



Settlement and recruitment of fish in mussel farms

Lucy H. Underwood^{1,2,*}, Andrew G. Jeffs^{1,2}

¹School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand

²Institute of Marine Science, University of Auckland, Private Bag 92019, Auckland, New Zealand

ABSTRACT: Fish are thought to settle and recruit to shellfish and seaweed farms; however, there is little published evidence to support this assumption. Shellfish and seaweed farms increase structural complexity and epibiota productivity, which may attract settling fish larvae. In this study, fish settlement and recruitment patterns into 2 aquaculture habitats, mussel–kelp co-culture and mussel farm monoculture, were compared to 2 adjacent natural habitats, soft-sediment seafloor and rocky reef, within a settlement season. Standard monitoring units for the recruitment of fish (SMURFs) were used, as they are a common and reliable method for measuring temporal and spatial variability in fish settlement and recruitment among habitat types. The communities of fish species settling and recruiting to both sets of aquaculture and natural habitats were equivalent. This was most likely due to the artificial 3D structure of the mussel farm habitats functioning in a similar manner to the structural complexity of a rocky reef habitat. Further, there was indication that for at least the most abundant fish species, *Fosterygion lapillum*, the 2 aquaculture habitats were of sufficient quality to support growth from settlement to juvenile size classes (i.e. in mussel monoculture habitat 65% were newly settled in December, and 86% were of juvenile size class by February). Overall, these findings provide foundational quantitative evidence of the interactions that fish have with mussel farms and increases the understanding of restorative opportunities for aquaculture operations.

KEY WORDS: Mussel farm · Fish recruitment · Fish settlement · Restorative aquaculture · Co-culture · SMURFs

1. INTRODUCTION

Aquaculture structures operate as artificial habitats which can host a wide diversity of sessile biofouling species and provide shelter, food and nursery habitat to a range of mobile wild fish species (Dealteris et al. 2004, Callier et al. 2018, Theuerkauf et al. 2022). While it is known that fish, including juveniles, can aggregate around aquaculture structures, or temporarily occupy these structures, there is little published evidence that fish directly recruit to shellfish or seaweed farms (Tallman & Forrester 2007). There is some limited evidence for fish farms, where wild demersal and pelagic fish of settlement to juvenile size have been observed to inhabit sea cages, indicating that aquaculture structures can provide habitat for larval settlement and recruitment of fish (Valle et al.

2007, Fernandez-Jover et al. 2009, Fernandez-Jover & Sanchez-Jerez 2015). These fish recruits appear to benefit from the habitat functions provided by the artificial habitat, including the protection it provides from predation. Seaweed farms have been identified as potential nursery habitat for juvenile fish, particularly in tropical environments; however, there is no direct evidence that fish are recruiting to the farms or that the composition and abundances of fish recruits is the same or varies from those found in natural habitats (Hehre & Meeuwig 2016, Tano et al. 2017, Kelly et al. 2020). A few published studies have investigated the use of shellfish aquaculture operations as nursery habitat for fish (Dealteris et al. 2004, Powers et al. 2007, Tallman & Forrester 2007). For example, juvenile fish on hard clam *Mercenaria mercenaria* aquaculture structures were utilising epibiota in a similar

*Corresponding author: lund481@aucklanduni.ac.nz

manner to nearby natural seagrass habitats (Powers et al. 2007). It is important to delineate between the settlement and recruitment functions of aquaculture structures so that the true extent of the contribution of aquaculture habitats to the overall production and biomass of wild fish populations can be quantified, because aquaculture structures may only act as an attractive habitat for recruits that have settled elsewhere (Barrett et al. 2022, Theuerkauf et al. 2022).

The green-lipped mussel *Perna canaliculus* is the most significant aquaculture species in New Zealand, with approximately 5500 ha in current (2022) production and over 15 000 ha of space approved for expanding production (Stenton-Dozey & Broekhuizen 2019, Aquaculture New Zealand 2020). This scale of expansion has caused public concern surrounding the potential ecological effects of these farms in coastal waters (Stenton-Dozey & Broekhuizen 2019). There is a negative perception towards these farms, partly because there is a lack of evidence to support the positive contribution mussel farms may make to coastal ecosystems (Stenton-Dozey & Broekhuizen 2019). Green-lipped mussels are grown on longline farming systems (Jefferies et al. 1999) that are known to provide artificial habitat for fish (Theuerkauf et al. 2022); however, it is unknown how fish interact with the mussel farm habitat and what aspects of their life history are involved (Stenton-Dozey & Broekhuizen 2019). In particular, there is, to our knowledge, no published evidence that larval fish settle within mussel farms, despite the presence of juvenile fish within mussel farms, which would otherwise suggest that these fish may be the result of settlement events within the farm (Morrissey et al. 2006, Stenton-Dozey & Broekhuizen 2019, Theuerkauf et al. 2022). Green-lipped mussel farms host a range of biofouling taxa including kelp (*Ecklonia radiata* and *Undaria pinnatifida*) and other macroalgal species typical of rocky reef habitats in the region (Woods et al. 2012). Coastal fish frequently recruit into macroalgae, as it provides shelter from predators, hosts a range of macroinvertebrates, and increases habitat complexity (Connell & Jones 1991, McDermott & Shima 2006, Shelamoff et al. 2020). Besides hosting biofouling macroalgae, mussel farms also support a wide range of productive fauna and provide physical structure, which appears to attract fish, including juvenile recruits (Carbines 1993, Morrissey et al. 2006, McLeod et al. 2014).

Standard monitoring units for the recruitment of fishes (SMURFs) are commonly used as a reliable method to measure temporal and spatial variability in fish settlement and recruitment, including among dif-

ferent habitats (Ben-David & Kritzer 2005, Valles et al. 2006, Arney et al. 2017). SMURFs provide a representative sample of the fish settlers and/or recruits that are naturally present in the surrounding habitat (Ammann 2004, Ben-David & Kritzer 2005, Arney et al. 2017). Studies indicate that SMURFs are less discriminatory than other sampling methods, as they attract the settlers and recruits of a range of fish species from within the sampled habitat (Ammann 2004, Valles et al. 2006). Other methods for sampling fish settlers and recruits include light traps, towed nets and diver visual surveys. However, light traps preferentially attract fish species that have strong phototaxis, most often at the late larval stage, while towed nets are ineffective at sampling among structures, and diver visual surveys are of limited use due to the small size and cryptic behaviour of settlers (Ammann 2004, Carassou et al. 2008, Guyah et al. 2021).

The placement of SMURFs within a habitat allows for assessment of the habitat-specific settlement cues present, with SMURFs functioning as temporary settlement substrate to capture fish settlers present in the environment (Ammann 2004, Shima & Swearer 2009, Swearer & Shima 2010). SMURFs have previously measured fish settlement and recruitment across a range of habitat types. These include a comparison of kelp canopy densities in a defined near-shore environment, in fringing reefs across a coastline, in artificial reefs with varied culvert densities, and kelp habitats of varied structural complexity within one embayment (Siddon et al. 2008, Valles et al. 2008, Jones & Mulligan 2014, Arney et al. 2017). Therefore, even at small scales, the homogenous design of SMURFs enables direct comparisons among habitat types. The design of SMURFs ensures that larger predatory individuals are excluded (Ammann 2004, Ben-David & Kritzer 2005). Fish recruits have the ability to move in and out of the SMURF structure during the post-settlement period such that the abundance of recruits in the SMURFs reflects the post-settlement processes operating within the habitat, although the retention of recruits within SMURFs is also influenced by species-specific behaviour and is partly dependent on the complexity of the adjacent habitat types (Ammann 2004, Ben-David & Kritzer 2005, Shelamoff et al. 2020). Where space is more available and predation rates low, recruits may not associate with SMURFs long-term; however, they may still utilise them temporarily during post-settlement processes (Shelamoff et al. 2020).

Few studies using SMURFs have directly compared patterns of fish recruitment among habitat types over a relatively small spatial scale. Within a

confined area, larval supply is expected to be similar across a range of adjacent habitats, facilitating direct comparisons of the influence of habitat on fish settlement and recruitment. By deploying SMURFs in aquaculture habitats and adjacent natural habitats within a locality with a similar larval supply, it should be possible to isolate the relative influence of the aquaculture habitats on the settlement and recruitment of fish within the various habitats. In so doing, it will improve the understanding of the role of aquaculture activities on the recruitment of coastal fish, which in turn can help direct aquaculture development and restorative aquaculture efforts (Arney et al. 2017, Gentry et al. 2020, Theuerkauf et al. 2022).

The overall aim of this research was to determine, for the first time globally, whether shellfish farms directly provide habitat for local fish settlement and recruitment. In particular, our research tested the hypothesis that the relative contribution of aquaculture habitats (mussel farm with a high density of kelp *E. radiata* and *U. pinnatifida*) [co-culture] and a mussel farm with a low density of kelp [monoculture] to fish recruitment would be equivalent to the contribution of natural habitats (soft-sediment seafloor with limited physical structure and natural rocky reef).

2. MATERIALS AND METHODS

2.1. Sample site

This study was conducted at the mouth of the Coromandel Harbour in northern New Zealand ($36^{\circ} 48' 28.7''$ S, $175^{\circ} 26' 18.8''$ E (Fig. 1)). The study site is influenced by both incoming tidal flows from the north and surface currents which flow longshore down the coastline (Oldman et al. 2007, Norrie 2019). Most coastal fish in New Zealand, such as triplefin species *Fosterygion* spp., have a larval period of at least 1 mo, and will therefore be exposed to the hydraulic conditions for dispersal throughout the local area (Kingsford & Choat 1985, Shima & Swearer 2009). Only one shallow coastal study site was chosen to standardise larval supply as much as possible and to reduce the amount of natural variability among replicates. The study site was subject to homogeneous natural processes, particularly surface currents that provide larval supply and a tidal range of close to 4 m. The sampled aquaculture habitats were located within 3 blocks of an operational longline green-lipped mussel farm, consisting of a series of 2 parallel backbone lines held near the surface by large plastic

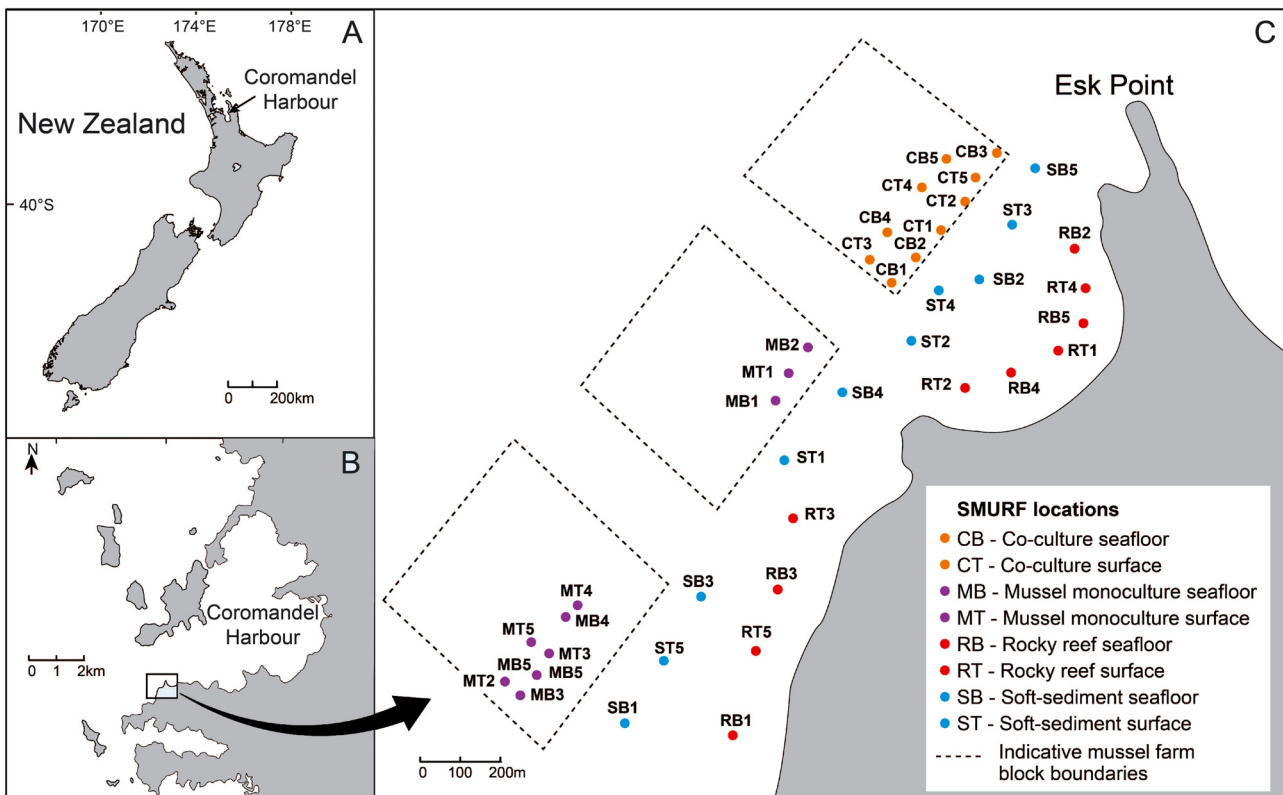


Fig. 1. Location of standard monitoring units for the recruitment of fish (SMURFs) at Esk Point, Coromandel

floats that support suspended loops of dropper rope with attached mussels which extend to approximately 8 m deep and hang above the seabed that ranged from 12–15 m deep. Monoculture aquaculture habitat (Habitat M) was where green-lipped mussels are cultured on dropper lines with minimal kelp (*Ecklonia radiata*, *Undaria pinnatifida*) biofouling, whereas co-culture habitat (Habitat C) was where green-lipped mussels were present with a high density of associated growing kelp. The natural reef habitat (Habitat R) traverses along the adjacent coast, is comprised of hard rock with thick kelp cover, and ranges from 5–9 m deep. The natural soft-sediment habitat (Habitat S) was located in an area between the natural rocky reef and mussel farm habitats where depth ranged from 8–9 m and consisted of an area of seafloor with sand and fine silt sediment composition.

2.2. Sample design

The SMURFs used for the study were constructed to the specifications of Ammann (2004) but reduced in length by 0.1 m due to the width of commercially available plastic mesh. Two sampling depths were

used for aquaculture habitats, 3 m below surface ('surface') and 8 m below surface ('seafloor'), with the intention of detecting any differences in fish recruits in the water column (surface SMURFs) and in the vicinity of the benthic zone (seafloor SMURFs). Where the natural bathymetry allowed, natural habitat SMURFs were placed at the same depths as aquaculture habitats. However, some of the reef areas were slightly shallower than 8 m deep and so were placed 1 m off the seabed. Ten SMURFs were placed in alternating surface and seafloor depths at least 30 m apart within the 4 habitat types (i.e. M, C, S, and R) (Fig. 2). The SMURFs placed in mussel farm habitats (C and M) were attached to a mooring line and tied directly to the mussel farm backbone. SMURFs placed in Habitats R and S were attached to a mooring line with an anchor and surface buoy.

The SMURFs were deployed on 7 December 2020, and then fish were removed from each SMURF 2 d either side of a new moon on 16 December 2020, 14 January 2021 and 11 February 2021, as recruitment can be impacted by the lunar cycle (McFarland et al. 1985, Ben-David & Kritzer 2005, Kohn 2011). A 3 mo period was chosen to represent the key seasonal period during which coastal fishes are present in the nearshore environment and to maximise the capture

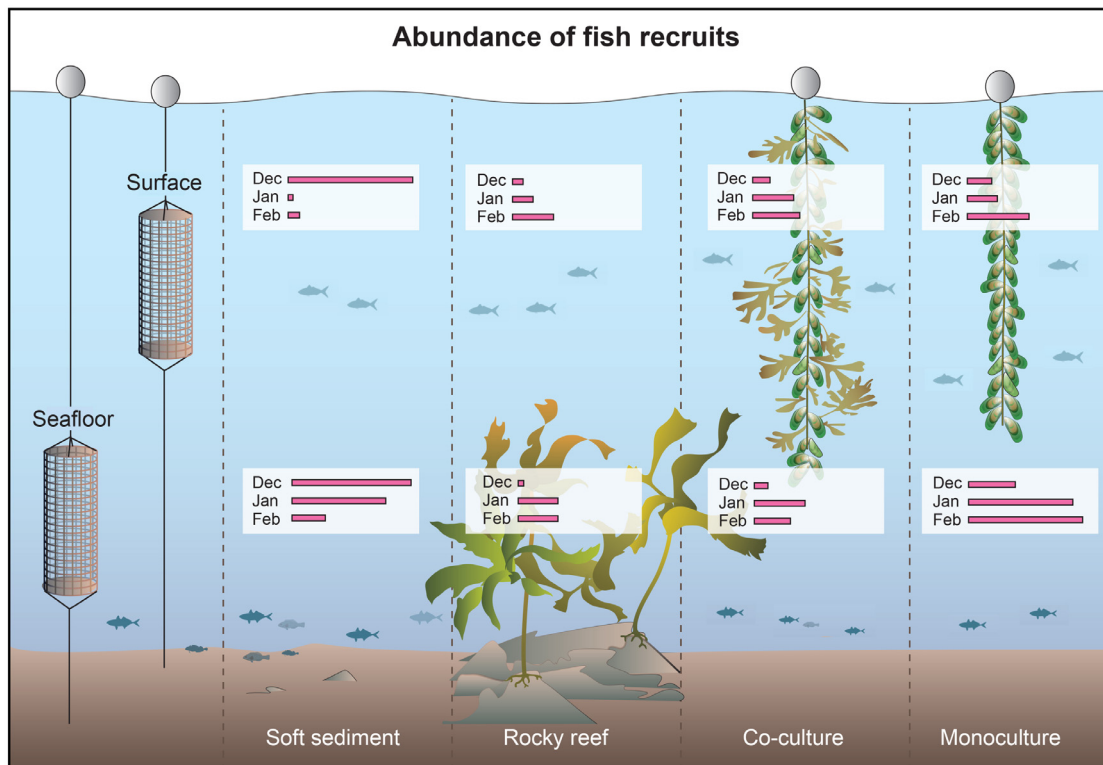


Fig. 2. Visual representation of the SMURF sample design and the 4 habitat types. Bar plots show the differences in the total abundance of fish recruits within each depth and month combination

of a variety of settling reef fish. For example, triplefin *Fosterygion* spp. stop settling by February, and spotty *Notolabrus celidotus* begin settling early December and finish in February (Jones 1984, Carbines 1993, Kohn & Clements 2011). Therefore, month was included as a key variable in the analysis of fish settlement and recruitment, as the sequential months are expected to identify the seasonal transition of settling fish into the various habitat types. Fish within each SMURF were removed by slowly lifting the SMURF to near the surface, at which point a large scoop net (5 mm mesh size) was used to retrieve the SMURF to a boat. As each SMURF was drawn to the surface, fish retreated further into the artificial habitat cover, so that any loss of recruits during the retrieval process was minimal (Ammann 2004, Kohn 2011). Each SMURF was flushed and shaken into a fish bin with saltwater to release individuals. Where an appropriate identification could be undertaken without a specimen, fish were photographed with a reference measure, weighed and released immediately. If they could not be readily identified, they were euthanized immediately in a salt ice slurry. After euthanasia, fish were preserved in 90% isopropyl for processing. The research was compliant with the American Veterinary Medical Association's Guidelines for the Euthanasia of Animals: 2020 edition (<https://www.avma.org/sites/default/files/2020-02/Guidelines-on-Euthanasia-2020.pdf>). SMURFs were then redeployed to the same location.

2.3. Sampling handling and classification

Fish were measured (total length [TL], mm), counted, and identified to the lowest taxonomic level possible. Common triplefin (*F. lapillum*) were split into 3 size classes: 0–30 mm TL, newly settled individuals; 31–50 mm TL, juveniles; >51 mm, adults (McDermott & Shima 2006). Additionally, settlement-sized individuals for each fish species were separated out to describe patterns in settlement among habitat types. Previous otolith studies have indicated that ~20 mm TL is the size of triplefin species at settlement (Paulin & Roberts 1992, Kohn & Clements 2011). Similarly, the size at settlement for orange clingfish *Dellichthys trnskii* is <20 mm (Conway et al. 2018), leatherjacket *Parika scaber* <35 mm (Kingsford & Milicich 1987), and *Trachurus* spp. <25 mm (Beveren et al. 2016). Age cohort investigation was only conducted on *F. lapillum*, as this was the only species with sufficient catches from the SMURFs to make this analysis feasible.

2.4. Species diversity and evenness

Shannon-Wiener diversity and evenness indices were calculated for each habitat for each month as they take into account the number of species and abundance of fish species caught and better describe the overall fish community. Indices were calculated per SMURF for each of the 3 mo. The following equations were used to calculate species diversity (H') and species evenness (E):

$$H' = -\sum p_i \ln p_i \quad (1)$$

where p_i = proportion of S made up of the i th species:

$$E_{H'} = H' / \ln S \quad (2)$$

where S = the total number of species in the community.

2.5. Biofouling and habitat assessment

A biofouling assessment was undertaken to quantify the biomass of kelp in the 2 aquaculture habitats. Six 0.5 m sections each of randomly selected dropper lines from Habitats M and C were stripped (Fig. 1). Replicates from each habitat were evenly split between the 2 depth ranges (surface and seafloor) to characterise the equivalent SMURF sampling locations ($n = 3$ per habitat–depth combination). Dropper lines were lifted with a crane onto a mussel barge, where all material attached to the rope was removed, bagged, chilled, and transported to the laboratory. In the laboratory, the material was sorted into broad taxonomic groups or dominant species where appropriate (e.g. kelp) and wet weighed so that the different biofouling groups could be proportionately quantified.

The natural reef was characterised for the percentage cover of *E. radiata* covering the rocky reef surfaces only, so that the differences in kelp cover among aquaculture and natural habitats could be compared. This was a high-level indicative classification to confirm that the rocky reef was a habitat dominated by *E. radiata*, which is typical of the coastline of north-eastern New Zealand. An underwater video recorder was suspended beneath a free diver within the reef area, and the resulting video footage was used to randomly select 29 still images of the rocky reef surface from which estimates of macroalgal canopy cover across the rocky surfaces could be estimated (Bennion et al. 2019). This was calculated as a percentage of the total rocky surface area covered in macroalgae.

2.6. Statistical analyses

A linear mixed effects model was used with restricted maximum likelihood (REML) estimates to model total fish and *F. lapillum* abundance over the 3 sampling events for the SMURFs. A constant of 0.5 was added to all raw abundance values to remove zeros from the data set, and variables were logged to account for skewed data. Random intercepts (REML estimates) were fit for each SMURF sampling unit at each month to account for repeated measures. Where the overall model results were significant, 'emmeans' post-hoc analyses were used to compare each of the combinations among the 3 interacting factors used in the sampling design (habitat, month, depth).

H' and *E* did not conform to parametric assumptions, even after transformation of the proportional indices (Scariano & Davenport 1987). Consequently, multi-pairwise Kruskal-Wallis comparisons were used, with a correction for inflated error. Such an approach to analyses of these data is sufficiently statistically conservative to provide adequate protection for type I errors caused by α inflation from multiple testing and sequential sampling from static SMURF positions (Lee & Lee, 2018). Post-hoc analyses were conducted if significant differences were identified across all scenarios of the 3 interacting factors used in the sampling design (habitat, month, depth).

To compare fish communities among habitat types, non-metric multidimensional scaling (NMDS) was conducted based on Bray-Curtis distances with 999 permutations for the fish species data per SMURF. An ordination plot was produced for a 2D representation of the ordination.

To compare the biofouling between the 2 aquaculture habitat types and confirm the differences between the monoculture and co-culture farm habitats, a PERMANOVA on the biomass of biofouling groups based on Bray-Curtis distances with 999 permutations was done, with comparisons between habitat (M and C) and depth (surface and seafloor) as factors.

A linear mixed effects model was used to model mean *F. lapillum* length (TL) for habitat and month. Random intercepts were fit for each SMURF sampling unit at each month to account for repeated measures. Where the overall model results were significant, 'emmeans' post-hoc analyses were used to compare each of the combinations among the 2 interacting factors (habitat, month). Fisher's exact test was used to compare the proportions of the abundance of settlers to post-settled *F. lapillum* individuals among habitats for the month of December. December was the only month where settlement-sized individuals

were recorded and was used to understand differences in fish settlement among habitat types.

All statistical analyses and plots were produced using R statistical software v4.0.4 (R Core Team, 2021), with the exception of the NMDS plot, which was produced on PAST statistical software (version 4.0.4) (Hammer et al. 2001). All analyses used a significance $\alpha = 0.05$. All means are presented as mean \pm SE.

3. RESULTS

3.1. Abundance of species

Overall, a total of 730 fish from 9 distinguishable species, classified to the lowest taxonomic level possible, were captured in the SMURFs during the 3 sampling events. Only one replicate SMURF was lost, from Habitat S (ST1) during the February sampling. Over all depths combined, aquaculture habitats (i.e. C and M) collected 373 fish, while natural habitats (i.e. S and R) collected 357 fish. The common triplefin was the dominant species collected at all habitats and comprised roughly 74% of the total catch (Fig. 3). The December collection included schooling mackerel *Trachurus* spp. at settlement size, which comprised roughly 15% of the total catch for the month. The other 7 species were at low abundances across all months and comprised the remaining 11% of the total catch. Common triplefin, orange clingfish, and *Pseudophycis barbata* were the only species found within all habitat types. The total number of species (i.e. species richness) found within the 4 habitats was similar, with monoculture and reef habitats containing 7 species and soft-sediment and co-culture containing 6 species. Few individual fish were captured at settlement size, common triplefin ($n = 56$ across all habitats), *Dellichthys trnskii* ($n = 2$ in Habitats S and R), leatherjacket ($n = 3$ in Habitat S) and mackerel spp. ($n = 108$ in Habitat S).

Overall, there were significant differences in the mean abundance of fish sampled in SMURFs between the 2 depths and among and within 4 habitats sampled over 3 mo ($\chi^2_{23} = 85.24$, $p < 0.0001$) (Figs. 2 & 4). The main factor effects of depth were significant, as were the interactions of habitat \times month, habitat \times depth, and month \times depth (Table 1). Post-hoc analyses identified the most significant interactions related to Habitat S in December (i.e. characterised by catches of groups of settling mackerel *Trachurus* spp.). Significant interactions related to depth of SMURF sampling were applicable for Habitats S and M in January and

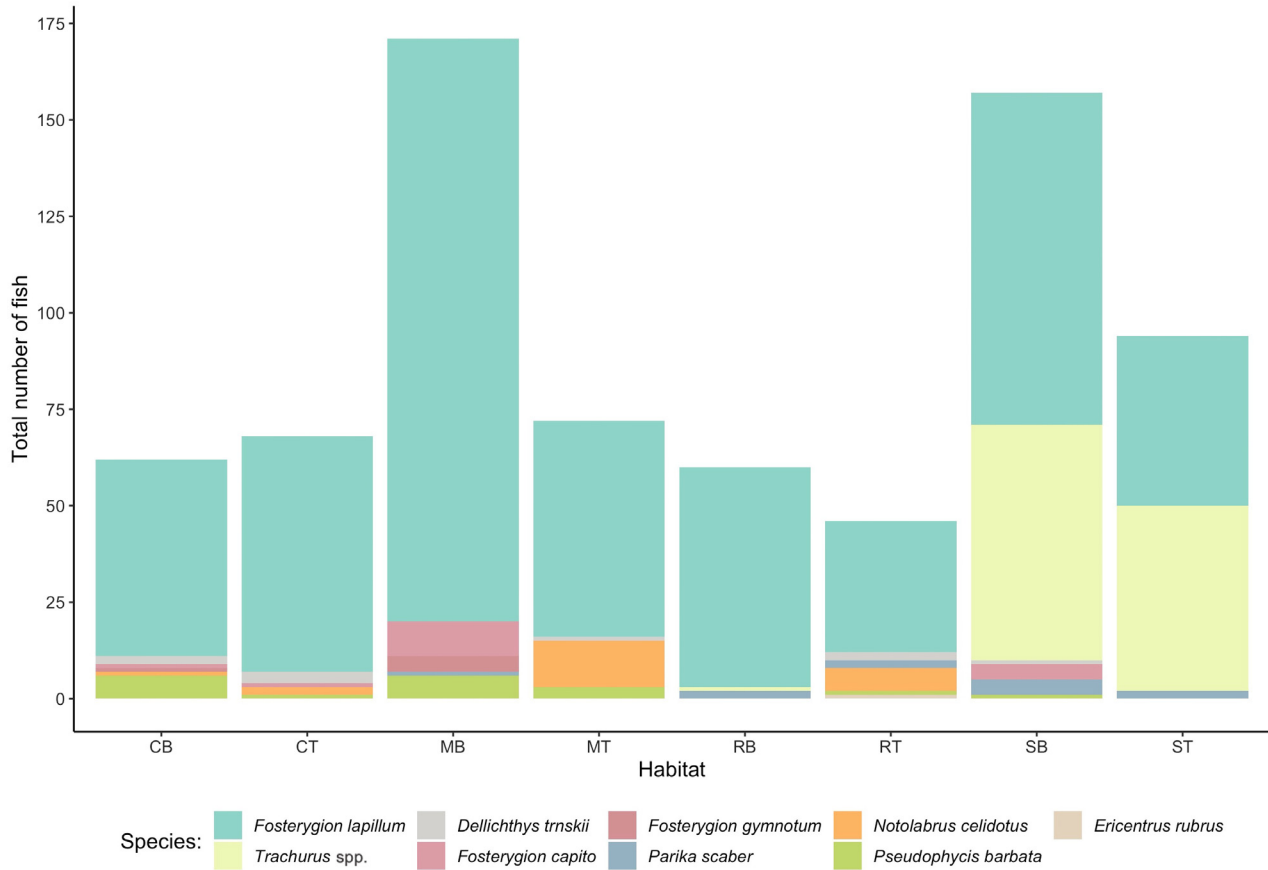


Fig. 3. Total catches of different fish species caught in SMURFs pooled from 3 sampling events (monthly) between December 2020 and February 2021 at co-culture (C), monoculture (M), reef (R) and soft-sediment (S) habitats. Each habitat is split into surface (T) and seafloor (B) depths (n = 5 for each habitat, depth, and month combination)

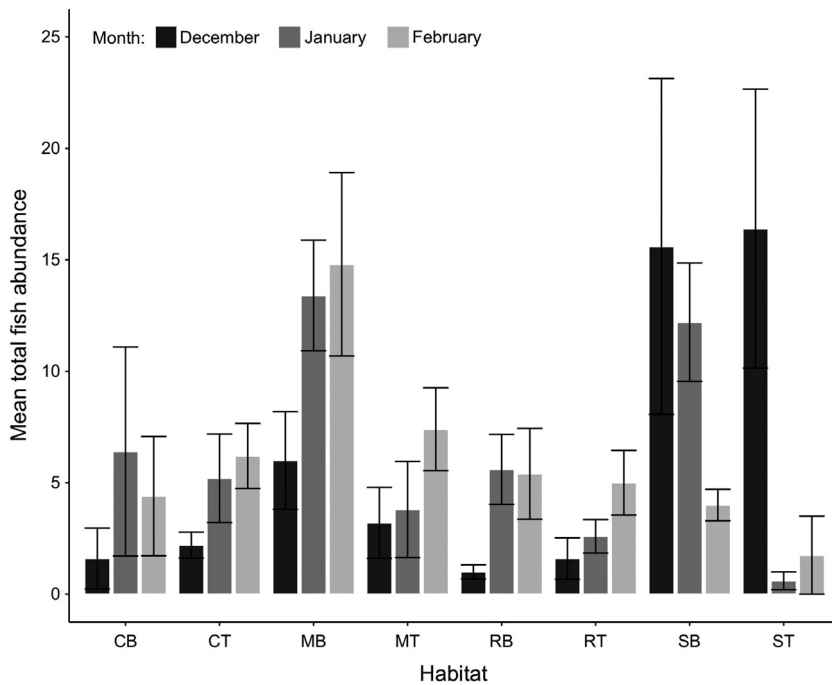


Fig. 4. Mean (\pm SE) abundance of all fish species from 3 monthly sampling events in SMURFs placed in 4 habitats (C: co-culture; M: monoculture; R: reef; S: soft-sediment) and 2 depths (B: seafloor; T: surface)

Table 1. Summary statistics for total and *Fosterygion lapillum* abundance counts within the 4 habitats sampled over 3 mo based on linear mixed effects model fit with restricted maximum likelihood (REML)

Variable	Model	Predictors	df	F	p
Total abundance	Linear mixed model fit by REML with random intercepts for each unique combination	Habitat	3	2.81	0.055
		Month	2	2.66	0.078
		Depth	1	5.52	0.025
		Habitat: Month	6	7.95	<0.0001
		Habitat: Depth	3	4.61	0.009
		Month: Depth	2	5.78	0.005
		Habitat: Month: Depth	2	1.29	0.270
<i>F. lapillum</i> abundance	Linear mixed model fit by REML with random intercepts for each unique combination	Habitat	3	2.29	0.097
		Month	2	4.57	0.014
		Depth	1	5.70	0.023
		Habitat: Month	6	3.26	0.007
		Habitat: Depth	3	4.71	0.008
		Month: Depth	2	7.52	0.001
		Habitat: Month: Depth	6	1.91	0.092

Habitat S in February, when seafloor SMURFs had a higher abundance than surface SMURFs (Fig. 4, Table S1 in the Supplement; www.int-res.com/articles/suppl/q015p085_supp.pdf). Significant interactions related to month were only evident for Habitat R, where abundance was higher in January and February seafloor SMURFs compared to December (Fig. 4, Table S1). Significant interactions contrasted by habitat identified both M and C surface habitats in February with higher abundance compared to Habitat S. In January, Habitat C at the surface also had a higher abundance than Habitat S (Fig. 4, Table S1).

There were overall differences in the mean abundance of *Fosterygion lapillum* in the SMURFs between the 2 depths within 4 habitats sampled over 3 mo ($\chi^2_{23} = 73.90$, $p < 0.0001$) (Fig. 5). The main factor effects of depth and month were significant, as were the interactions of habitat \times month, habitat \times depth, and month \times depth (Table 1). Significant interactions contrasted by depth mostly indicated that seafloor SMURFs had higher *F. lapillum* abundance than surface SMURFs within Habitats S, M, and C (Fig. 5, Table S2). Significant interactions contrasted by month indicated a significant increase in *F. lapillum* abundance over time for Habitats R and M, while there was a decrease over time for Habitat S. Significant interactions contrasted by habitat indicated that Habitats M and C surface SMURFs in February had higher *F. lapillum* abundance than the

Habitat S, and Habitat M seafloor had a higher abundance than the C habitat for the same depth–month combination (Fig. 5, Table S2).

3.2. Species diversity and evenness

There were overall significant differences in the diversity of fish sampled in the SMURFs between the 2 depths and among and within the 4 habitats sampled over 3 mo, as measured by H' (Kruskal-Wallis, $\chi^2_{23} = 44.94$, $p = 0$) (Fig. 6a). Post-hoc analysis of the 3 interacting factors (month, habitat, depth) could not

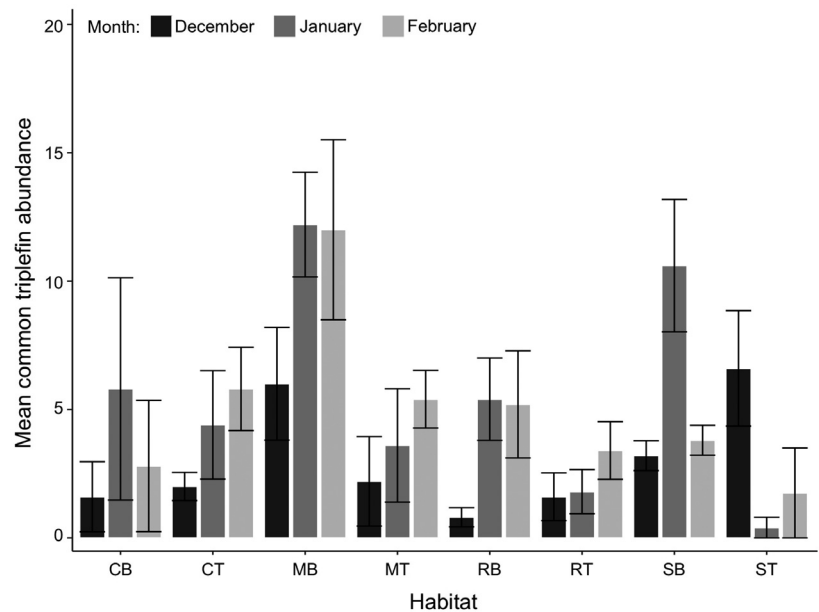


Fig. 5. Mean (\pm SE) abundance of common triplefin at 3 sampling events in SMURFs placed in 4 habitats (C: co-culture; M: monoculture; R: reef; S: soft-sediment) and 2 depths (B: seafloor; T: surface)

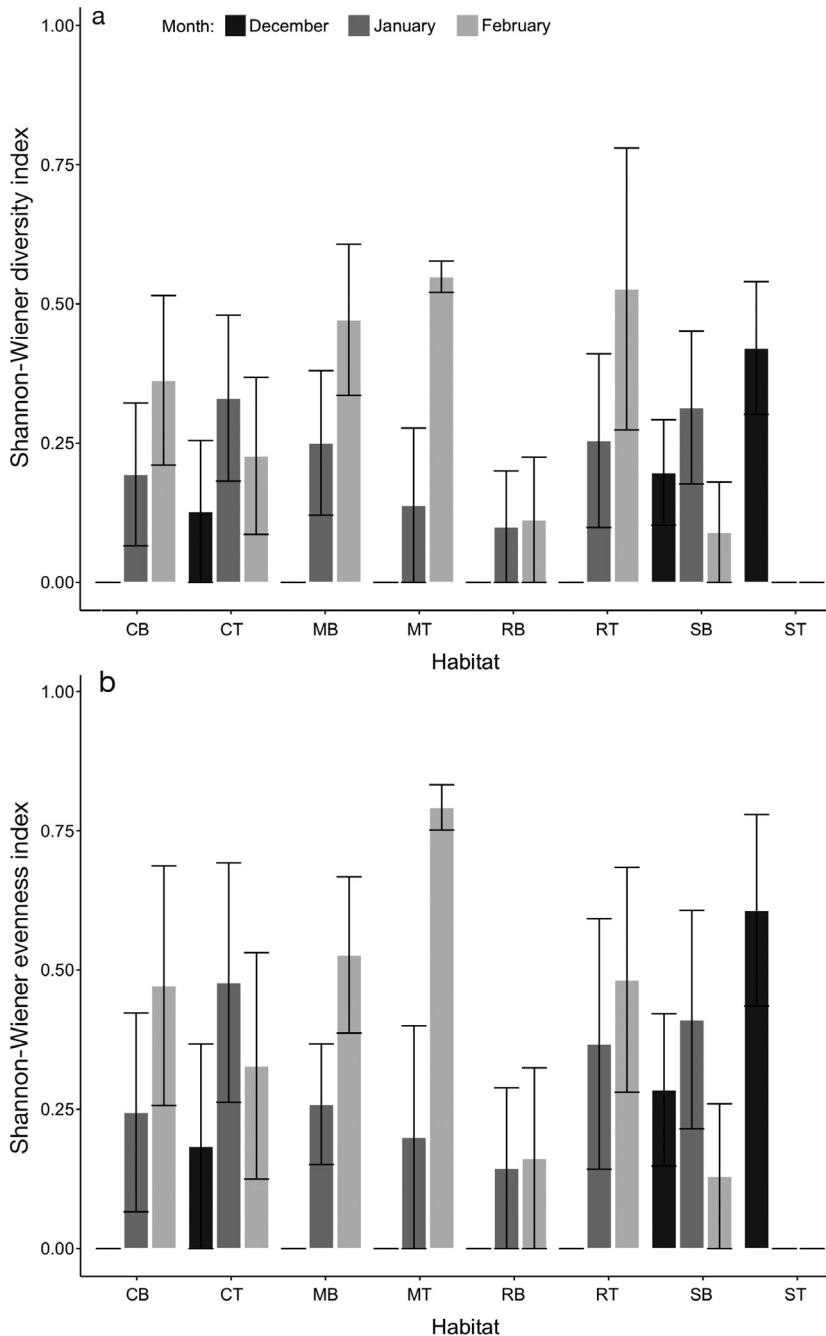


Fig. 6. Comparison of mean (\pm SE) Shannon-Wiener (a) diversity index and (b) species evenness index for all fish caught in SMURFs for 4 habitats (C: co-culture; M: monoculture; R: reef; S: soft-sediment), 2 depths (B: seafloor; T: surface) at 3 monthly sampling events

detect any differences in the main effect of habitat (Table S3). Similarly, there were overall significant differences in the evenness of fish sampled in the SMURFs between the 2 sampled depths within 4 habitats sampled over 3 mo as measured by E (Kruskal-Wallis $\chi^2_{23} = 44.13$, $p = 0.01$) (Fig. 6b). However, post-hoc analyses were unable to distinguish

any differences in the main effect of habitat due to the dominance of *F. lapillum* throughout all 4 sampled habitats (Table S4).

3.3. Fish communities at different habitats

The ordination analysis identified that the communities of fish arriving in SMURFs among habitat types were similar, with every habitat type overlapping considerably (Fig. 7). Habitats C and S appear to have had more variation in the composition of fish communities arriving in SMURFs, while Habitat M had the least variation.

3.4. Size distribution of *F. lapillum*

Overall, for all habitats, the size of *F. lapillum* increased from December to February (Fig. 8). In December 2020, the 20–30 mm size class had the highest overall abundance, whereas by February 2021, the 40–50 mm size class was the most abundant among habitats. Settlers (<22 mm TL) were caught at all habitats, but only in the December sample, with the highest abundance of settlement-sized individuals present in Habitats S and M ($n = 33$ and 12 , respectively), and the lowest in Habitats C and R ($n = 5$ and 6 , respectively). However, the proportion of settlers to post-settled individuals in December differed significantly among habitats (Fisher exact test, $p < 0.0001$). In this month, settlers constituted a greater proportion of all the sampled *F. lapillum* in Habitats S and R (67 and 50% of total catch, respectively) and the least proportion in Habitats C and M (27 and 29% of total catch, respectively).

There were overall differences in the mean length of *F. lapillum* in the SMURFs among the 4 habitats sampled over 3 mo ($\chi^2_{11} = 368.98$, $p < 0.0001$) (Fig. 9). The main factor effects of habitat and month and month \times habitat were significant (Table 2). Post-hoc analyses indicated that the significant interaction was mostly driven by the differences in the rate of in-

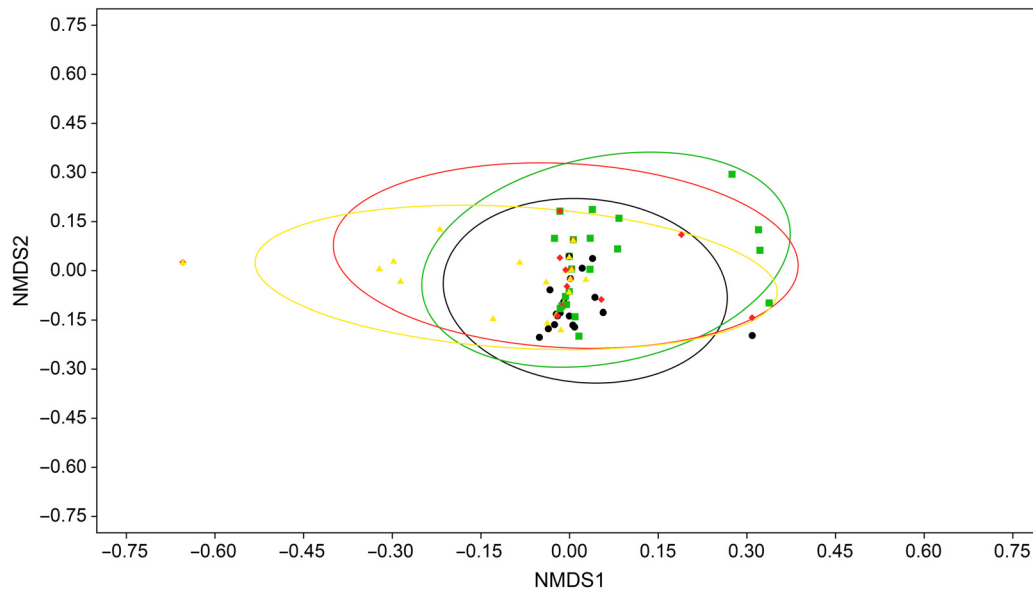


Fig. 7. Non-metric multidimensional scaling (NMDS) plot of fish communities sampled within SMURFs and split into habitat for 2 depths and for 3 mo of sampling. Yellow: soft-sediment habitat; green: co-culture habitat; black: monoculture habitat; orange: reef habitat; 95 % ellipses displayed

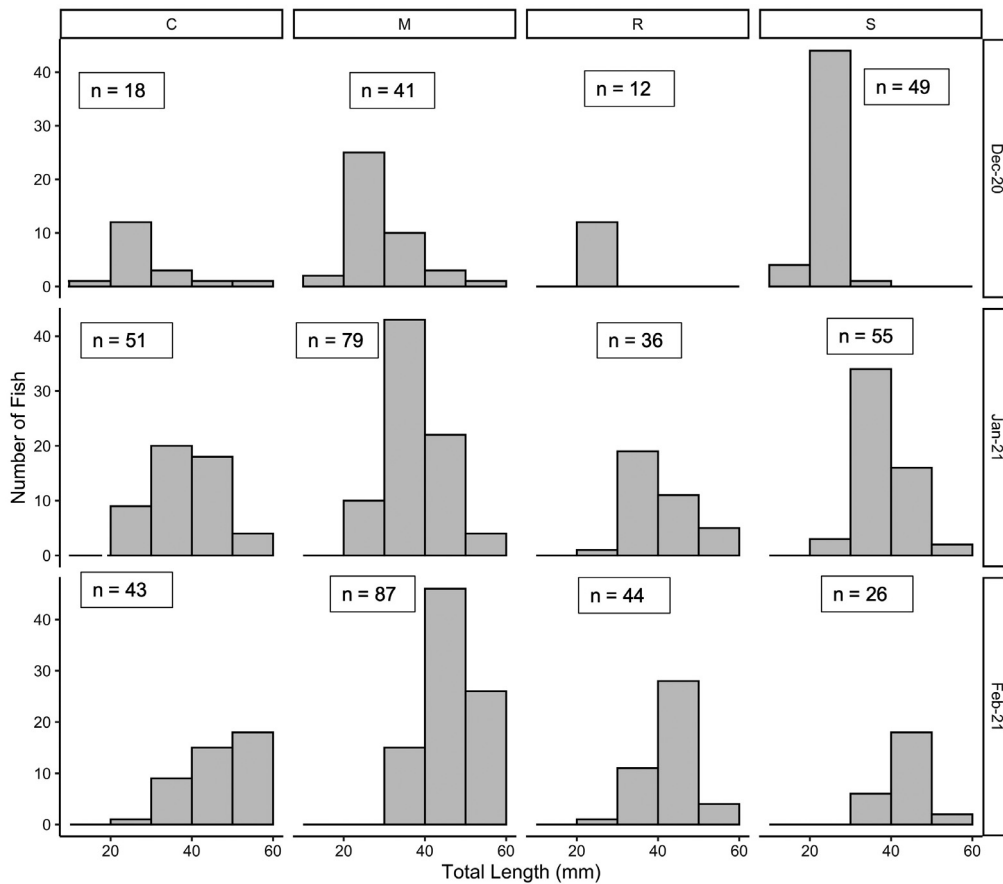


Fig. 8. Distribution of common triplefin *Fosterygion lapillum* in different size classes for total length (mm) from samples collected with SMURFs from 4 habitats (C: co-culture; M: monoculture; R: reef; S: soft-bottom) per month (December 2020, January 2021, February 2021) and for 2 depths combined

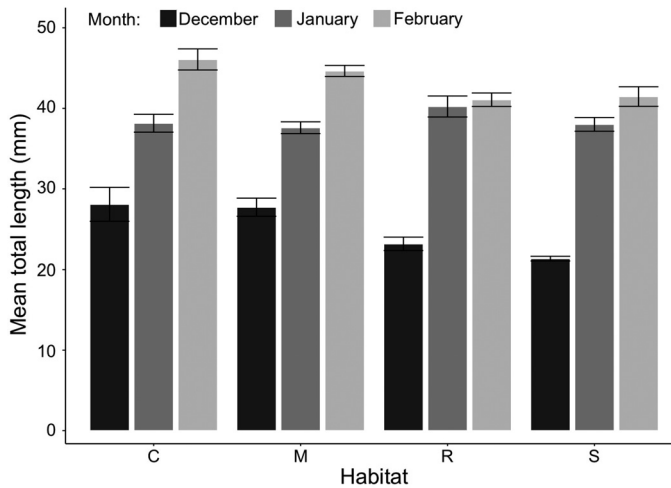


Fig. 9. Mean (\pm SE) total length (mm) of common triplefin *Fosterygion lapillum* from samples collected from SMURFs sampling 4 habitats (C: co-culture; M: monoculture; R: reef; S: soft-bottom) over 3 mo (December 2020, January 2021, February 2021)

crease in the size of fish over time for all habitat types. Among these, *F. lapillum* only showed a significant increase in size between December and January and December and February for natural habitats (i.e. Habitats R and S), whereas in aquaculture habitats (i.e. Habitats C and M), there was a significant increase in size for all month combinations (Fig. 9, Table S5). The *F. lapillum* sampled from Habitat S were also significantly smaller in December compared to Habitats C and M, but not Habitat R. The recruits of *F. lapillum* sampled in February in Habitat R were significantly smaller (by 12%) than those sampled from Habitat C ($p = 0.034$, $C = 46.1 \pm 1.3$ vs. $R = 41.1 \pm 0.8$ mm). There were no significant differences in mean size between Habitats C and M within any month.

3.5. Biofouling communities

Overall, 13 coarse groupings were identified within biofouling samples taken from the 2 aquaculture habitats, based on dominant species or ecological

function. PERMANOVA analysis of the biomass of biofouling identified significant differences between Habitat C and M biofouling communities ($F_{(1,8)} = 4.98$, $p = 0.045$). No significant differences were identified between sampled depths ($F_{(1,8)} = 0.91$, $p = 0.42$), or for the interaction of habitat \times depth ($F_{(1,8)} = 0.05$, $p = 0.96$). Habitat C had a more diverse range of biofouling, which included a higher percentage biomass of kelp *Ecklonia radiata* ($C = 9.0 \pm 1.6\%$, $M = 0.1 \pm 0.0\%$).

Overall, Habitat R was characterised by rocky reef with extensive canopy cover of *E. radiata* ($46.0 \pm 4.8\%$). Variability in cover was due to patches of reef without kelp, as well as the intermittent presence of other species of seaweeds, e.g. *Carpophyllum* spp. and *Cystophora* spp., that were mixed in places with *E. radiata*.

4. DISCUSSION

4.1. Comparison of fish communities among habitats

While it is acknowledged that the habitat value of aquaculture structures to fish has been identified, the results from this study provide some of the first evidence that fish larvae are specifically settling into aquaculture habitats and successfully establishing in the habitat after settlement (Tallman & Forrester 2007, Callier et al. 2018, Barrett et al. 2022). This distinction is important as it indicates that larval settlers and recruits have a direct association with aquaculture habitats and are not only utilising or aggregating within the habitat at later stages of development. Furthermore, the 2 examined aquaculture habitats enabled the recruitment of fish at rates equivalent to adjacent natural habitats. A similar suite of fish species was found to be recruiting to each of the 4 habitats that were sampled with SMURFs over 3 mo, with species richness being similar and the fish communities in the aquaculture versus natural habitats being indistinguishable by NMDS analysis. Similarly, comparisons of the diversity and evenness of fish sampled could not detect any broadscale differences among

Table 2. Summary statistics for *Fosterygion lapillum* length within the 4 habitats sampled over 3 months based on linear mixed effects model fit with restricted maximum likelihood (REML)

Variable	Model	Predictors	df	F	p
<i>F. lapillum</i> mean length	Linear mixed model fit by REML with random intercepts for each unique combination	Habitat	3	4.48	0.009
		Month	2	199.15	<0.0001
		Habitat: month	6	4.00	0.001

the 4 habitats. All of the significant interactions for evenness were related to samples from the SMURFs that comprised only one species (common triplefin), which resulted in an evenness score of zero. Common triplefin are highly territorial and competitive, which may have contributed to the dominance and singularity of this species captured in SMURFs (Jones 1988, Carbines 1993, Willis & Anderson 2003).

The overall consistency of fish communities indicates a similar pattern of arrival of fish larvae at all 4 habitats. However, there was some variation in the presence of the uncommon species, which may indicate some possible fine-scale differences in use by the recruits of some fish species. For example, juvenile orange clinid *Ericentrus rubrus* was only present in one sample taken at a surface reef habitat. The orange clinid prefers rocky reef habitat where specific species of brown algae, *Carpophyllum* and *Cystophora*, are present, and these macroalgae were at very low densities in co-culture habitat (Clements et al. 2014). Additionally, recruits of the spotty *Notolabrus celidotus* were consistently absent from soft-sediment habitats throughout the sampling period but were present in aquaculture and reef habitats. Spotty are associated with macroalgae during recruitment and, as they reach juvenile sizes, will seek structural complexity, such as mussel lines, mussel farm anchor blocks, or rocky reef habitat (Carbines 1993, Morrisey et al. 2006). SMURFs did not catch any settlement-sized spotty (<2 cm), which is the age class that has a stronger association with brown macroalgae (Jones 1984, Carbines 1993, Morrisey et al. 2006). In the present study, robust triplefin *Fosterkygion gymnotum* was only sampled in aquaculture habitats, i.e. a total of 1 in Habitat C and 4 in Habitat M. This species has previously been observed to have relatively wide habitat preferences, including artificial structures, such as wharf piles (Jawad 2008), while the abundance of this species in reef habitats is associated with more complex rocky reef habitat without kelp (Shelamoff et al. 2020). Therefore, in the present study, the aquaculture infrastructure likely provided the structural complexity of habitat preferred by the cryptobenthic recruits of the robust triplefin.

4.2. Comparison of habitats for settlement of fish larvae

Recruits of the common triplefin dominated the catches from SMURFs, with a smaller proportion being of settlement size (i.e. 56 out of total of 541). This

species is commonly found in high abundances in coastal reef and hard rock habitats in New Zealand and has strong thigmotactic responses during settlement (Ammann 2004, Valles et al. 2006, Kohn 2011). In December, common triplefin settlers were sampled in SMURFs in all habitats and depths, although their abundance varied markedly among habitat types. SMURFs in Habitat S in December had the highest abundance of common triplefin settlers. In contrast, Habitats C and R had the lowest abundance of common triplefin settlers. Habitats M had double the number of settlers compared to Habitats C, but only a third as many as were sampled in the Habitat S. Common triplefin settlers were absent from all samples from all habitats for January and February sampling, indicating that there was a discrete settlement pulse within December only during the experimental timeframe. Settlement may also have occurred prior to December, with post-settled individuals also observed within the December sampling. Common triplefin are known to have a broad range of settlement habitats, exhibiting strong thigmotaxis and a preference for cryptic habitats (Connell & Jones 1991, Willis & Anderson 2003, McDermott & Shima 2006). The initial high abundance of settlers sampled in the SMURFs placed in the Habitat S suggests that settling larvae were available to settle throughout the 4 habitats within this study location.

Recently settled *Trachurus* spp. were only found at high abundance in SMURFs Habitat S (n = 108), 1 present in reef habitat in December only and none in the other 2 habitats. Mackerel species are pelagic and have strong schooling behaviour, but are attracted to physical structures in order to avoid predation in the water column (Valle et al. 2007, Fernandez-Jover et al. 2009, Beveren et al. 2016). Therefore, it is unlikely that settling mackerel larvae were seeking reef habitat for settlement (Beveren et al. 2016). The subsequent absence of this species from all sampled SMURFs in January and February, other than 1 individual in Habitat S, highlights their short period of larval settlement, with settled and established individuals presumably moving into pelagic habitat or subject to mortality.

Post-hoc analyses indicated that seafloor SMURFs captured more recruits than surface SMURFs in Habitats S and M. This was unexpected, as the sample area was shallow; therefore, vertical stratification was unlikely to have congregated settling individuals at certain depths. However, interactions related to depth were mostly present in January and February and so within the post-settlement period rather than the settlement period. It is likely the differences in

habitat between the 2 depths (i.e. close to the sea-floor) had driven the differences in recruits at depth within these habitat types.

4.3. Comparison of habitats as nurseries for fish recruits

The vast majority of fish sampled within this study were of post-settled size, i.e. overall total of 169 settlers versus 561 post-settlers, all species combined. Cryptobenthic species (i.e. common triplefin) have small home ranges and are territorial in nature, which means they do not travel far after settlement (Connell & Jones 1991, Morrisey et al. 2006). The isolation of the aquaculture habitats suggests that these recruits had become resident in the habitat prior to the settlement period observed in this study.

The artificial 3-dimensional structures of the mussel farm habitats provided a similar function as in the physical structural complexity that a rocky reef system provides, if not more so (i.e. total common triplefin abundance in February in Habitat M = 87 vs. Habitat R = 44). Habitats C and M also showed a significant increase in size of *F. lapillum* recruits between all months, whereas natural habitats (S and R) only showed an initial significant increase in December, but not thereafter. The combination of survival and growth is important, as it strongly indicates that these artificial aquaculture habitats are of sufficient quality to host settlers, recruiting juveniles and adults (Morrisey et al. 2006, Shelamoff et al. 2020). Three-dimensional aquaculture structures along with established biofouling and mussels present on the aquaculture structures likely support post-settled individuals through the provision of food and shelter, similar to the habitat function of naturally occurring shellfish reefs (McLeod et al. 2014, Cheminée et al. 2015, Wilson et al. 2017). Specifically, natural *Perna canaliculus* reefs that occur on soft-sediment seafloors have been found to have a 13.7 times higher density of small fishes compared with nearby areas of bare soft-sediment seafloor, most likely due to the physical structure providing shelter and increased abundance of invertebrates as food for fish provided by the mussel reef habitat (McLeod et al. 2014). The lack of quantification of secondary production in shellfish farms makes it difficult to compare the relative importance of the feeding opportunities for fish recruits with natural shellfish beds (Alleway et al. 2019). In the present study, SMURFs placed in aquaculture habitats were observed to host a wide range of mobile fauna with a dominance of benthic crustaceans, particularly

crabs and glass shrimp species, together with a diverse range of amphipod and copepod species (L. H. Underwood pers. obs.). Because SMURFs were hung directly off the shellfish aquaculture infrastructure, the mobile fauna accumulating in SMURFs were representative of those species associating with the aquaculture habitat. These small mobile species are an important food source for triplefin recruits, juveniles, and adults (Jones 1988, Feary et al. 2009). Unlike some other demersal fish recruits which may only utilise nursery habitats for shelter but feed in the adjacent water column (i.e. snapper *Pagrus auratus* recruits), it is the combination of shelter and food that is important for these cryptobenthic fish species (Jones 1988, Parsons et al. 2014, Parsons et al. 2020).

In a 2-dimensional soft-sediment habitat, there was limited physical habitat structure to support fish recruits, resulting in the subsequent decline observed in the abundance of recruits sampled by SMURFs in Habitat S over time (i.e. a significant decline in *F. lapillum* recruits and total fish recruits at surface Habitat S from December–January and December–February). A range of habitats can promote settlement of triplefins, although they exhibit subsequent age-specific mortality when recruits outgrow less complex habitat, resulting in decreasing abundance (Connell & Jones 1991). The lack of food or shelter within habitats with limited structural and biogenic complexity may increase density-dependent and density-independent mortality in fish recruits, as there is greater competition among individuals for resources and more predation mortality during this vulnerable life stage (Connell & Jones 1991, Johnson, 2007, Cheminée et al. 2015). Other than mortality, reductions in growth rate are also associated with lower-complexity habitats (Cheminée et al. 2015, Ermgasen et al. 2016, Lefcheck et al. 2019), such as the significantly greater increase in mean size of common triplefin from January to February sampled in the aquaculture habitats (C and M) versus Habitat S.

Overall, settlers were available within each habitat type and subsequently settled into the temporary substrate provided by the SMURFs. However, the qualities of habitats appeared to be more important to the subsequent establishment of settlers, with marked differences in the retention and growth of common triplefin observed among the 4 sampled habitats. Both aquaculture habitats outperformed Habitat S for both the retention and growth of common triplefin. Further, the mean length of *F. lapillum* was significantly greater in aquaculture habitats compared to Habitat R in February, suggesting more rapid growth. Overall, the results indicate that the

structural complexity of habitat, and the complex interactions of physical and biological factors which habitat structure supports (i.e. less predation, reduced competition, increased food availability), drive the different trends in abundance and diversity of fish recruits over time within a habitat. However, separate experiments would be required to confirm these driving mechanisms. While this study has only used one spatial location, the data provides a foundational understanding of the settlement and recruitment patterns and of the degree of natural variability which occurs at a small scale. This variability will need to be carefully managed for future studies that seek to undertake sampling over a wider range of locations.

5. CONCLUSION

The results of this study indicate that aquaculture and natural habitats provide suitable habitat for the settlement of fish that are typical to natural coastal rocky reef habitats within the vicinity. Aquaculture habitats also supported post-settled individuals through recruitment and appear to provide a nursery habitat function. In soft-sediment habitats, although supporting the settlement of fish, there was a decline in individuals over time, which suggests that settlers were unable to be supported by the habitat, likely due to the lack of physical structure. There were also indications that, for at least one species, the common triplefin, the 2 aquaculture habitats examined are of sufficient quality to support the growth of fish from settlement to juvenile size classes. The presence of kelp in the co-culture aquaculture habitat versus mussels alone did not affect these observed patterns of fish recruitment, suggesting that the presence of kelp does not enhance structural or secondary production of the habitat in a manner that improves settlement and establishment outcomes for fish recruits. Overall, the results provide evidence that shellfish aquaculture infrastructure can provide suitable habitat for the recruitment of fish that is comparable with natural habitat and that it further extends the ecosystem services provided by such aquaculture activities.

Data availability. The data underlying for this article will be shared on reasonable request by the corresponding author.

Acknowledgements. We thank Gold Ridge Marine farms for providing access to the mussel farm sites and for logistic support and the New Zealand Marine Farmer's Association (MFA) for their support. Thanks also to Esther Stuck and Peter Schlegel, who endured long days of field work. We are

grateful to the Nature Conservancy for financial support for this research and to the Ministry of Business, Innovation & Employment's Endeavour Fund (RJGHT1901).

LITERATURE CITED

- ✦ Alleway HK, Gillies CL, Bishop MJ, Gentry RR, Theuerkauf SJ, Jones R (2019) The ecosystem services of marine aquaculture: valuing benefits to people and nature. *Bioscience* 69:59–68
- ✦ Ammann AJ (2004) SMURFs: standard monitoring units for the recruitment of temperate reef fishes. *J Exp Mar Biol Ecol* 299:135–154
- ✦ Aquaculture New Zealand (2020) New Zealand greenshell mussel spat strategy. National Institute of Water & Atmospheric Research, Christchurch
- ✦ Arney RN, Froehlich CYM, Kline RJ (2017) Recruitment patterns of juvenile fish at an artificial reef area in the Gulf of Mexico. *Mar Coast Fish* 9:79–92
- ✦ Barrett LT, Theuerkauf SJ, Rose JM, Alleway HK and others (2022) Sustainable growth of non-fed aquaculture can generate valuable ecosystem benefits. *Ecosyst Serv* 53: 101396
- ✦ Ben-David J, Kritzer J (2005) Early life history and settlement of the slender filefish, *Monacanthus tockeri* (Monacanthidae), at Calabash Caye, Turneffe Atoll, Belize. *Environ Biol Fishes* 73:275–282
- ✦ Bennion M, Fisher J, Yesson C, Brodie J (2019) Remote sensing of kelp (Laminariales, Ochrophyta): monitoring tools and implications for wild harvesting. *Rev Fish Sci Aquacult* 27:127–141
- ✦ Beveren EV, Klein M, Serrão EA, Gonçalves EJ, Borges R (2016) Early life history of larvae and early juvenile Atlantic horse mackerel *Trachurus trachurus* off the Portuguese west coast. *Fish Res* 183:111–118
- ✦ Callier MD, Byron CJ, Bengtson DA, Cranford PJ and others (2018) Attraction and repulsion of mobile wild organisms to finfish and shellfish aquaculture: a review. *Rev Aquacult* 10:924–949
- ✦ Carassou L, Ponton D, Mellin C, Galzin R (2008) Predicting the structure of larval fish assemblages by a hierarchical classification of meteorological and water column forcing factors. *Coral Reefs* 27:867–880
- Carbines GD (1993) The ecology and early life history of *Notolabrus celidotus* (Pisces: Labridae) around mussel farms in the Marlborough Sounds. MSc Dissertation, University of Canterbury, Christchurch
- ✦ Cheminée A, Merigot B, Vanderlift MA, Francour P (2015) Does habitat complexity influence fish recruitment? *Mediterr Mar Sci* 17:39–46
- ✦ Clements KD, Holleman W, Williams JT (2014) *Ericentrus rubrus*. The IUCN Red List Threat Spec 2014:e.T179005 A1558366. <https://dx.doi.org/10.2305/IUCN.UK.2014-3.RLTS.T179005A1558366.en>. (accessed May 2021)
- ✦ Connell SD, Jones GP (1991) The influence of habitat complexity on post recruitment processes in a temperate reef fish population. *J Exp Mar Biol Ecol* 151:271–294
- ✦ Conway KW, Stewart AL, Summers AP (2018) A new species of sea urchin associating clingfish of the genus *Dell-ichthys* from New Zealand (Teleostei, Gobiesocidae). *ZooKeys* 740:77–95
- Dealteris JT, Kilpatrick BD, Rheault RB (2004) A comparative evaluation of the habitat value of shellfish aquaculture gear, submerged aquatic vegetation and a non-

- vegetated seabed. *J Shellfish Res* 23:867–874
- ✦ Ermgassen PSE, Grabowski JH, Gair JR, Powers SP, Jones J (2016) Quantifying fish and mobile invertebrate production from a threatened nursery habitat. *J Appl Ecol* 53: 596–606
- ✦ Feary D, Wellenreuther M, Clements K (2009) Trophic ecology of New Zealand triplefin fishes (Family Tripterygiidae). *Mar Biol* 156:1703–1714
- ✦ Fernandez-Jover D, Sanchez-Jerez P (2015) Comparison of diet and otolith growth of juvenile wild fish communities at fish farms and natural habitats. *ICES J Mar Sci* 72: 916–929
- ✦ Fernandez-Jover D, Sanchez-Jerez P, Bayle-Sempere JT, Arechavala-Lopez P, Martinez-Rubio L, Jimenez JAL, Lopez FJM (2009) Coastal fish farms are settlement sites for juvenile fish. *Mar Environ Res* 68:89–96
- ✦ Gentry RR, Alleway HK, Bishop MJ, Gillies CL, Waters T, Jones R (2020) Exploring the potential for marine aquaculture to contribute to ecosystem services. *Rev Aquacult* 12:499–512
- ✦ Guyah N, Webber M, Prospere K (2021) An assessment of the larval fish diversity within a coastal marine reserve. *Reg Stud Mar Sci* 43:101655
- Hammer Ø, Harper DA, Ryan PD (2001) PAST: paleontological statistics software package for education and data analysis. *Palaeontol Electronica* 4:9
- ✦ Hehre EJ, Meeuwig JJ (2016) A global analysis of the relationship between farmed seaweed production and herbivorous fish catch. *PLOS ONE* 11:e0148250
- ✦ Jawad LA (2008) Second revision of the New Zealand triplefin genus *Forsterygion* Whitley and Phillips, 1939 (Pisces: Tripterygiidae). *J Nat Hist* 42:2943–2989
- Jeffs AG, Holland RC, Hooker SH, Hayden BJ (1999) Overview and bibliography of research on the greenshell mussel (*Perna canaliculus*), from New Zealand waters. *J Shellfish Res* 18:347–360
- ✦ Johnson DW (2007) Habitat complexity modifies post-settlement mortality and recruitment dynamics of a marine fish. *Ecology* 88:1716–1725
- ✦ Jones GP (1984) Population ecology of the temperate reef fish *Pseudolabrus celidotus* Bloch & Schneider (Pisces: Labridae). I. Factors influencing recruitment. *J Exp Mar Biol Ecol* 75:257–276
- ✦ Jones GP (1988) Ecology of rocky reef fish of north-eastern New Zealand: a review. *NZ J Mar Freshw Res* 22:445–462
- ✦ Jones M, Mulligan T (2014) Juvenile rockfish recruitment in Trinidad Bay, California. *Trans Am Fish Soc* 143:543–551
- ✦ Kelly ELA, Cannon AL, Smith JE (2020) Environmental impacts and implications of tropical carrageenophyte seaweed farming. *Conserv Biol* 34:326–337
- ✦ Kingsford MJ, Choat JH (1985) The fauna associated with drift algae captured with a plankton-mesh purse seine net. *Limnol Oceanogr* 30:618–630
- ✦ Kingsford MJ, Milicich MJ (1987) Presettlement phase of *Parika scaber* (Pisces: Monacanthidae): a temperate reef fish. *Mar Ecol Prog Ser* 36:65–79
- Kohn PE (2011) The influence of habitat type on fish recruitment to standard monitoring units in Northern New Zealand. MSc Dissertation, The University of Auckland
- ✦ Kohn YY, Clements KD (2011) Pelagic larval duration and population connectivity in New Zealand triplefin fishes (Tripterygiidae). *Environ Biol Fishes* 91:275–286
- ✦ Lee S, Lee DK (2018) What is the proper way to apply the multiple comparison test? *Korean J Anesthesiol* 71:353–360
- ✦ Lefcheck JS, Hughes BB, Johnson AJ, Pfirrmann BW and others (2019) Are coastal habitats important nurseries? A meta-analysis. *Conserv Lett* 12:e12645
- ✦ McDermott CJ, Shima JS (2006) Ontogenetic shifts in microhabitat preference of the temperate reef fish *Forsterygion lapillum*: implications for population limitation. *Mar Ecol Prog Ser* 320:259–266
- McFarland WN, Brothers EB, Ogden JC, Shulman MJ, Birmingham EL, Kotchian-Prentiss NM (1985) Recruitment patterns in young French grunts, *Haemulon flavolineatum* (family Haemulidae), at St. Croix, Virgin Islands. *Fish Bull* 83:413–426
- ✦ McLeod I, Parsons D, Morrison M, Van Dijken S, Taylor R (2014) Mussel reefs on soft sediments: a severely reduced but important habitat for macroinvertebrates and fishes in New Zealand. *NZ J Mar Freshw Res* 48:48–59
- ✦ Morrisey DJ, Cole RG, Davey NK, Handley SJ, Bradley A, Brown SN, Madarasz AL (2006) Abundance and diversity of fish on mussel farms in New Zealand. *Aquaculture* 252:277–288
- Norrie C (2019) Quantifying population connectivity of marine larvae: hydrodynamic modelling and shell microchemistry methods to determine larval dispersal of *Perna canaliculus*. PhD dissertation, University of Auckland
- Oldman JW, Hong J, Stephens S, Broekhuizen N (2007) Verification of Firth of Thames hydrodynamic model. (No. 326.). Auckland Regional Council, Auckland
- ✦ Parsons D, Sim-Smith C, Cryer M, Francis M and others (2014) Snapper (*Chrysophrys auratus*): a review of life history and key vulnerabilities in New Zealand. *NZ J Mar Freshw Res* 48:256–283
- ✦ Parsons DM, Buckthought D, Edhouse S, Lohrer AM (2020) The paradox of the Hauraki Gulf snapper population: testing the nursery habitat concept. *PSZNI: Mar Ecol* 41: e12582
- Paulin CD, Roberts C (1992) The rock pool fishes of New Zealand: Te Ika Aaria O Aotearoa. Museum of New Zealand Te Papa Tongarewa, Wellington
- ✦ Powers MJ, Peterson CH, Summerson HC, Powers SP (2007) Macroalgal growth on bivalve aquaculture netting enhances nursery habitat for mobile invertebrates and juvenile fishes. *Mar Ecol Prog Ser* 339:109–122
- R Core Team (2021). R: a language and environment for statistical computing (version 4.1.0; R studio version 1.4.1106). R Foundation for Statistical Computing, Vienna
- ✦ Scariano SM, Davenport JM (1987) The effects of violations of independence assumptions in the one-way ANOVA. *Am Stat* 41:123–129
- ✦ Shelamoff V, Layton C, Tatsumi M, Cameron MJ, Edgar GJ, Johnson CR (2020) High kelp density attracts fishes except for recruiting cryptobenthic species. *Mar Environ Res* 161:105127
- ✦ Shima JS, Swearer SE (2009) Spatially variable larval histories may shape recruitment rates of a temperate reef fish. *Mar Ecol Prog Ser* 394:223–229
- ✦ Siddon EC, Siddon CE, Stekoll MS (2008) Community level effects of *Nereocystis luetkeana* in southeastern Alaska. *J Exp Mar Biol Ecol* 361:8–15
- ✦ Stenton-Dozey J, Broekhuizen N (2019) Provision of ecological and ecosystem services by mussel farming in the Marlborough Sounds. A literature review in context of the state of the environment pre- and post-mussel farming. Prepared for Marine Farming Association, National Institute of Water & Atmospheric Research, Christchurch,

https://www.marinefarming.co.nz/site_files/24792/upload_files/Fullreport_28.07.2021update.pdf?dl=1

- ✦ Swearer SE, Shima JS (2010) Regional variation in larval retention and dispersal drives recruitment patterns in a temperate reef fish. *Mar Ecol Prog Ser* 417:229–236
- ✦ Tallman JC, Forrester GE (2007) Oyster grow-out cages function as artificial reefs for temperate fishes. *Trans Am Fish Soc* 136:790–799
- ✦ Tano SA, Eggertsen M, Wikström SA, Berkström C, Buriyo AS, Halling C (2017) Tropical seaweed beds as important habitats for juvenile fish. *Mar Freshw Res* 68. doi:10.1071/MF16153
- ✦ Theuerkauf SJ, Barrett LT, Alleway HK, Costa-Pierce BA, St. Gelais A, Jones RC (2022) Habitat value of bivalve shellfish and seaweed aquaculture for fish and invertebrates: pathways, synthesis and next steps. *Rev Aquacult* 14:54–72
- ✦ Valle C, Bayle-Sempere JT, Dempster T, Sanchez-Jerez P, Giménez-Casalduero F (2007) Temporal variability of wild fish assemblages associated with a sea-cage fish farm in the south-western Mediterranean Sea. *Estuar Coast Shelf Sci* 72:299–307
- ✦ Valles H, Kramer DL, Hunte W (2006) A standard unit for monitoring recruitment of fishes to coral reef rubble. *J Exp Mar Biol Ecol* 336:171–183
- ✦ Valles H, Kramer DL, Hunte W (2008) Temporal and spatial patterns in the recruitment of coral-reef fishes in Barbados. *Mar Ecol Prog Ser* 363:257–272
- ✦ Willis TJ, Anderson MJ (2003) Structure of cryptic reef fish assemblages: relationships with habitat characteristics and predator density. *Mar Ecol Prog Ser* 257:209–221
- ✦ Wilson SK, Depczynski M, Holmes TH, Noble MM, Radford BT, Tinkler P, Fulton CJ (2017) Climatic conditions and nursery habitat quality provide indicators of reef fish recruitment strength. *Limnol Oceanogr* 62: 1868–1880
- ✦ Woods C, Floerl O, Hayden B (2012) Biofouling on Green-shell™ mussel (*Perna canaliculus*) farms: a preliminary assessment and potential implications for sustainable aquaculture practices. *Aquacult Int* 20:537–557

*Editorial responsibility: Tim Dempster,
Melbourne, Victoria, Australia;
Christine Paetzold, Oldendorf/Luhe, Germany
Reviewed by: G. Ozbay, K. Toledo-Guedes and
1 anonymous referee*

*Submitted: February 15, 2022
Accepted: February 8, 2023
Proofs received from author(s): March 15, 2023*