

Density-dependent habitat selection in marine flatfish: the dynamic role of ontogeny and temperature

Benjamin J. Laurel*, Allan W. Stoner, Thomas P. Hurst

Fisheries Behavioral Ecology Program, Alaska Fisheries Science Center, NOAA, Hatfield Marine Science Center, Newport, Oregon 97365, USA

ABSTRACT: Changes in habitat use with increasing conspecific density are well-documented, but such patterns are likely to be dynamic over the lifespan of the organism and responsive to changes in the environment. In the laboratory, we examined how habitat selection was mediated by ontogeny (6, 8 and 12 mo) and temperature (4 and 9°C) in 2 juvenile, marine flatfish species: Pacific halibut *Hippoglossus stenolepis* and northern rock sole *Lepidopsetta polyxystra*. In a set of initial trials at 9°C, groups of same-aged juvenile flatfish (6, 8 or 12 mo) of either halibut or rock sole were given the choice of 2 habitats—fine sand (preferred) and coarse gravel (unpreferred)—at 1 of 6 densities (0.4 to 12.2 fish m⁻²). A second set of trials was conducted at 4°C using 8 mo juvenile fish of both species over the same range of densities. At 9°C, density-dependent habitat selection was observed among all treatment groups. As juveniles increased in age in the 9°C treatments, both species began occupying the less-preferred gravel habitat at lower densities. However, at 4°C, density-dependent habitat selection varied between species. Sand habitat supported higher densities of juvenile Pacific halibut at 4°C whereas no change was observed in northern rock sole. Juvenile Pacific halibut activity was also lower than rock sole at 4°C, suggesting that competitive interactions (e.g. interference, territoriality etc.) and/or physiological demands of halibut is sufficiently reduced at this temperature to increase the carrying capacity of the preferred habitat. Together, these results indicate that temperature, ontogeny and density interact to yield unique habitat selection patterns in fish, mechanisms that may be important in area-abundance relationships.

KEY WORDS: Density-dependence · Habitat selection · Carrying capacity · Pacific halibut · Northern rock sole

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INTRODUCTION

Density-dependent habitat selection (DDHS) is an important component of the spatial dynamics of many organisms (Morris 2003). The concept that conspecific density influences habitat decision-making was first formalized by Fretwell & Lucas (1970) in the 'ideal free distribution' and is based on the assumption that a preferred habitat's fitness value (i.e. intrinsic suitability) is reduced at higher densities, such that secondary habitats, originally considered less suitable at low densities, increase in their relative value. Therefore spatial patterns in populations can be temporally dynamic through fluctuations in abundance without changes occurring in the characteristics or availability of habi-

tats (Kramer et al. 1997). Such principles form the basis from which conceptual and quantitative models of DDHS are derived.

DDHS models are particularly useful in describing spatial dynamics of marine fish species. Marine fish populations undergo large fluctuations in abundance, resulting from recruitment variability (e.g. Myers et al. 1997), fishing mortality (Fisher & Frank 2004) and latitudinal shifts in components of the population resulting from climate change (Perry et al. 2005). Consequently, the application of DDHS models to examine spatial patterns in marine fish population has received broad attention (Myers & Stokes 1989, MacCall 1990). The analyses used to describe DDHS are based on relationships between abundance and area occupied, the

*Email: ben.laurel@noaa.gov

assumption being that increasing population size results in increased use of marginal habitats distributed over a larger area (Gaston et al. 1997). In contrast, at low abundance, populations are concentrated in small areas of high quality habitat. Often the fish densities in these small, contracted areas are high enough to keep fishing profitable (Hutchings 1996), thereby creating a 'double jeopardy effect' as a higher proportion of the population is fished at lower population sizes without any increase in effort (Harley et al. 2001). Therefore, understanding the patterns and mechanisms of range contraction and expansion is a critical component of fisheries management and conservation.

Surprisingly few studies have explicitly examined DDHS as a mechanism in marine systems despite the implicit evidence revealed by area-abundance relationships. Although DDHS is often invoked as a mechanism of changing spatial pattern in marine fish populations, the measures of habitat suitability are often assumed, borrowed or ignored (e.g. Marshall & Frank 1995, Hutchings 1996, Blanchard et al. 2001). Habitat suitability is a dynamic measure mediated by behavior (Laurel et al. 2004), ontogeny (e.g. Livingston 1988) and the environment (e.g. Cunjak 1988) and its quantification is critical to the interpretation of area-abundance relationships in marine systems. Largely for these reasons, Gaston et al. (1997) conclude that DDHS is only one of several mechanisms by which changes in abundance can affect area of occupancy in a population. We should therefore be cautious in interpreting particular spatial patterns in marine systems as evidence of DDHS without additional explicit examinations of behavior, especially in situations where environmental conditions and regional age-structures of the population are integrated into a single, large-scale analysis, i.e. ocean-basin regions over multiple years using trawl-net survey data. There is a clear need for controlled, experimental studies to firstly determine the relevance of DDHS in spatial patterns in marine fish species and secondly to understand how such patterns vary among species, age and different environmental conditions.

Juvenile flatfish are ideal model marine species with which to examine DDHS. Flatfish experience an increase in density as they settle from the water column to a 2-dimensional demersal habitat, after which they demonstrate distinct preference for discrete habitats (Gibson 1994). These habitats are often particular sediments (Gibson & Robb 1992, Stoner & Ottmar 2003) or a combination of sediment and other habitat characteristics (e.g. emergent structures, depth, temperature; Pihl & van der Veer 1992, Jager et al. 1993, Abookire & Norcross 1998, Phelan et al. 2001, Goldberg et al. 2002). More importantly in the context of DDHS, these preferred habitats are constantly in a dynamic state of flux (Stoner et al. 2001) such that their

availability may be high in one year and almost absent in another (A. W. Stoner unpubl. data). Pacific halibut *Hippoglossus stenolepis* ('halibut' hereafter) and northern rock sole *Lepidopsetta polyxystra* ('rock sole' hereafter) are 2 commercially important species that co-occur in the Gulf of Alaska and are relatively well-studied in terms of their general distribution in the first year after settlement. Both species are found extensively in coastal nursery areas and have been shown to prefer small-grain sandy sediment (Norcross et al. 1999, Stoner & Abookire 2002, Stoner et al. 2006). Rock sole arrive at nursery grounds in June-July and settle at ~20 to 40 mm TL, whereas halibut arrive slightly later in early August and settle at larger sizes (Hurst unpubl. data). In general, these and other flatfish species show an ontogenetic shift in tolerance from fine to coarser sediment types, presumably because of an increased ability to bury in such substrate (Gibson & Robb 1992, Stoner & Ottmar 2003).

In this study, we explicitly measure DDHS in juvenile halibut and rock sole based on laboratory observations of distribution and behavior. We further examine whether DDHS is regulated by changes in ontogeny and temperature using ranges similar to those experienced by halibut and rock sole in their first year after settlement in the Gulf of Alaska. Specifically, we hypothesized that DDHS would result in increased use of marginal habitats at high fish density but that rates of expansion into those habitats would be species-, ontogen- and temperature-specific.

MATERIALS AND METHODS

Field collections and holding. Age-0 juvenile halibut (50 to 70 mm TL) and northern rock sole (20 to 40 mm TL) were collected from nearshore areas (7 to 20 m depth) around Kodiak Island, Alaska, in late summer 2004 and again in 2005. Fish were held for several days at the Alaska Fisheries Science Center (AFSC) Kodiak Laboratory, before being shipped overnight in insulated containers to the AFSC laboratory in Newport, Oregon. Fish were initially held in 64 × 45 × 23 cm holding tanks before being transferred to a series of 183 cm diameter round tanks for extended holding. Fish were held at densities of <2 fish m⁻² in the round tanks and fed daily a combination of thawed brine shrimp and commercial fish food (1 to 2 mm diameter pellets). However, during the experimental period, feeding was reduced to 3× weekly.

Experimental arena. Experimental work was conducted in 5 replicate circular arenas (1.83 m diameter × 0.75 m depth). Two habitats of equal area and shape (tank halves) were provided on each tank bottom: a fine sand (0.65 mm) and a coarse granule substrate

(2 to 4 mm). We assigned higher suitability to the sand habitat *a priori* based on previous sediment-size studies with these species (Stoner & Ottmar 2003). Each sediment type covered the tank bottom to a depth of 5 cm and the sediments were periodically cleaned and smoothed between trials. Indirect, incandescent lighting was set on a 12:12 h light:dark photoperiod to simulate day-night conditions found in the Gulf of Alaska during Sep-Oct. Light levels at the surface of the arena averaged 5.8×10^{-1} and 6.0×10^{-6} $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ during light and dark periods respectively.

A video camera was mounted above each tank to monitor the activity of fish. Video recording and tank monitoring was conducted in a separate control room which had the capabilities of simultaneously recording video from all 5 experimental tanks. Cameras were focused on the substrate field of each tank to maximize the likelihood of viewing cryptically colored fish along the bottom. Fish that were higher in the water column (i.e. at the air-water interface) were plainly visible because of their high contrast, even though they were not entirely in focus.

Density experiment. Three age groups of fish were used in experiments: 6, 8 & 12 mo (Table 1). Sizes (mm TL \pm SD) of these age groups differed slightly between halibut (6 mo: 78.5 ± 8.7 ; 8 mo: 98.6 ± 10.7 ; 12 mo: 133.6 ± 21.4) and rock sole (6 mo: 46.0 ± 4.6 ; 8 mo: 64.7 ± 7.4 ; 12 mo: 110.7 ± 13.4) due to larger size-at-settlement and faster growth rates of Pacific halibut during their first year (Hurst unpubl. data). Six densities of each species and age combination were used: 0.4, 0.8, 1.5, 3.0, 6.1 and 12.2 fish m^{-2} , corresponding to 1, 2, 4, 8, 16 and 32 fish per tank. Some of the densities used in this experiment far exceed those observed naturally for YOY rock sole and halibut on nursery grounds (0.1 to 1.5 fish m^{-2} ; Stoner et al. 2006). However, we purposely included higher densities to determine if and when the mechanisms of DDHS begin and plateau. The experimental tanks were maintained at $9 \pm 0.8^\circ\text{C}$, falling well within the range of temperatures (4 to 11°C) experienced by these flatfish species in nursery areas around Kodiak Alaska (Ryer et al. 2007). We withheld food from any treatment group for a 24 h period prior to the beginning of any trial to insure that the fish would be sufficiently active to explore the different substrata (see Stoner & Ottmar 2003)

We introduced fish to the center of tanks in removable holding rings at 1400. After ca. 30 s, trials were initiated by removing center rings and allowing fish full access to the tank bottom. Trials were run for a period of 24 h (12 h light; 12 h dark), after which a partition was quickly lowered to divide the substrates and prevent further movement between habitat types. The partition drop took 2 to 3 s and generally caused fish to bury in place, but in 2 instances trials were re-run

because fish crossed habitats during the procedure. We then collected, counted and measured fish to the nearest mm TL before returning them to a secondary holding tank. Replicate trials were interspersed among tanks such that every treatment combination was conducted at least once in each of the 5 experimental set-ups. Each treatment combination (density \times age \times species) was replicated 5 times with the exception of low density treatments (0.4 and 0.8 fish m^{-2}), which were replicated 7 to 10 times to address the issues of high variance associated with low numbers of fish. Trials were run daily, after which fish were returned to a recovery tank for a 1 to 2 wk period. Following this recovery period, fish were either reused for additional trials for that age group or used in cold temperature trials 3 mo later (see below). However, the probability of reselecting the same group of fish for any trial never exceeded our statistical alpha of 0.05.

We conducted a second set of low-temperature trials ($4 \pm 0.7^\circ\text{C}$) using 6 mo old halibut and rock sole. Fish were acclimated to 4°C at 1°C d^{-1} in separate holding tanks and held there for a 7 wk period prior to being used for any trial. We used identical protocols and replication for the experiments conducted at 4°C as those described for 9°C .

The effects of temperature on activity levels of fish were measured on a per capita basis. We videotaped 8 mo old halibut and rock sole at 4 and 9°C for 5 min periods at 4 stages during the trial (0.25, 3.5, 18.5 and 23.5 h), corresponding to 14:15, 17:30, 08:30 and 13:30 h, respectively. Videotapes of trials were archived and subsequently uploaded to a computer for image analysis. Activity was analyzed by overlaying a grid which divided the tank into 4 equal radial sections. One line separated habitats and a perpendicular line divided each habitat in half. The degree of line crossing by fish was used as an index of activity for each treatment. The amount of total line crossing was then divided by the total number of fish in that treatment to generate a per capita activity measure. Movement was mostly saltatory and could be quantified by scanning the entire field of view for activity. However, at higher densities (i.e. >8 fish per tank), single line sections were examined separately to ensure all activity was quantified in the tank.

Statistical analyses. Determination of whether fish used habitat in a density-dependent manner was initially examined by plotting the percentage of fish occupying gravel habitat against total fish density in the trial. A significant relationship between these variables of any kind (e.g. linear, asymptotic etc.) indicates DDHS. If DDHS was detected, we used General Linear Models (GLMs) to determine whether species and ontogeny significantly affected such relationships. However, the use of only 1 age group at cold tempera-

tures did not permit analysis of DDHS in a single, fullfactorial model. Therefore, multiple GLMs were run on subsets of the data. Two GLMs used 'fish density' as a covariate to examine the effects of (1) 'species' and 'age' and (2) 'species' and 'temperature' on the proportion of fish in gravel habitat. 'Fish density' was used as a covariate since DDHS was already established from the initial analysis. We constructed an additional GLM to correct for size-at-age differences within and between flatfish species. Halibut are larger than rock sole at a given age and it was uncertain whether species effects were simply driven by size differences. Individual weights were calculated using length-weight conversions for the size ranges of fish used during the experiment (T. P. Hurst unpubl. data). The size-corrected model used 'total biomass' as a covariate (i.e. total fish biomass in the arena) with 'density' and 'species' as explanatory variables. The biomass of fish in gravel was used as the response variable. Interaction terms were added between 'species' and 'density' as well as between 'density' and 'total biomass.' Multiple regression was additionally used to determine the significance and relative amount of variance explained by total 'fish density' and 'total biomass' on gravel habitat use (biomass). Changes in overall per capita activity level were examined using 'species' and 'temperature' as explanatory variables and 'fish density' as a covariate in a GLM.

In most instances, data were $\ln(y+10)$ transformed prior to statistical analysis, in order to meet the assumptions of normality. Residuals from each statistical test were subsequently examined for homogeneity to assure the data met such assumptions. However, if data could not be successfully transformed, new p-values were generated from randomization tests (Manly

Table 1. GLM results for the effect of age (6, 8 and 12 mo) and species (halibut and rock sole) on the proportion of fish in gravel habitat at 9°C

Source	SS	df	MS	F-ratio	p
Age	11.44	2	5.72	6.73	0.002
Species	5.39	1	5.39	6.34	0.013
Age × Species	1.871	2	0.936	1.10	0.335
Density	321.06	1	321.06	377.68	<0.001
Error	159.82	193	0.85		

1991). This was done by randomizing the dataset 5000 times while holding the explanatory variables constant. New p-values were calculated by the proportion of randomizations with *F*-ratios greater than or equal to the observed *F*-ratio.

RESULTS

Both flatfish species spilled over into gravel habitat at higher rates with increasing density and age, therefore providing evidence of DDHS (Fig. 1). Results from the GLM also indicated that DDHS was age-dependent for both halibut and rock sole (Table 1). Higher rates of gravel habitat use occurred in halibut at a given age, but this was possibly due to a larger size-at-age in juvenile halibut. Using a GLM that standardized for these growth differences (i.e. using tank biomass as a covariate) indicated rock sole used gravel habitat more readily at a given size than halibut ($F_{1,237} = 17.54$, $p < 0.001$). In 12 mo old rock sole, there was also a significant difference in size between fish occupying gravel and sand at the end of each trial (i.e. larger fish occupied gravel habitat) but these differences were not observed in any other age groups for either species (Table 2).

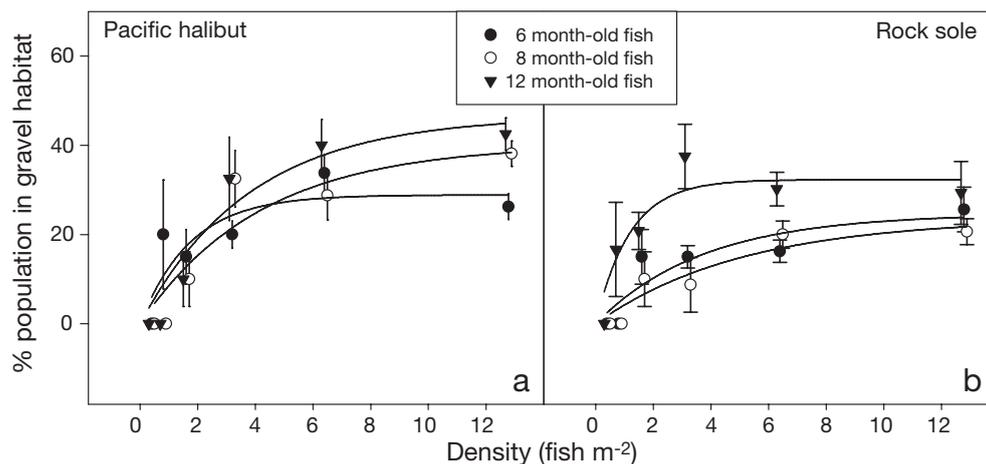


Fig. 1. Increased fish density and age result in proportionally higher use of unpreferred gravel over preferred sand habitat: (a) halibut, (b) rock sole, at varying ontogenetic stages (6, 8 and 12 mo old) and densities. Points: 5 to 10 replicates \pm 1 SE

Table 2. Summary of mean sizes (± 1 SE) of juvenile flatfish age groups following density-dependent habitat selection, i.e. size in sand or gravel. *Significant effect in size difference of fish between sand and gravel habitats ($p < 0.008$)

Age (mo)	Temp. (°C)	Overall size (n = 310–332)	Size in sand (n = 192–275)	Size in gravel (n = 34–120)
Halibut				
6	9	78.5 \pm 0.5	78.7 \pm 0.6	77.9 \pm 0.9
8		98.6 \pm 0.6	98.9 \pm 0.8	98.0 \pm 1.0
12		133.6 \pm 1.3	134.8 \pm 1.6	130.8 \pm 2.3
8	4	89.0 \pm 0.6	88.8 \pm 0.6	90.9 \pm 2.5
Rock sole				
6	9	46.0 \pm 0.3	46.0 \pm 0.3	46.0 \pm 0.5
8		64.7 \pm 0.4	64.7 \pm 0.5	64.9 \pm 1.2
12		110.7 \pm 0.7	109.3 \pm 0.9	113.3 \pm 1.1*
8	4	65.5 \pm 0.5	65.3 \pm 0.6	66.7 \pm 1.3

A significant interaction was found between biomass and density ($F_{5,237} = 30.14$, $p < 0.001$) on habitat use in both species (Fig. 2). The multiple regression, using tank density and total fish biomass in the tank as regressors, resulted in good fits for both halibut ($R^2_{\text{adj}} = 0.75$; $F_{2,97} = 143.54$, $p < 0.001$) and rock sole ($R^2_{\text{adj}} = 0.74$; $F_{2,97} = 142.36$, $p < 0.001$). Individually, both of the model components 'biomass' and 'density' significantly contributed to this relationship for halibut (biomass $t_{97} = 5.23$, $p < 0.001$; density $t_{97} = 7.46$, $p < 0.001$) and rock sole (biomass $t_{97} = 10.59$, $p < 0.001$; density $t_{97} = 2.00$, $p = 0.048$). However, an examination of the standardized regression coefficients from the multiple regression indicated that biomass was a better predictor for use of gravel habitat for rock sole (biomass = 0.758, density = 0.143) whereas density was a better indicator for halibut (biomass = 0.386, density = 0.551).

The analysis of thermal effects in DDHS revealed a significant interaction between species and temperature ($F_{1,115} = 7.536$, $p = 0.007$). Analyzing by species, halibut use of gravel habitat was significantly reduced at 4°C whereas no effect was observed for rock sole at those temperatures (Table 3, Fig. 3).

Table 3. GLM results for the effect of temperature (4 and 9°C) on proportion of halibut and rock sole in gravel habitat

Source	SS	df	MS	F-ratio	p
Halibut					
Temperature	2190.10	1	2190.10	18.78	<0.001
Density	4790.68	1	4790.68	41.09	<0.001
Error	6646.17	57	116.60		
Rock sole					
Temperature	19.69	1	19.69	0.16	0.689
Density	3042.54	1	3042.54	24.97	<0.001
Error	6946.07	57	121.86		

Overall per capita activity increased with increasing density for both flatfish species at 9°C (Fig. 4), and much of the activity at higher densities occurred in the water column rather than the sediment surface. We also noticed that relatively less activity occurred towards the end of the experiment, i.e. 23.5 h. However, the GLM indicated a significant interaction between species and temperature ($F_{1,347} = 16.62$; $p < 0.001$), the consequence of little to no activity observed at 4°C in juvenile halibut (Fig. 4). For species examined separately, the analysis indicated a significantly lower activity rate at 4°C for both halibut ($F_{1,172} = 29.75$; $p < 0.001$) and rock sole ($F_{1,172} = 10.16$, $p = 0.002$).

DISCUSSION

Density-dependent habitat selection

Juvenile halibut and rock sole increased their proportional use of marginal habitat (i.e. gravel) with increasing conspecific density, a pattern that is consistent with other taxa such as mammals (e.g. Meisser et al. 1990), insects (e.g. Krasnov et al. 2002), birds (Jensen & Cully 2005) and reptiles (e.g. Massot et al. 1994). To date there have been few explicit tests of DDHS in marine fish species (juvenile pollock *Pollock virens*, Rangley & Kramer 1998; juvenile cod *Gadus morhua* and *G. ogac*, Laurel et al. 2004; gag *Myxeroperca microlepis*, Lindberg et al. 2006) despite the multitude of studies describing area-abundance relationships in marine environments (see Shepherd & Litvak 2004 for review). In flatfish, fine grained sand substrates are preferred over relatively coarser grained substrates (Stoner & Ottmar 2003), most likely because flatfish are more capable of burying in such habitats as a means of reducing predation (Ryer et al. 2004; although see Manderson et al. 2000) or finding food (Livingston 1987). The increased use of coarse grained habitats at higher densities suggests the fitness benefits of sand (e.g. anti-predator or foraging) may be compromised at such densities, although this has yet to be examined explicitly.

Given the strong DDHS patterns observed in the laboratory for both species, it is clear that field studies will need to determine the extent to which such processes occur and contribute to larger scale spatial patterns. The settlement period in halibut and rock sole can be protracted (~2 mo, T. P. Hurst unpubl. data), such that late arriving settlers may use a broader range of habitats because preferred habitats

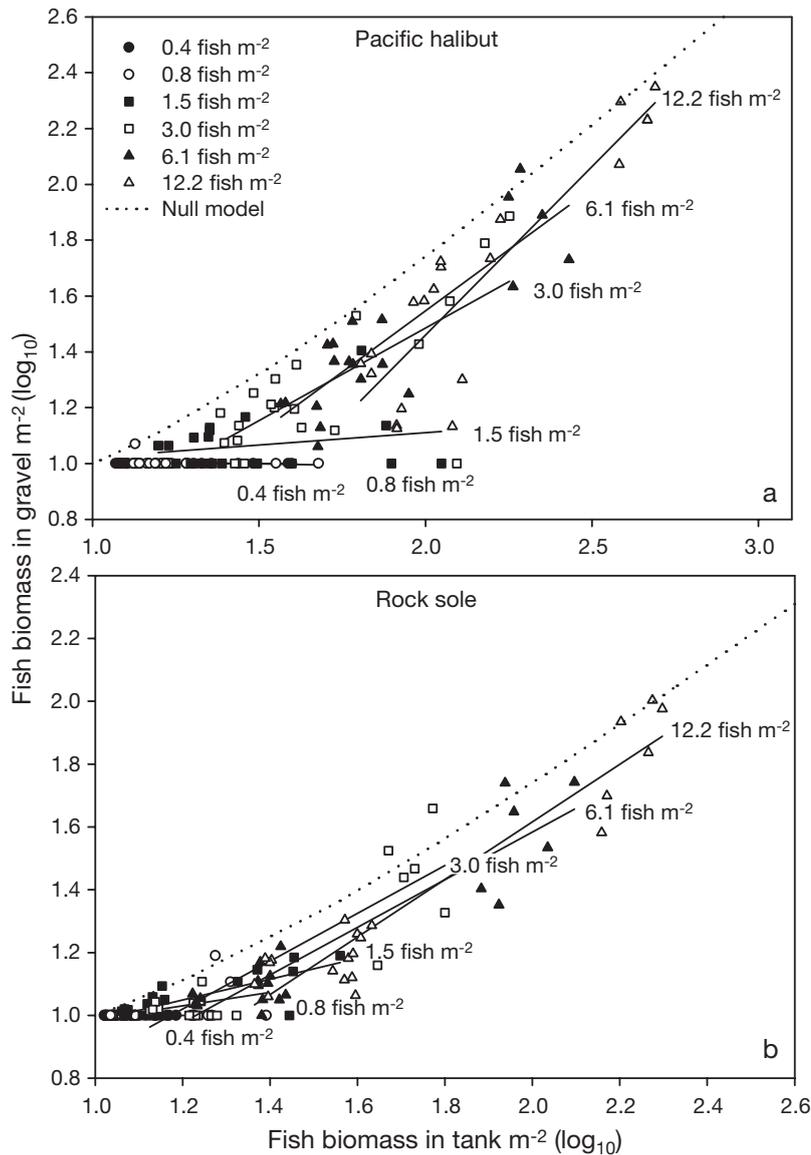


Fig. 2. Combined effects of density and ontogeny (i.e. fish biomass) on habitat use in (a) halibut and (b) rock sole. Slopes indicate rates of gravel habitat use with ontogeny at a given density. Null model (i.e. no habitat preference) represented by single dotted line

are saturated with conspecifics. Space-limitation at the time of settlement is well-documented in reef environments and can lead to negative density-dependent growth, condition and survival (Sweatman 1983, Stimson 1990, Schmitt & Holbrook 1996, Holbrook & Schmitt 2002, Osenberg et al. 2002). Such processes may also occur in flatfish. Nash & Geffen (2000) suggest that space-limitation in Age 0 juvenile plaice *Pleuronectes platessa* in nursery areas is the principle determinant of year-class strength in the Irish Sea. Unfortunately, the absence of fisheries survey data for the age classes of the species examined in this study precludes a similar analysis.

With the exception of halibut at 4°C, activity rates increased with density among treatment combinations. Juvenile flatfish often demonstrate avoidance response to other approaching fish (Ryer et al. 2004), and it is possible that the flatfish observed in this study move in order to simply avoid such interactions. In no instances did we observe territoriality or other agonistic behavior (e.g. fin nipping, chasing, etc.), but given the scale of the experimental apparatus it is possible that such behavior was too subtle to quantify from video. Regardless, the reduction in activity towards the end of a trial suggests that the distribution of fish among habitats had become relatively stable.

The interactive effects of ontogeny and density were important predictors of habitat use in both species. As expected, increasing fish biomass in the tank corresponded with an increase in fish biomass in the gravel habitat. However, density changed the slope of this relationship. At low densities (i.e. <1 fish m⁻²) there was very little effect of biomass (i.e. shallow slope), but as densities increased in the tank, so too did the sensitivity of fish to biomass. At the highest densities, the slope of the relationship resembled the null model, i.e. an even distribution between both sand and gravel. However, the multiple regression indicated halibut were slightly more sensitive to the effects of density whereas habitat use by rock sole was better explained by biomass. These differences may be a consequence of the higher observed activity levels in halibut. At 9°C, halibut line-crossing activity was nearly 2× greater than rock sole at higher densities. Higher activity levels in halibut have also been noted in other comparative flatfish studies (Ryer et al. 2004). Rock sole are considered risk-averse and have generally low activity whereas halibut are active, pursuing more motile prey, and only reduce activity in the presence of a predator, i.e. are more risk-sensitive (Lemke & Ryer 2006). Juvenile halibut have been shown to have greater preference for emergent structures (Stoner & Titgen 2003, Ryer et al. 2004) as well as a greater tolerance for occupying large grained sediments (Stoner & Ottmar 2003) compared to rock sole. We suspect that these behavioural dissimi-

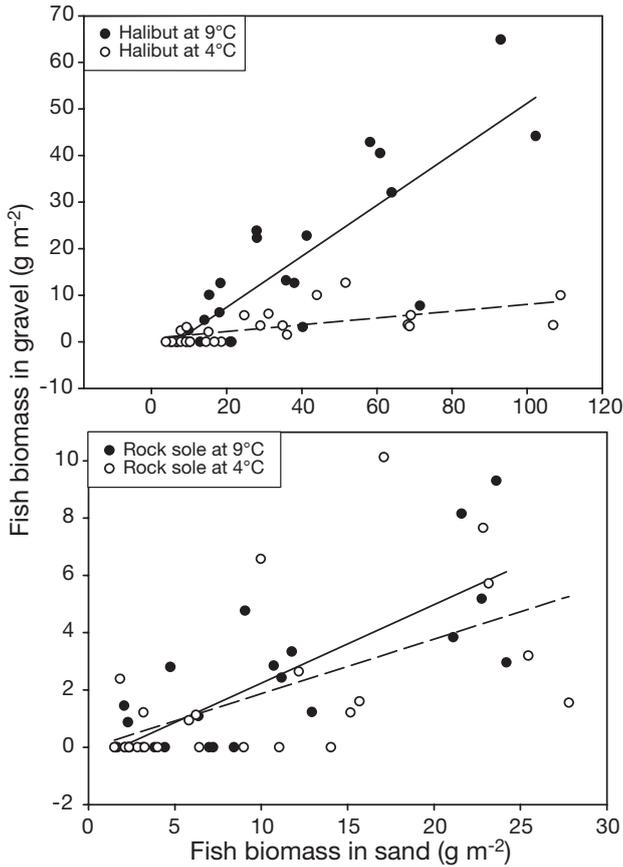


Fig. 3. Lower temperatures (4°C) reduce density-dependent habitat selection in juvenile halibut but not in rock sole. Densities of fish are converted to biomass to standardize for size-at-age differences between and within species. Points represent biomass distribution of varying densities (0.4 to 12.2 fish m⁻²) of 8 mo old juvenile fish in sand and gravel habitat following a 24 h trial

larities may have contributed to the small differences in explained variance in the multiple regression.

Ontogeny and temperature effects

Our study demonstrates that DDHS changes rapidly during the early ontogeny of marine fish, largely as a result of high growth rates during this period. Large juveniles more readily occupied sand habitat at lower densities. However, it is difficult to determine the degree to which such changes in DDHS were size-dependent or the result of changes in intrinsic habitat suitability. For example, ontogenetic changes in habitat preference occur as fish move from nursery habitats to sub-adult and juvenile habitats (e.g. Harden-Jones 1968, Livingston 1988). Rock sole also show greater preference for structured habitat in their second year of development (Ryer et al. 2007), and generally, flat-

fish occupy a broader range of substrate types as they grow (Gibson & Robb 1992, Stoner & Ottmar 2003). However, given the fact that biomass explained a large amount of variance when all ontogenetic stages were combined, we suspect that the trends observed in this study were not entirely the result of increased tolerance to coarse grained substrates. Regardless, given that DDHS is highly sensitive to ontogenetic change, we recommend that future studies analyze abundance-area relationships by year class (e.g. Blanchard et al. 2005) or at finer scales (e.g. quarterly) during early life history stages where growth rates are highest.

An alternative approach would be to collapse age classes into a single biomass measure, e.g. 'biomass'-dependent habitat selection. For example, the DDHS of 8 large (i.e. 12 mo old) rock sole closely resembled the DDHS of 32 small (i.e. 4 mo) rock sole. Biomass explained a high degree of variance in habitat use when 'biomass' and 'age' were examined simultaneously in the multiple regression, most likely because it is autocorrelated with age yet can account for size-at-age variation. Using biomass rather than density measures would be especially suitable in situations where partitioning the data into multiple age-groups is problematic.

The DDHS response of the 2 flatfish species differed markedly at 4°C, most likely stemming from differences in the thermal physiology of halibut and rock sole. In a separate growth study, halibut grew 48% faster than rock sole at warm (10°C) temperatures whereas rock sole grew 16% faster than halibut at cold (2°C) temperatures (Hurst & Abookire 2006). These

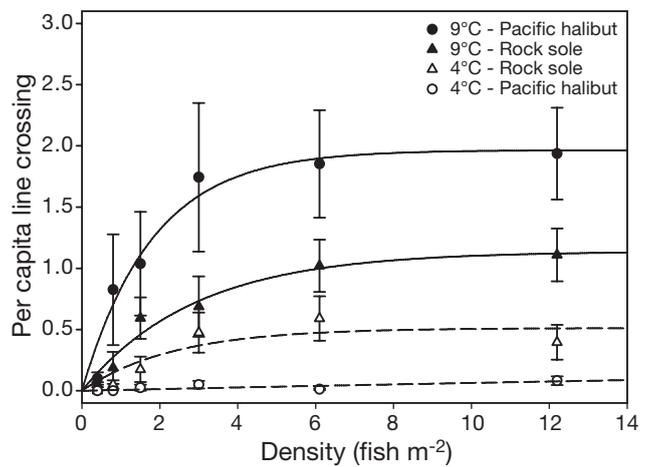


Fig. 4. Lower temperatures (4°C) reduce activity in Pacific halibut to higher extent than in northern rock sole at higher temperature (9°C). Activity levels are represented by line-crossing activity occurring at 5 min intervals at 0.25, 3.5, 18.5 and 23.5 h into a 24 h trial period. Points represent mean (n = 5) ± 1 SE

physiological differences most likely form the base mechanism by which DDHS varied between the species at warm and cold temperatures. Studies have shown that thermally induced spatial patterns are magnified in juveniles because they lack the ability to make large migrations to warmer water and/or do not require increased energetic intake for spring spawning (Olla et al. 1974, Parker 1990). However, adult fish also change their distribution in response to density and temperature. For example, Atlantic cod in the southern Gulf of St. Lawrence tend to occupy colder water in years of high abundance, possibly as a means of reducing competition for food (Swain & Kramer 1995). Fish often use cold water habitats to enhance the efficiency of digestion and energy utilization of food (Hughes & Grand 2000). Alternatively, low temperatures may differentially affect the susceptibility to predation. For example, overwintering fish seek alternative habitats (e.g. rock crevices, substrates) where predation can be reduced, even at high costs of successfully acquiring food (e.g. Olla et al. 1974, Cunjak 1988, Parker 1990, Griffith & Smith 1993). It is therefore reasonable to predict that temperature will change the 'carrying capacity' of a particular habitat depending on how the organism's physiology changes.

Temperature can have profound effects on the distribution of fish populations (e.g. Perry et al. 2005), and thermal habitats are sometimes preferred over patches with higher abundances of food and energetic gain (Garner et al. 1998, Wildhaber 2001). Blanchard et al. (2005) examined DDHS in Atlantic cod using temperature as a direct measure of habitat suitability (i.e. optimal temperature for growth), but these patterns were examined independently of other habitat variables. From our study it is clear that temperature can mediate habitat suitability and should be incorporated into DDHS models, especially at scales which encompass a range of temperatures. Otherwise temperature has the potential to magnify or mask area-abundance relationships, most notably when temperature covaries across the same spatial gradient in which distribution is measured (Shepherd & Litvak 2004).

Relevance to management and conservation

There is an increasing emphasis on understanding essential fish habitats (EFH) and our data, along with a growing body of studies, suggests that we need to incorporate dynamic measures of habitat suitability into habitat modeling (e.g. Manderson et al. 2002, Stoner 2003). The recent mandates in the USA to better integrate habitat and fisheries management (e.g. EFH under the National Habitat Plan; Schmitt 1999)

has placed greater pressure on fisheries scientists to understand how habitat influences the vital rates and productivity of fish populations. In addition, the increasing interest in using spatial management strategies such as marine protected areas (MPAs) has also made it important to understand how marine fish spillover from reserves to repopulate neighbouring regions outside the reserve (Lawton 1993, NRC 2000). DDHS is therefore especially important to management today.

To date, the application of DDHS theory has been largely limited to large-scale studies examining range contraction and expansion through population fluctuations. Abundance-area relationships have been detected for numerous marine species, including Atlantic cod (Swain & Wade 2003, Blanchard et al. 2005), herring *Clupea harengus* (Ulltang 1980), yellowtail flounder *Limanda ferruginea* (Brodie et al. 1998, Simpson & Walsh 2004) and several flatfish species in the eastern Bering Sea (McConnaughey 1995). In contrast, no such relationship has been detected in other species e.g. English sole *Parophrys vetulus* (Sampson 1994) and rock sole (McConnaughey 1995). Of the 32 stocks examined on the Scotian shelf, only half demonstrated some significant relationship between population abundance and areal extent of distribution (Fisher & Frank 2004). The inconsistent trends among species may be more a consequence of scale rather than behavioural differences. In the laboratory, movement between habitats is unrestricted, but may be restricted in the field if (1) distances separating those habitats are too large and/or the costs of movement are too high (Tyler & Gilliam 1995), (2) physical barriers or predators separate those habitats (Kennedy & Gray 1997) or knowledge of alternative, more 'ideal' habitats is absent (Milinski 1994). Shepherd & Litvak (2004) also note that patterns resembling DDHS can emerge in large scale studies of marine fish populations through spatially autocorrelated changes in density-independent factors (see Gaston et al. 1997 for review). We are therefore uncertain as to how behavioral patterns observed in the laboratory translate to large scale patterns of distribution in these species. MacCall (1990) suggested that marine fish move along habitat preference gradients, offering a mechanism by which habitat selection occurs at scales larger than their perceptual range of the individual. However, it is recognized that the assumptions of the ideal free distribution and consequently DDHS are violated at the largest scales (Lima & Zollner 1996). Therefore, the DDHS observed in this study, and the secondary roles of temperature and ontogeny, may be most applicable to localized areas (e.g. embayments, nursery areas etc.) rather than cross-shelf or ocean basin regions of the entire managed population(s).

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