

REVIEW PAPER

Role of habitat in mediating mortality during the post-settlement transition phase of temperate marine fishes

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(Received 26 October 2006, Accepted 20 December 2006)

The transition phase describes a distinct post-settlement stage associated with the recruitment to benthic habitats by pelagic life stages. The habitat shift is often accompanied by feeding shifts and metamorphosis from larval to juvenile phases. Density-dependent settlement, growth and mortality are often the major factors controlling recruitment success of this phase. Habitat use also becomes more pronounced after settlement. The role of habitat-mediated post-settlement mortality is elucidated by focusing on the early life history of Atlantic cod (*Gadus morhua*) and cunner (*Tautoglabrus adspersus*) in the north-west Atlantic. In these species, settlement can occur over all bottom types, but habitat-specific differences in post-settlement mortality rates combined with size and priority at settlement effects on growth and survival determine recruitment and eventual year-class strength. These results and those from other temperate marine fish species along with work on tropical reef species emphasize the generality of habitat-based density-dependent mortality during the transition phase and its potential for population regulation. These results have implications for fisheries management and can be used to outline a procedure to assist managers in identifying and managing essential transitional habitats including the potential role of marine protected areas in habitat conservation.

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Key words: Atlantic cod; cunner; habitat; post-settlement mortality; predation; transition phase.

INTRODUCTION

Teleost fishes are speciose and exhibit complex life histories, which are generally defined by external fertilization, high fecundity, small offspring size and little parental care. In contrast to freshwater fish species, marine fish species generally produce smaller pelagic eggs, and as a consequence few species exhibit parental care (only 16% of marine families compared with 60% in fresh water) (Freedman & Noakes, 2002). The combination of small offspring size (and lack of parental care) leads to high fecundities, high mortality rates,

increased rates of dispersal and limited control over habitat choice at the larval stage. Although recent work in coral reef species has shown that pelagic juveniles can swim directionally towards inshore nursery areas (Leis & McCormick, 2002), most other species of pelagic larvae and juveniles are considered to be passive drifters in the plankton and thus relatively unselective of habitat. Density-independent factors are thought to control the success of the early life-history stages (Hixon & Webster, 2002). Many researchers have concluded that year-class strength of marine fishes is set during this 'critical period' when mortality rates are very high (Hjort, 1914; Marr, 1956; Cushing, 1969, 1975; May, 1974; Houde, 1987; Beyer, 1989; Brander & Hurley, 1992).

THE TRANSITION PHASE

The term 'transition phase' describes a distinct post-settlement stage associated with the recruitment to benthic habitats by pelagic life stages (Kaufman *et al.*, 1992). The habitat shift is often accompanied by feeding shifts and metamorphosis from larval to juvenile phases. Kaufman *et al.* (1992) proposed that the post-settlement transitional phase is a complex and widespread phenomenon in coral reef fishes and that it may determine future population structure. Density-dependent settlement, growth and mortality are probably the major factors controlling recruitment variability and success of this phase, and many have argued that the critical period occurs in the post-larval or juvenile phase rather than the larval phase (Sissenwine, 1984; Peterman *et al.*, 1988; Hollowed & Bailey, 1989; Wooster & Bailey, 1989; Bailey & Spring, 1992; Beverton & Iles, 1992; Bradford, 1992; Campana, 1996; Bradford & Cabana, 1997; Van der Veer & Leggett, 2005). Sissenwine (1984) concluded that the relative importance of specific life stages in determining future year-class strength depends on their duration and the respective mortality rates experienced during each stage as well as the scale at which data are gathered.

Leis (1991) suggests that most coral reef fish species are flexible with respect to the length of larval life, competency to settle and whether settlement occurs before or after metamorphosis to the juvenile stage. He also states that the transition from the pelagic environment to the reef environment is probably dangerous for various reasons. First, the settler must travel through the 'wall of mouths' that surrounds many reefs. Second, the settler, presumably being well adapted both morphologically and behaviourally to a pelagic lifestyle, must quickly become adapted to a reef environment. The transition phase is, therefore, a highly vulnerable period for reef animals and may lead to the evolution of behavioural flexibility (Stimson, 1990). Although it is not completely clear how most species cope with such a transition, there are a few examples of behaviours that seemingly have evolved as a response to high predation. These behaviours include burying in sand (Victor, 1983), settlement into intermediate habitats, forming schools (Breitburg, 1989) and settling into corals (Colin, 1975). The mode of attack, capture and ingestion of prey are also likely to change as the spectrum and habits of potential prey widen and differ from those in the plankton. However, the success of the transition phase is also partially dependent on the prior feeding history during the pelagic phase (McCormick & Molony, 1992).

Habitat use also becomes more pronounced after settlement, during which early benthic phases of fishes and invertebrates exhibit their narrowest and most selective habitat preferences (Langton *et al.*, 1996) with important consequences for recruitment. For example, natural selection for use of restricted feeding habits and predation risk taking by newly settled juvenile fishes can lead to recruitment limitation as a consequence of strong density-dependent mortality (Walters & Juanes, 1993). Much of the post-settlement mortality is attributed to predation (Steele & Forrester, 2002; Doherty *et al.*, 2004) and is often mediated by habitat complexity (Beukers & Jones, 1997).

The importance of habitat in mediating mortality during the transitional phase has not been broadly recognized in marine fishes, particularly in temperate waters (but see Hixon & Jones, 2005; Johnson, 2006*a, b*). Identification of such habitats is critical if one is to delineate and conserve essential fish habitat (EFH) for these species. EFH is defined as 'those waters and substrate necessary to fish for spawning, breeding, feeding or growth to maturity' (USDOC, 1996). After passage of the Sustainable Fisheries Act (SFA) in the United States in 1996, identification and description of EFH for more than 700 federally managed fish stocks became required as a way to protect and conserve the habitat of marine, estuarine and anadromous fishes (Schmitten, 1999). Yet, for many species the functional dynamics of habitat associations, particularly for juvenile stages, are not yet understood (Able, 1999; Able *et al.*, 2005).

The present review examines the transitional phase of two north-west Atlantic marine fish species Atlantic cod (*Gadus morhua* L.) and cunner [*Tautoglabrus adspersus* (Walbaum)], and highlights the importance of habitat use for density-dependent mortality during this early phase of the life history. These two species, one commercially important and the other not, have been among the most studied Atlantic temperate fishes with respect to habitat use during the transitional phase and thus provide valuable case studies for generalization. The widespread generality of habitat-mediated post-settlement mortality and its potential as a regulatory process is sought by briefly examining results of studies using other temperate and tropical reef fishes. The results are then extended to consider their relevance for definitions and management of EFH.

ATLANTIC COD

Cod undergo a series of pelagic stages from egg to larvae to juveniles. Eggs and larvae primarily drift along predominant currents to nursery areas. Larvae are found in relatively broad (chemically) but simple (physically) pelagic habitats with little habitat choice. Parental provisioning is limited to energy contained in yolk sacs, and as is the case with most marine fish species, no direct parental care is offered. However, some important indirect and maternal effects have been identified (Chambers & Waiwood, 1996; Marteinsdottir & Steinarsson, 1998; Cardinale & Arrhenius, 2000; Vallin & Nissling, 2000; Berkeley *et al.*, 2004). Adults spawn in particular locations and at specific times to presumably maximize larval survival and the probability of reaching juvenile nurseries. The match-mismatch hypothesis has outlined how the interaction between timing of spawning and food dynamics can substantially regulate

survival in cod (Beaugrand *et al.*, 2003) and haddock (*Melanogrammus aeglefinus* L.) (Platt *et al.*, 2003). Studies on many other species (including cod) have suggested that altered oceanographic conditions (as might be expected from climate change) can alter migration routes and thereby affect spawning location and timing (Sims *et al.*, 2001; Walther *et al.*, 2002; Beaugrand *et al.*, 2003; Juanes *et al.*, 2004).

Larvae undergo metamorphosis to the pelagic juvenile phase at *c.* 12 mm and settle to bottom habitats at sizes ranging from 25 to 80 mm, and undergo a shift from pelagic to benthic prey (Lomond *et al.*, 1998). This broad range of settlement sizes is geographically variable and is apparently due, in part, to different definitions of 'settlement'. This lack of consensus on the definition of settlement has led to a debate as to whether the process is gradual or abrupt depending on whether diet, distribution or physiology is focused on (see review in Gorman, 2004). Habitat use at the transitional phase from pelagic to benthic habitats narrows towards complex bottom habitats (primarily large gravel and cobble) and selective use. As cod grow and mature, habitat use broadens in depth and habitat complexity (Langton *et al.*, 1996).

Cod recruitment, size structure and survivorship are probably a function of habitat-based variation in predation and vulnerability immediately after settlement. Tupper & Boutilier (1995a) demonstrated that habitat-specific differences in predation risk could account for post-settlement distribution. In their system, cod settled equally over four different habitats (reef, cobble, seagrass and sand), but after a few days densities were highest in the most complex (defined by substratum rugosity) habitats (reef and cobble) and least dense in sand, with seagrass containing intermediate densities with a strong statistical relationship between post-settlement survival and substratum rugosity, suggesting competition for refuge sites. However, they also found that efficiency of the main cottid predators (measured as capture success) decreased with increasing habitat complexity, which suggested that in addition to potential competition for space, differential rates of survival might also be due to habitat-based differences in predation mortality. As might be expected, young-of-year cod select more complex habitats when in the presence of predators (Gotceitas & Brown, 1993). Other studies examining field distributions of age 0 cod have found that small cod were most abundant in shallow (<10 m) vegetated sites particularly during the day (Grant & Brown, 1998a; Linehan *et al.*, 2001), and in the laboratory, habitat utilization has been shown to be less selective at night probably as a response to reduced predation (Borg *et al.*, 1997). A field manipulation study using tethered cod as prey, showed that age 0 cod mortality rates increased with depth, were higher during the day and in unvegetated habitats, and mean predator size also increased with depth suggesting that the observed distribution patterns were antipredator behaviour responses to habitat-based mortality patterns in juvenile cod (Linehan *et al.*, 2001). A further large-scale habitat manipulation showed that settling cod can respond to such changes; cod abundance increased in sites enhanced by addition of simulated eelgrass and declined in sites where eelgrass had been removed (Laurel *et al.*, 2003). These results suggest that in contrast to Tupper & Boutilier's (1995a) results, when examined at a larger scale, cod may select complex habitats to settle in and in some situations aggregate after settlement. The differing results may be

due to density-dependent effects; in years of large abundance, preferred habitats may be saturated leading to indiscriminant settlement or dispersal (Grant & Brown, 1998*b*). Large abundances of conspecifics also leads to habitat-use behaviour modification perhaps as a way to exploit lower quality habitat (sand) when high-quality (eelgrass) habitat is filled (Grant & Brown, 1998*b*; Laurel *et al.*, 2004). Furthermore, juvenile cod form tighter aggregations when over sand compared with eelgrass perhaps as a response to increased predation risk in sand habitats (Laurel *et al.*, 2004). These results suggest that habitat suitability may be dynamic and a function of changes in density of recently settled fish.

A rapid transition to benthic habitats would accelerate use of the structurally more complex bottom habitats as individuals develop their cryptic colouration. Clearly the transition to bottom habitats should occur at 'optimum' times in the life history. Modelling and field studies on cod in Norway have shown that in fact this habitat shift occurs at minimum mortality to growth ratios as predicted by Werner & Gilliam (1984) (Godo *et al.*, 1989; Salvanes *et al.*, 1994). Once cod settle, they defend territories around a shelter site. Fish that settle earlier and/or larger, grow faster and hold larger territories suggesting an important role for competition for space in the early post-settlement phase (Tupper & Boutilier, 1995*b*). Smaller/late cod are at a disadvantage in competing for the limited high-quality shelter sites and inhabit areas of low habitat complexity, where they will experience higher mortality due to predation. Similarly, in juvenile Nassau grouper (*Epinephelus striatus* Bloch), ontogenetic habitat shifts are consistent with the minimization of mortality to growth highlighting the role of behavioural responses to size-dependent predation risk (Dahlgren & Eggleston, 2000).

Variation in size (and age) at settlement may also be a consequence of habitat availability and habitat-based vulnerability to predation. Cod settle earlier in nearshore than offshore habitats probably as a response to predator distributions (Gorman, 2004). The combination of restricted nearshore movements, diurnal shoaling and preference for structurally complex habitat observed in newly settled cod are probably mechanisms for predator avoidance and suggest that predation risk is very high at these early life stages (Grant & Brown, 1998*a, b*). In a similar example, juvenile winter flounder (*Pseudopleuronectes americanus* Walbaum) show dynamic spatial and temporal settlement patterns mediated by habitat and predators (Manderson *et al.*, 2002, 2003, 2004, 2006). Juvenile Pacific halibut (*Hippoglossus stenolepis* Schmidt) showed preference for structured bottom (mainly sponges) over sand in the laboratory (Ryer *et al.*, 2004). In the field, mortality was greater over sand bottoms primarily because of the effect on predator-prey interactions. Predator-prey encounter rates decreased and pursuits were hindered in the sponge habitat leading to more successful escape by the juvenile halibut (Ryer *et al.*, 2004).

These habitat-specific distributions can be tracked at higher scales and into larger size classes. Using data from the long-term (1962–1987) Newfoundland northern cod trawl survey, Anderson & Gregory (2000) showed that geographical distribution of young cod (<2 years) was density dependent and spatially limited to preferred seabed habitats. In years when their range expanded onto the shelf, they experienced higher levels of cannibalism by older cod that show

broader geographic distribution and are less dependent on bottom habitats. Their results suggest that density-dependent habitat processes moderate survival during the early juvenile stages leading to recruitment variation and probably setting of year-class strength early in the life history (Sundby *et al.*, 1989). Similarly, regional differences in the strength of density-dependent mortality among juveniles from 11 populations on the Norwegian Skagerrak coast were explained by variation in the availability of bottom structure (Fromentin *et al.*, 2001).

CUNNER

Cunner (*T. adspersus*) is a temperate labrid fish found primarily in nearshore reefs ranging from Newfoundland to New Jersey. They have a larval life of *c.* 3 weeks, followed by a 3–4 week settlement period (Gleason & Recksiek, 1990; Levin, 1991, 1993, 1994). After settlement, cunner are closely site attached and strongly associated to structure (Olla *et al.*, 1975; Pottle & Green, 1979; Levin, 1991). Cunner use structure as shelter during the nightly period of torpor (Green & Farwell, 1971; Tupper & Boutilier, 1997). Levin (1994) showed that post-settlement loss (mostly due to mortality because of cunner's site attachment) was more than 99%, unrelated to the pattern of settlement, but was sensitive to the spatial arrangement of the habitat. Similar to cod, Tupper & Boutilier (1997) found that in St Margaret's Bay, Nova Scotia, cunner settlement was independent of habitat type (and adult density) but that recruitment success was positively correlated with habitat complexity probably as a function of habitat-based differences in predation mortality since growth was unrelated to habitat complexity. This result led them to conclude that habitat-mediated post-settlement processes are critical to recruitment and population dynamics of cunner. In a similar study in coastal Massachusetts, Nitschke *et al.* (2002) found strong evidence for density-dependent mortality in the post-settlement phase and that small changes in habitat structure across reefs over the recruitment season can lead to variability in recruitment. Thus, reefs that decreased in complexity experienced higher cunner mortality.

OTHER TEMPERATE FISHES

Researchers working on other temperate reef fishes have also noted the importance of habitat structural complexity in determining levels of density-dependent mortality, particularly affecting predation as the mechanism of mortality. For example, Anderson (2001) showed that the structural complexity of giant kelp [*Macrocystis pyrifera* (Agardh)] provided a refuge for juvenile kelp perch (*Brachyistius frenatus* Gill) and that along with the aggregative response of their main predator, kelp bass [*Paralabrax clathratus* (Girard)], were responsible for predator-induced compensatory mortality. For newly settled plaice (*Pleuronectes platessa* L.) in the North Sea, sediment structure (Pihl & Van der Veer, 1992) and algal cover (Wennhage, 2002) affect vulnerability to predation, yet settling fish prefer bare sediment patches probably as a response to potential

hypoxia and lowered prey levels in algal covered patches (Wennhage & Pihl, 1994). In New Zealand, distribution and densities of the adult blennioid fish, *Forsterygion varium* (Forster), were highly dependent on post-settlement mortality, with highest early juvenile mortality occurring within habitats of low complexity during the first week after settlement (Connell & Jones, 1991). In contrast, Levin *et al.* (1997) found that differential predation could not explain differences in recruitment of pinfish (*Lagodon rhomboides* L.) between vegetated and unvegetated habitats, instead selection of eelgrass habitats may be a function of habitat-specific differences in growth rate. More recently, Johnson (2006a, b) has shown that the effect of structural habitat complexity on the strength of density-dependent mortality differs as a function of scale; at small scales increased habitat complexity led to stronger density-dependent mortality, at larger scales the effect was reversed. Johnson attributes this difference to scale-dependent differences in predator response.

TROPICAL REEF FISHES

Results of research on tropical reef fishes are consistent with the general conclusions outlined above for temperate reef fishes and other temperate demersal fishes (Table I). For example, in a recent study focusing on the transition phase of a tropical surgeonfish [*Naso unicornis* (Forsskål)], c. 60% of potential settlers were lost during settlement independent of cohort size (Doherty *et al.*, 2004). However, post-settlement mortality was density dependent (9–20%/day) and thought to be mostly due to predation. Unfortunately, this study did not examine potential habitat-specific differences in survival. Refuge from predation also appears to be an important component of density-dependent mortality in coral reef fishes. Forrester & Steele (2004) detected strong density-dependent mortality in plots with few refuges. In contrast, in plots with abundant refuges, mortality was density independent, whereas predators were independent of prey density or refuges. Variation in site quality can mask strong density-dependent effects as shown for the six bar wrasse [*Thalassoma hardwicke* (Bennett)] in Moorea (Shima & Osenberg, 2003). Higher quality sites received greater settlement, which obscured patterns in post-settlement density dependence leading to a phenomenon termed 'cryptic density dependence', which may be common in reef fish studies where habitat quality is not measured. A review of the relative importance of density dependence in reef fish populations concluded that 17 of 20 species analysed experienced the strongest density-dependent per capita mortality usually shortly after settlement (Osenberg *et al.*, 2002). However, it is important to note that density-dependent mortality will only be detected when densities are large enough so that it can be distinguished from density independence (Osenberg *et al.*, 2002). Although most studies have concluded that predation is the primary factor modifying settlement and subsequent recruitment patterns through density-dependent mortality, the strength of the effect varies across prey species, reflecting differences in prey behaviour (Booth, 2002; Webster, 2002) and can be a function of reef spatial structure and heterogeneity (Overholtzer-McLeod, 2004; Hixon & Jones, 2005).

TABLE I. Examples of the role of habitat in mediating settlement, post-settlement distribution and mortality of age 0 and juvenile Atlantic cod, cunner and other temperate fishes

Species	Type of habitat mediation	Reference
Atlantic cod	Habitat use narrows towards complex habitats during transition phase	Langton <i>et al.</i> (1996)
	Habitat-specific differences in predation risk account for post-settlement distribution	Tupper & Boutilier (1995a)
	Select more complex habitats when in the presence of predators	Gotceitas & Brown (1993)
	Most abundant in shallow vegetated sites particularly during the day	Grant & Brown (1998a), Linehan <i>et al.</i> (2001)
	Habitat utilization is less selective at night	Borg <i>et al.</i> (1997)
	Mortality rates increase with depth, are higher during the day and in unvegetated habitats	Linehan <i>et al.</i> (2001)
	Abundance responds to complex habitat availability	Laurel <i>et al.</i> (2003)
	Habitat discrimination can be effect of conspecific density	Grant & Brown (1998b), Laurel <i>et al.</i> (2004)
	Form tighter aggregations when over more complex habitats	Laurel <i>et al.</i> (2004)
	Settlement occurs at minimum mortality to growth ratios	Godo <i>et al.</i> (1989), Salvanes <i>et al.</i> (1994)
	Fish that settle earlier and/or larger, grow faster and hold larger territories	Tupper & Boutilier (1995b)
	Settle earlier in nearshore than offshore habitats probably as a response to predator distributions	Gorman (2004)
	Geographical distribution is density dependent and spatially limited on preferred seabed habitats	Anderson & Gregory (2000)
	Regional variability in the strength of density-dependent mortality explained by bottom structure availability	Fromentin <i>et al.</i> (2001)
	Cunner	Site attached and strongly associated to structure

TABLE I. Continued

Species	Type of habitat mediation	Reference
	Use structure as shelter during the nightly torpor	Green & Farwell (1971), Tupper & Boutilier (1997)
	Mortality unrelated to the pattern of settlement, but sensitive to habitat spatial arrangement	Levin (1994)
	Settlement is independent of habitat type and adult density but recruitment success is positively correlated with habitat complexity	Tupper & Boutilier (1997)
	Habitat-specific density-dependent mortality and recruitment variability	Nitschke <i>et al.</i> (2002)
Other temperate fishes		
Winter flounder	Dynamic spatial and temporal settlement patterns mediated by habitat and predators	Manderson <i>et al.</i> (2002, 2003, 2004, 2006)
Pacific halibut	Preference for structured bottom over sand; mortality greater over sand; predatory encounter rates, pursuits and capture success declines with habitat complexity	Ryer <i>et al.</i> (2004)
Kelp perch	Predator-induced compensatory mortality in complex habitat	Anderson (2001)
North Sea plaice	Sediment structure and algal cover affect vulnerability to predation	Pihl & Van der Veer (1992), Wennhage (2002)
Blennioid fish	Highest mortality occurred within low complexity habitats	Connell & Jones (1991)
Pinfish	Differential predation could not explain differences in habitat-specific recruitment of pinfish	Levin <i>et al.</i> (1997)
Rockfish spp.	Effect of structural habitat complexity on the strength of density-dependent mortality differs as a function of scale	Johnson (2006a, b)

CONCLUSIONS

The conclusion from a variety of work on temperate and tropical fishes is that high levels of density-independent mortality occur at the larval and settlement phases. However, population regulation probably occurs soon after settlement

as reflected by the substantial levels of density-dependent mortality experienced during this phase. Much of this mortality is due to piscivorous predators corroborating earlier ideas on the importance of predation on juveniles as a regulatory mechanism (Sissenwine, 1984; Rothschild, 1986; Houde, 1987; Myers & Cadigan, 1993; Walters & Juanes, 1993). The point that has not been strongly emphasized to date and which is highlighted in this paper is the widespread role of habitat in mediating these mortality levels leading to distortions of settlement patterns and regulation of recruitment patterns (Tupper & Boutilier, 1995a, 1997; Linehan *et al.*, 2001; Steele & Forrester, 2002). Settling fishes may or may not settle into refuge habitats (depending on species, location, scale and density), but their distribution patterns are very much determined by habitat-based differences in predation rates; complex habitats offer more protection whereas simple habitats lead to higher vulnerabilities (Fig. 1). Thus, even those species where settlement is not habitat specific show habitat-based patterns of recruitment. However, habitat quality and its suitability for growth and survival may be a dynamic process determined by spatial and temporal variation in regulatory processes (Manderson *et al.*, 2002; Laurel *et al.*, 2004). The trade-off between seeking refuge and the necessity to grow to larger less-vulnerable sizes ultimately leads to selection for 'time allocation patterns' that directly translate to stock-recruitment relationships (Walters & Juanes, 1993).

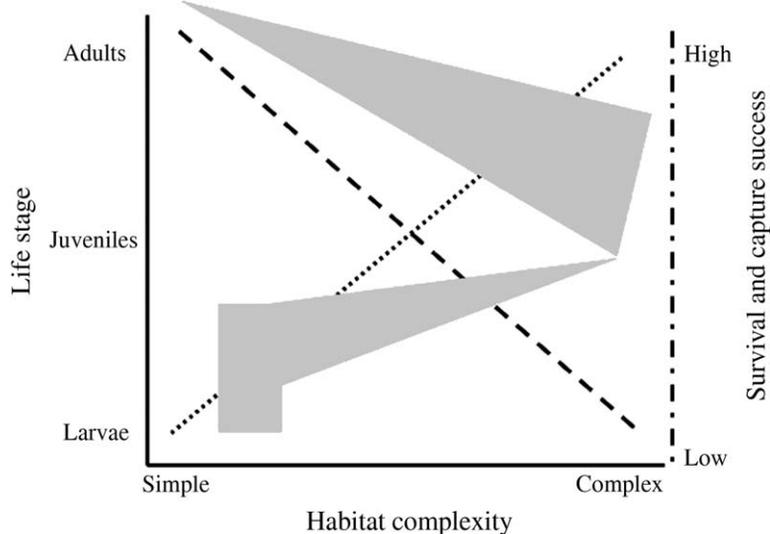


FIG. 1. An illustration of the role of habitat in mediating distribution and mortality levels of transition-phase fishes. The filled areas represent ontogenetic spatial relationships of temperate reef fishes, particularly Atlantic cod and cunner. At the early post-settlement stage, juveniles exhibit their narrowest and most selective habitat preferences for complex habitats (redrawn from Figure 1 in Langton *et al.*, 1996). Juvenile fishes experience higher survival in complex habitats (.....; see for example Tupper & Boutilier, 1995a, 1997) probably as a result of the relationship between capture success and habitat complexity in piscivorous predators (----; see for example Tupper & Boutilier, 1995a, 1997). It is important to note that mortality rates at the juvenile phase are often density dependent and almost always size based (*i.e.* mortality declines as fish size increases).

MANAGEMENT IMPLICATIONS

The clear importance of habitat to the early post-settlement phases of demersal marine fishes such as cod and cunner suggests that habitat management should focus on 'critical' habitats used during these stages and these habitats should be considered 'essential fish habitat' for these and many other fish species. Recent work has concluded that based on limited empirical evidence many populations are limited by juvenile habitat availability, even though model predictions suggested that juvenile habitat should rarely be limiting to adult abundances compared with recruitment and adult carrying capacity (Halpern *et al.*, 2005). Juvenile habitat availability could thus be used to identify areas for protection as has been done for adult stages. For example, adult cod show high levels of site specificity in the Irish Sea (Hinz *et al.*, 2003) suggesting that observed distributions could be used to delineate EFH assuming cod habitat selection operates according to an ideal free distribution (Shepherd & Litvak, 2004).

Description of EFH has also led to the identification and management of potential threats to EFH and the growing concern over destruction and degradation of aquatic habitats. It is primarily the complex bottom habitats and their associated macrofauna that are most vulnerable to damage from fishing gear (Auster, 1998; Collie *et al.*, 2000; Kaiser *et al.*, 2002) and the rate of such destruction is increasing (Watling & Norse, 1998). Bottom trawls and dredges can alter the seafloor and reduce habitat structure leading to redistribution of juvenile fish to less preferred habitat (Ryer *et al.*, 2004) and to increased mortality due to predation. For example, Lindholm *et al.* (1999) showed that in the laboratory, for 0 year cod under the threat of predation in a variety of habitats selected to mimic the range of impacts from fishing gear, survivorship increased with habitat complexity probably due to decreased predator efficiency. These results are consistent with those from field studies and highlight the potential impact of habitat alteration by fishing activity on juvenile survivorship and eventual recruitment of cod and other demersal species. Because reductions in habitat complexity (and biodiversity) can be directly related to increases in fishing effort (Auster, 1998; Engel & Kvitek, 1998), overfishing of commercial stocks can have both direct and indirect mortality effects.

Langton *et al.* (1996) proposed a habitat-based management scheme for commercially important species, including Atlantic cod, to assist managers in prioritizing scientific information when managing EFH. Previous work had shown that the critical habitat for cod was that used by the early post-settlement phases. The argument was based on the relatively broad but simple habitat used by the pelagic phases, narrowing to a complex but selective habitat choice as early benthic phases, and broadening again in depth and habitat complexity as cod grow and mature. They concluded that economically important fisheries that have relatively small essential habitats and habitats that are important for more than one target species rank higher in terms of management priority. However, in order to implement such a habitat-based management scheme, more work is required to quantify juvenile habitats, to understand in what situations juvenile habitat is EFH and its use leads to bottlenecks in adult phases of stage-structured species (see review in Halpern, 2004), and to weigh the

social and economic demands against the biological constraints involved in managing essential habitat (Langton *et al.*, 1996).

Identifying EFH is complex, because it is species and stage specific, and will also exhibit interannual variability (Able, 1999). For example, Scharf *et al.* (2006) working with multiple predator and prey fish species not only showed that prey survivorship increased with habitat complexity for all predator–prey combinations but also found important species-specific effects related to differences in predator and prey behaviour. These results suggest that the impact of reduced habitat complexity may be more severe for some species than others. Further quantification of life-history habitat couplings is necessary for management of EFH and will increasingly determine location and extent of protected areas, an effective method to protect habitat and fish/invertebrate populations dependent on such limited habitat (Sobel & Dahlgren, 2004). Recent reviews of the effectiveness of marine reserves have concluded that they often result in increases in the abundance, diversity and productivity of marine organisms (Lubchenco *et al.*, 2003 and references therein). Many of these changes are due to reduced mortality and decreased habitat destruction (Lubchenco *et al.*, 2003). The focus to date has been on adult stages and large spatial scales (Langton & Auster, 1999; Hinz *et al.*, 2003), but clearly future research must also concentrate on the dynamics of the early benthic life stages and their habitat requirements.

I thank Dick DeGraaf, Dave King and Keith Nislow for the invitation to speak at the habitat use symposium in New Zealand for which I first put these ideas together. The invitation to speak at the Fish Habitat Ecology and Conservation FSBI Symposium by John Armstrong and Michel Kaiser allowed me to further refine these ideas and encouraged me to finish the manuscript. Many colleagues and, in particular, John Manderson, Paul Nitschke and Mark Tupper have helped to shape my thinking about the role of habitat in marine fishes. I am grateful to the US Forest Service and FSBI for generous travel funds. Partial support was also provided by a Hatch Grant from the University of Massachusetts. The writing was completed while I was a Sabbatical Fellow at the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (Grant number DEB-0553768), the University of California, Santa Barbara, and the State of California. This paper is dedicated to the memory of Dr Joe Brown who recognized early the importance of habitat for the early life-history stages of both freshwater and marine fishes.

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