, it may be crucial to remain in an appropriate tidepool that can safely harbour them for extended periods of time during low tide.

Using a similar statistical approach to that of Yoshiyama *et al.* (1992), no difference was found between the two species in site fidelity. Using the White & Burnham (1999) approach, however, some support for a species difference in site fidelity was found. This study also found no difference in site fidelity between the sexes or with size for either species, based on both approaches. It should be stressed, however, that the sample
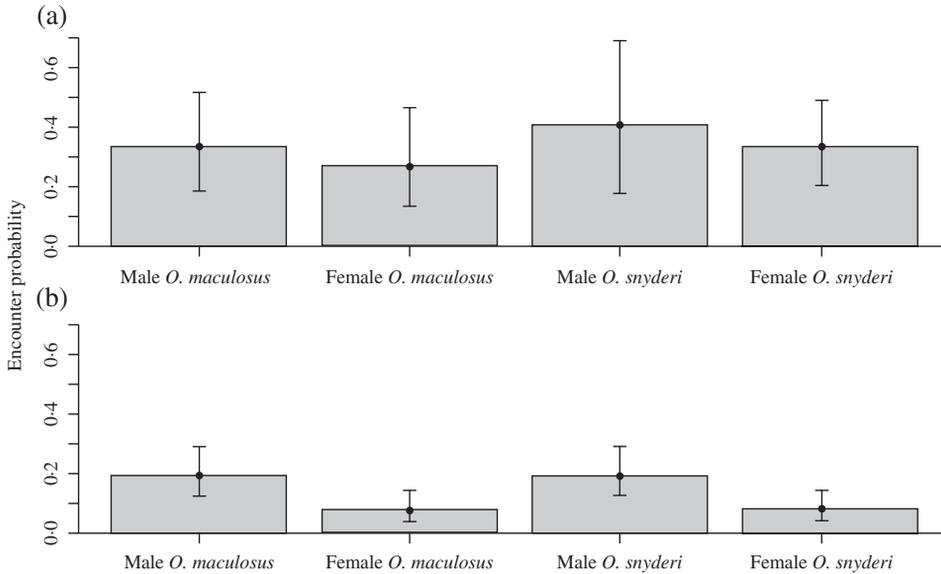
(a)

(b)

FIG. 2. Encounter probability by species and sex. Model-averaged estimates of encounter probability for each sex-specific species group with unconditional s.e. bars, separated as (a) the control sculpin group and (b) the displaced sculpin group.

sizes in this study are relatively small and therefore likely to lead to type II statistical error (failing to detect an effect that is present). With that caveat in mind, it appears that sex and size are not good predictors of site fidelity, but species identity receives some support in the White & Burnham (1999) modelling approach. Overall, this behaviour may be a general characteristic of both species and possibly extends to other sculpins as well.

HOMING ABILITY

These results also support the work of Yoshiyama *et al.* (1992) showing that both *O. maculosus* and *O. snyderi* have strong homing ability. This study found no difference in either species for homing ability based on size, which is in contrast to the findings of Yoshiyama *et al.* (1992) and others (Green, 1971*b*; Craik, 1981). For *O. maculosus*, this study found no difference in homing ability between the sexes using a similar statistical approach to Yoshiyama *et al.* (1992), but it did find strong support for a sex difference in homing after accounting for encounter probability.

While this work found that both species are able to return to home pools after displacement, this ability diminishes with displacement distance for both species combined and for *O. maculosus*. Prior to this study, the maximum demonstrated homing ability for intertidal sculpins was 85 m in *O. snyderi* (Yoshiyama *et al.*, 1992) and 122 m in *O. maculosus* (Khoo, 1974) and this study extends the maximum homing distance to 179 m for *O. snyderi* and 218 m for *O. maculosus*. Both of these distances represent the maximum distance that each species was displaced in this study and suggests that they may be capable of greater homing distances. This maximum distance homing behaviour for both species was performed across a wide expanse (*c.* 150 m) of sand
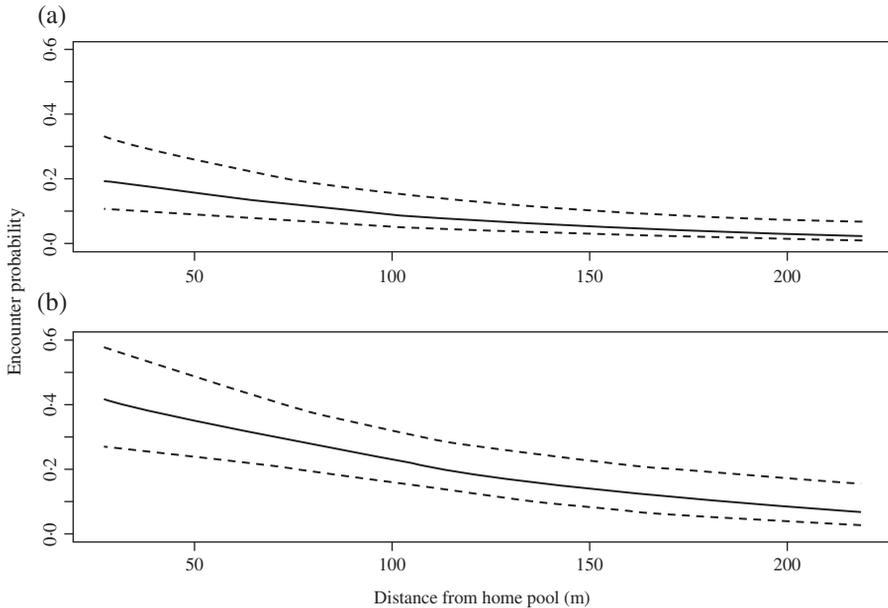
(a)

(b)

Distance from home pool (m)

FIG. 3. Encounter probability (both species combined). ____, encounter probability decreases with distance individual sculpins were displaced from their home pool. _ _ _, 95% C.I. Encounter probability estimates are from the best-fitting model for displaced sculpins (which included sex and distance displaced), separated for (a) females and (b) males.

and silt bottom subtidal area (Fig. 1) that is not typical habitat for these species (Miller & Lea, 1972; Ramon & Knope, 2008; Knope & Scales, 2013) and probably offers little refuge from predation. It is also important to note that these distances are a minimum estimate of homing distance, as the fishes may not have swum in a direct line from their transplant pool to their home pool (or immediate vicinity).

HOW DO SCULPINS ORIENT TO THEIR HOME POOLS AND NAVIGATE TO THEM?

Khoo (1974) experimentally tested the home site fidelity of non-experimentally altered *O. maculosus* individuals against those that were experimentally blinded or
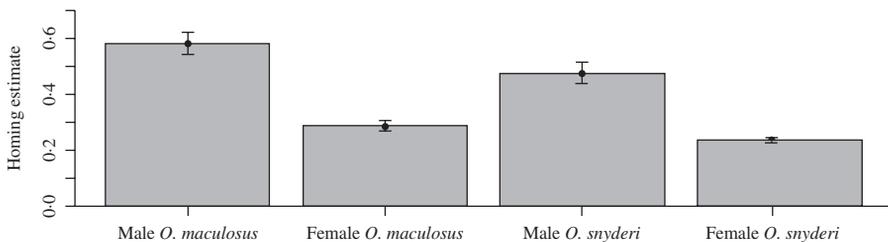

FIG. 4. Homing estimates by species and sex. Estimates of homing based after accounting for encounter probability for each sex-specific species group with error bars plotting the variance of each estimate.

TABLE III. Homing estimates (h). Sex-specific species group parameter estimates of homing probability and the difference in these estimates based on sex (in *Oligocottus maculosus* alone) and based on species (comparing only females)

Parameter	Estimate	Variance
$h_{\text{Male}O.maculosus}$	0·582	0·0403
$h_{\text{Female}O.maculosus}$	0·290	0·0177
$h_{\text{Female}O.snyderi}$	0·236	0·0083
Category	Difference	*P*-value
Sex (*O. maculosus*)	0·292	<0·05
Species (females only)	0·0544	>0·05

anosmic (unable to smell) and found a significant reduction in site fidelity for *O. maculosus* individuals that were both blind and anosmic as compared with unaltered individuals. Furthermore, Khoo (1974) found no significant difference in site fidelity between *O. maculosus* that were only blind or only anosmic as compared with unaltered *O. maculosus*, indicating that having only the sense of vision or only the sense of smell is sufficient to maintain site fidelity, but *O. maculosus* lose site fidelity if they lose both senses.

The homing ability of *O. snyderi* and *O. maculosus* indicate these species have navigational abilities. Khoo (1974) also investigated the sensory basis of homing in *O. maculosus* and found that olfaction played a pivotal role in individuals returning to home tidepools. In fact, blind *O. maculosus* individuals were significantly better at homing than anosmic individuals and were in some cases equal in homing ability to unaltered sculpins (Khoo, 1974). These results indicate that vision may not be as important of a sensory channel as olfaction for homing ability in these fishes (Khoo, 1974), as is the case for some other homing fishes, such as salmonids (Hara, 1970), but it is not well understood how olfaction as a homing sense is influenced by the variable

TABLE IV. Homing estimates (h) with individual covariate predictors. Estimates of slope and intercept from a regression of homing estimates for each sex-specific species group and (a) body size and of (b) distance displaced using the observed data. *P*-values are calculated by comparing the distribution of slope and intercept estimates for each sex-specific species group generated in the permutation test with the slope and intercept values calculated from the observed displaced sculpin data. Male *Oligocottus snyderi* are not included due to low sample size

Group	Slope	*P*-value	Intercept	*P*-value
(a) Homing estimates (h) *v.* body size				
Male *Oligocottus maculosus*	0·0007	>0·05	0·238	<0·05
Female *O. maculosus*	0·0005	>0·05	0·205	>0·05
Female *O. snyderi*	0·0011	>0·05	0·479	>0·05
(b) Homing estimates (h) *v.* distance displaced				
Male *O. maculosus*	−0·003	<0·001	0·674	<0·001
Female *O. maculosus*	−0·003	<0·001	0·566	<0·001
Female *O. snyderi*	−0·005	<0·01	1·161	>0·05

movement of water in intertidal, compared with riverine systems. In addition, it is not clear if natural odours provide 'map' information (*i.e.* give geographic position information), or if perhaps, rather than serving directly in navigational information to these sculpins, odours activate non-olfactory navigational systems (Jorge, 2011).

The question, however, remains, can chance alone explain the reappearance of a sculpin in its original pool? This probability is likely to be a function of the amount of alternative habitat available to displaced individuals. Since a vast amount of alternative suitable habitat is available at Sunset Cove (Fig. 1), this suggests that the fishes did actually home and their return is unlikely to be accounted for by chance alone (Yoshiyama *et al.,* 1992). Why then, do fishes return to their home pools or immediately adjacent pools? During low tide stands, different intertidal pools may differ in habitability (*e.g.* some tidepools may drain completely) and the ability of fishes to recognize and return to pools that remain habitable during low tide could be critical to their survival. In addition, tidepools that offer protection from predators or are particularly food rich may attract fishes in environments where such sites are limited (Yoshiyama *et al.,* 1992).

IMPLICATIONS

Tidepools may represent islands in a biogeographical sense in that they are periodically isolated from the surrounding subtidal mainland and from each other (Altman & Taylor, 2003). Since intertidal sculpins show strong site fidelity to a home range of tidepools, this may lead to isolation and population subdivision somewhat akin to, although perhaps less extreme than, that found in freshwater lakes and oceanic islands. In addition, intertidal sculpins have life-history traits that might promote population subdivision. For example, their relatively small size (generally <10 cm L_T; Knope & Scales, 2013), short generation time (Green, 1971*a*; Yoshiyama & Sassaman, 1987) and limited larval dispersal potential (Marliave, 1986) suggest that they may have reduced potential for dispersal. This combination of high site fidelity and strong homing ability of adults with generally limited dispersal potential of larvae may facilitate speciation *via* disruptive selection without high levels of ongoing gene flow (Ramon, 2007) and may partially explain why sculpins are the most highly speciose component of the intertidal ichthyofauna of the North Pacific (Miller & Lea, 1972; Knope, 2013).

This study found that both *O. snyderi* and *O. maculosus* display high site fidelity to a home range of tidepools and strong homing ability, generally confirming the findings of Yoshiyama *et al.* (1992). Site fidelity was found not to be dependent on sex or size for either species tested. While both species were capable of homing, no difference in homing ability for either species based on size was found, but again only when using the White & Burnham (1999) approach that accounts for encounter probability, was a sex effect found on homing for *O. maculosus*. Also, homing generally decreased with increased displacement distance, but this was not statistically significant in *O. snyderi*. In addition, the maximum homing ability of both species was extended to the maximum displacement distances in this study, suggesting they may be capable of even greater homing distances. Lastly, increased replication of ecological studies can potentially improve the validity of single study findings.

Supporting Information

Supporting Information may be found in the online version of this paper:

TABLE SI. Distances between home pools and adjacent search pools, as measured with a transect tape (centre of pool to centre of pool). SA1, SB1, SC1, SD1, SD2, SE1 and SE2, where SA1 corresponds to search pool number one adjacent to home pool A, *etc*.

TABLE SII. Full set of models considered for (a) the control group and (b) the displaced group, ordered by best fit (lowest AIC and highest model weight). For both groups, the most general model included an additive sex and species effect, and body size as an individual covariate. In addition, the most general model for displaced sculpins included an individual covariate for distance and individuals were displaced from their home pool. Apparent survival is assumed equal to one in all models ($\Phi = 1$). The model set is fully nested and symmetric for all main effects, consisting of reduced parameter versions of the most general model. The term 'no factor' indicates that sex and species effects were not included in this model. Individual body size is called 'size' and the distance an individual was displaced from its home pool is abbreviated as 'dist'.

References

Altman, A. D. & Taylor, E. B. (2003). A molecular assessment of homing in the tidepool sculpin. *Journal of Fish Biology* **62,** 623–640. doi: 10.1046/j.1095-8649.2003.00052.x

Burnham, K. P. & Anderson, D. R. (2002). *Model Selection and Multimodel Inference*. New York, NY: Springer. doi: 10.1007/b97636

Craik, G. J. S. (1981). The effects of age and length on homing performance in the intertidal cottid, *Oligocottus maculosus* (Girard). *Canadian Journal of Zoology* **59,** 598–604. doi: 10.1139/z81-088

Cramér, H. (1946). *Mathematical Methods of Statistics*. Princeton, NJ: Princeton University Press.

Darwin, C. (1873). Origin of certain instincts. *Nature* **7,** 417–418. doi: 10.1038/007417a0

Fisher, R. A. (1935). *The Design of Experiments*. New York, NY: Hafner Publishing Company.

Fisher, R. A. (1974). In *The Collected Papers of R. A. Fisher*, Vol. 1−5 (Bennett, H., ed). Adelaide: University of Adelaide.

Gerking, S. D. (1959). The restricted movement of fish populations. *Biological Reviews* **34,** 221–242. doi: 10.1111/j.1469-185X.1959.tb02189.x

Gersbacher, W. M. & Denson, M. (1930). Experiments with animals in tidepools. *Publications of the University of Washington Puget Sound Marine Biological Station* **7,** 209–215.

Gotelli, N. J. & Ellison, A. M. (2004). *A Primer of Ecological Statistics*. Sunderland, MA: Sinauer Associates, Inc.

Green, J. M. (1971*a*). Field and laboratory activity patterns of the tidepool cottid, *Oligocottus maculosus* Girard. *Canadian Journal of Zoology* **49,** 255–264. doi: 10.1139/z71-036

Green, J. M. (1971*b*). High tide movements and homing behaviour of the tidepool sculpin *Oligocottus maculosus*. *Journal of the Fisheries Research Board of Canada* **28,** 383–389. doi: 10.1139/f71-051

Halverson, C. E. (1982). Habitat selection and other aspects of the ecology of some tidepool sculpins. PhD Dissertation, University of California, Berkeley, CA.

Hara, T. J. (1970). An electrophysiological basis for olfactory discrimination in homing salmon: a review. *Journal of the Fisheries Research Board of Canada* **27,** 565–586. doi: 10.1139/f70-059

Hasler, A. D. (1966). *Underwater Guideposts*. Madison, WI: University of Wisconsin Press.

Hixon, M. A. (1981). An experimental analysis of territoriality in the California reef fish *Embiotoca jacksoni* (Embiotocidae). *Copeia* **1981,** 653–665. doi: 10.2307/1444571

Jorge, P. E. (2011). Odors in the context of animal navigation. In *The Biology of Odors: Sources, Olfaction and Response* (Weiss, L. E. & Atwood, J. M., eds), pp. 207–226. Hauppauge, NY: Nova Science Publishers.

Kelly, C. D. (2006). Replicating empirical research in behavioral ecology: how and why it should be done but rarely ever is. *Quarterly Review of Biology* **81,** 221–236. doi: 10.1086/506236

Kerwath, S. E., Gotz, A., Attwood, C. G., Sauer, W. H. H. & Wilke, C. G. (2007). Area utilisation and activity patterns of roman *Chrysoblephus laticeps* (Sparidae) in a small marine protected area. *African Journal of Marine Science* **29,** 259–270. doi: 10.2989/AJMS.2007.29.2.10.193

Khoo, H. W. (1974). Sensory basis of homing in the intertidal fish *Oligocottus maculosus* Girard. *Canadian Journal of Zoology* **52,** 1023–1029. doi: 10.1139/z74-136

Knope, M. L. (2013). Phylogenetics of the marine sculpins (Teleostei: Cottidae) of the North American Pacific Coast. *Molecular Phylogenetics and Evolution* **66,** 341–349. doi: 10.1016/j.ympev.2012.10.008

Knope, M. L. & Scales, J. A. (2013). Adaptive morphological shifts to novel habitats in marine sculpin fishes. *Journal of Evolutionary Biology* **26,** 472–482. doi: 10.1111/jeb.12088

Laake, J. L. (2013). RMark: an R interface for analysis of capture-recapture data with MARK. *AFSC Processed Reports* **2013-01**, 25. doi: 10.1111/2041-210X.12065

Larson, R. J. (1980*a*). Competition, habitat selection, and the bathymetric segregation of two rockfish (*Sebastes*) species. *Ecological Monographs* **50,** 221–239. doi: 10.2307/1942480

Larson, R. J. (1980*b*). Influence of territoriality on adult density in two rockfish of the genus *Sebastes*. *Marine Biology* **58,** 123–132. doi: 10.1007/BF00396123

Larson, R. J. (1980*c*). Territorial behavior of the black and yellow rockfish and gopher rockfish (Scorpaenidae, *Sebastes*). *Marine Biology* **58,** 111–122. doi: 10.1007/BF00396122

Lohmann, K. J., Lohmann, C. M. F. & Endres, C. S. (2008). The sensory ecology of ocean navigation. *Journal of Experimental Biology* **211,** 1719–1728. doi: 10.1242/jeb.015792

Marliave, J. B. (1986). Lack of planktonic dispersal of rocky intertidal fish larvae. *Transactions of the American Fisheries Society* **115,** 149–154. doi: 10.1577/1548-8659(1986)115<149:LOPDOR>2.0CO;2

Matthews, K. R. (1990). An experimental study of the habitat preferences and movement patterns of copper, quillback, and brown rockfishes (*Sebastes* spp.). *Environmental Biology of Fishes* **29,** 161–178. doi: 10.1007/BF00002217

Mireles, C., Nakamura, R. & Wendt, D. E. (2011). A collaborative approach to investigate site fidelity, home range, and homing behavior of cabezon (*Scorpaenichthys marmoratus*). *Fisheries Research* **113,** 133–142. doi: 10.1016/j.fishres.2011.10.008

Nanami, A. & Yamada, H. (2008). Foraging rates and substratum selection in foraging activity of checkered snapper *Lutjanus decussatus* (Lutjanidae) in an Okinawan coral reef. *Journal of Fish Biology* **73,** 1444–1448. doi: 10.1111/j.1095–8649.2008.02026.x

Ramon, M. L. (2007). Molecular ecology of intertidal sculpins. PhD Thesis, University of California, Santa Cruz, CA.

Ramon, M. L. & Knope, M. L. (2008). Molecular support for marine sculpin (Cottidae; Oligocottinae) diversification during the transition from the subtidal to intertidal habitat in the Northeastern Pacific Ocean. *Molecular Phylogenetics and Evolution* **46,** 75–483. doi: 10.1016/j.ympev.2007.11.005

Richkus, W. A. (1978). A quantitative study of intertidepool movement of the wooly sculpin *Clinocottus analis*. *Marine Biology* **49,** 277–284. doi: 10.1007/BF00391140

White, G. C. & Burnham, K. P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study* **46,** 120–139. doi: 10.1080/00063659909477239

Whiteley, A. R., Gende, S. M., Gharrett, A. J. & Tallmon, D. A. (2009). Background matching and color change plasticity in colonizing freshwater sculpin populations following rapid deglaciation. *Evolution* **63,** 1519–1529. doi: 10.1111/j.1558-5646.2009.00627.x

Williams, G. C. (1957). Homing behavior of California rocky shore fishes. *University of California Publications in Zoology* **59,** 249–284.

Yoshiyama, R. M. (1981). Distribution and abundance patterns of rocky intertidal fishes in central California. *Environmental Biology of Fishes* **6,** 315–332. doi: 10.1007/BF00005760

Yoshiyama, R. M. & Sassaman, C. (1987). Geographical patterns of allozymic variation in three species of intertidal sculpins. *Environmental Biology of Fishes* **20,** 203–218. doi: 10.1007/BF00004955

Yoshiyama, R. M., Gaylord, K. B., Philippar, M. T., Moore, T. R., Jordan, J. R., Coon, C. C., Schalk, L. L., Valpey, C. J. & Tosques, I. (1992). Homing behavior and site fidelity intertidal sculpins (Pisces: Cottidae). *Journal of Experimental Marine Biology and Ecology* **160,** 115–130. doi: 10.1016/0022-0981(92)90114-P

Electronic Reference

Miller, D. J. & Lea, R. N. (1972). Guide to the coastal marine fishes of California. *California Department of Fish and Game Bulletin*, Sacramento, CA. Available at http://content.cdlib.org/ark:/13030/kt896nb2qd/