Chapter 8
Ecology of juvenile and adult stages of flatfishes: distribution and dynamics of habitat associations

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8.1 Introduction

The juvenile and adult stages of flatfishes are of past and continuing interest, largely because they are the focus of harvests by commercial and recreational fishermen from temperate to tropical waters of the world’s oceans and estuaries. As such, they have received much attention in the published literature, especially because of the recent Flatfish Symposia (see Preface), and as a result, many of the other chapters in this book. In fact, these complementary chapters such as those on reproduction (Chapter 4), trophic ecology (Chapter 9), age and growth (Chapter 7) and behaviour (Chapter 10) provide some boundaries for our own comments on the ecology of the juvenile and adult stages.

Our purpose is to review and synthesise the available information on the distribution and dynamics of habitat use for flatfishes including the roles that ontogeny, and short (tidal, diel, lunar, episodic) and long (annual, decadal) temporal scales have on habitat use and habitat quality, and thus identification of nurseries. We further define the limits of our treatment with a number of definitions.

8.2 Definitions

Ecology: The distribution and abundance of flatfishes in space and time.
Habitat: Often defined as simply the place where an animal lives (Krebs 1994) yet this is often very difficult to characterise more fully, partly because of the complex life history of flatfishes in which the different life history stages occupy different habitats. As an example, just for juveniles and adults these may include settlement habitats, nursery habitats, feeding habitats and spawning habitats. Furthermore, attempts to determine habitats are confounded by the high mobility of primarily benthic fishes such as flatfishes. We recognise this difficulty by focusing, whenever possible, on the dynamics of flatfish habitat associations. Wherever possible we make a distinction between habitat ‘use’ and habitat ‘selection’ (Kramer et al. 1997), assuming that distinction is available from individual papers.
Nursery: A habitat is a nursery of a species if its contribution per area to the production of recruits to the adult population is greater, on average, than production from all other juvenile
habitats (Beck et al. 2001). Furthermore, nursery habitats support greater adult recruitment from any contribution of four factors: (1) density, (2) growth and (3) survival of juveniles, and (4) movement to adult habitats.

*Juveniles:* The portion of the life history that, for most species, includes from settlement and/or the completion of metamorphosis to sexual maturity.

*Adults:* The portion of the life history from sexual maturity to senescence.

### 8.3 Distribution and ontogeny

Differences in ontogenetic state (e.g. juvenile vs adult for the purposes of this chapter) interact with seasonal fluctuations in abiotic (e.g. temperature, salinity, dissolved oxygen, substratum, depth) and biotic (e.g. predation, competition, food availability, parasites and disease) factors to produce differential distribution and habitat use at a variety of spatial and temporal scales (Gibson et al. 1996). Variability in one or a multitude of these factors may generate different levels of recruitment variation both within and among species. Therefore, given that many flatfishes are economically important, and given the recent emphasis placed on identifying and conserving essential fish habitat (NOAA 1996; Able 1999; Beck et al. 2001), understanding the effects of abiotic and biotic factors on the distribution dynamics of flatfishes during ontogeny is critical for those who need to make informed management decisions. Clearly, the degree to which we can address the above is limited by the scope of the published literature. Of the 15 recognised family level taxa of flatfishes (Chapter 2), only six are well represented in the literature (Paralichthyidae, Pleuronectidae, Bothidae, Scophthalmidae, Soleidae, Cynoglossidae), in large part because these families contain species of economic importance.

Many flatfish studies have aimed to identify which abiotic factors significantly influence the distribution of juveniles and adults belonging to a particular species, or species complex. Investigation of approximately 50 species from the Atlantic, 35 from the Pacific, two species from the Indian Ocean and one species from the Arctic Ocean, in addition to approximately 10 species from the Sea of Japan, China, Okhotsk and Bering seas, and four species from the Caribbean Sea, have concluded that a combination of variables – most often including depth, temperature, salinity and substratum type – are the best environmental predictors of habitat utilisation within a study area (e.g. Powell & Schwartz 1977; Kramer 1991; Jager et al. 1993; Szedlmayer & Able 1993; Vetter et al. 1994; Norcross et al. 1995; Allen & Baltz 1997; Albert et al. 1998; Rogers et al. 1998; Steves et al. 1999; Walsh et al. 1999; Sullivan et al. 2000; Stoner & Abookire 2002; Diaz de Astarloa & Fabré 2003; Stoner & Ottmar 2003). These variables, particularly temperature and salinity, may vary dramatically across seasons in temperate regions and may exhibit gradients at a variety of spatial scales. Other factors may vary over a range of spatial scales (e.g. depth and substratum type), but are more stable across seasons. Examination of these abiotic variables is common, perhaps because they are inexpensive to measure and fairly easy to quantify, and thus, the ubiquitous citation of these factors being correlated with flatfish abundance may be a methodological artifact. A caution noted in many studies is that while multivariate analyses may indicate that certain abiotic factors, or combinations of them, are correlated with patterns of distribution and abundance, they may not be the causal mechanisms responsible for producing these patterns. Instead,
Abiotic variables may be proxies for biological attributes of the habitat, such as reduced risk of predation or increased food availability and it is these that are truly responsible for controlling patterns of flatfish distribution. If so, flatfishes could use the gradients in abiotic factors to locate areas where the biotic factors are likely to match their habitat requirements. Biotic factors have been shown to affect the distribution of approximately 20 species of flatfishes from the Atlantic, 12 species from the Pacific and 2 species from the Indian Ocean, as well as approximately 14 species from the Sea of China and Japan.

A logical starting point for examining changes in flatfish distribution is settlement, given that the start of the juvenile stage coincides with settlement and/or the completion of metamorphosis for most species (see Toole et al. 1997 for some exceptions). Settlement patterns are governed by larval supply, but can be modified by larval behaviour and habitat selection during the settlement period. These changes can be expected to be particularly important over long temporal periods (see Sogard et al. 2001) or large spatial scales where habitat selection has a limited ability to operate. Pihl et al. (2000) examined the spatial variation in the abundance of newly settled plaice, Pleuronectes platessa, in the Swedish Skagerrak archipelago by sampling 32 isolated nursery grounds. Plaice settlement densities exhibited significant variation at several spatial scales from hundreds of metres to 200 km. Some of the variation could be explained by differences in habitat characteristics, but these patterns largely seemed to be obscured by differences in larval supply. In California flounder, Paralichthys californicus, a large proportion of the larvae settle on open coasts and subsequently migrate to more protected areas assumed to be nursery habitats (Allen & Herbinson 1990; Kramer 1991).

Species where the nurseries only constitute a limited part of the distribution range and/or species where the adults aggregate on spawning grounds must, by definition, have ontogenetic changes in distribution patterns. Furthermore, it appears that ontogenetic shifts in distribution during the juvenile and adult stages of flatfishes are a common phenomenon. In a North Carolina, USA estuary, four of seven species studied (summer flounder, Paralichthys dentatus; bay whiff, Citharinthys siptopeterus; blackcheek tonguefish, Symphurus plagiusa; and hogchoker, Trinectes maculatus) showed ontogenetic changes in distribution (Walsh et al. 1999), and in a Louisiana, USA estuary all of the four most common flatfish species (offshore tonguefish, Symphurus citivatium; bay whiff, fringed flounder, Eutroplus cossotus; and blackcheek tonguefish) showed similar changes (Allen & Baltz 1997). Both abiotic and biotic factors were considered to be important in the ontogenetic changes of juvenile flatfishes on the coast of Scotland (Gibson et al. 2002). It has been suggested that the nurseries of all flatfish species in Japanese waters seem to be located at the shallow end of the adult’s distribution range (Minami & Tanaka 1992). In some species the use of shallow habitats by small juveniles during early ontogeny is followed by movement of larger fish to deeper waters. One of the earliest records of the positive relationship between size-related ontogenetic shifts and depth was found in plaice (Heinke 1913), and the pattern was later termed ‘Heinke’s law’. This relationship has since been confirmed and demonstrated in a number of other flatfish species (e.g. McCracken 1963; Gibson 1973; Lockwood 1974; Dorel et al. 1991; Zimmerman & Goddard 1996). These shallow habitats for other species are often found in several types of coastal habitats such as open beaches (Riley et al. 1981; Pihl 1989), sheltered tidal flats (Kuipers 1977; Burke et al. 1991), and estuaries (Potter et al. 1990; Cabral & Costa 1999) including salt-marsh creeks (Rountree & Able 1992). These examples also show that shal-
low habitats are used by members of several different families of flatfishes (Paralicthryidae, Pleuronectidae, Scophthalmidae, Soleidae) and that recently settled flatfishes utilise shallow habitats in many parts of the world.

There are, however, exceptions to this pattern of settlement in shallow waters and subsequent dispersal into deeper habitats. In yellowtail flounder (*Limanda ferruginea*) on the Grand Banks of Newfoundland, there was no apparent ontogenetic change in distribution relative to depth and temperature and this was stable among year-classes and over the season (Walsh 1992). Witch (*Glyptcephalus cynoglossus*) along the Canadian east coast showed a negative relationship between fish size and depth during the summer (Powles & Kohler 1970). Despite the exceptions, there is mounting evidence suggesting that shallow-water habitats may enhance survival of early juvenile stages of a large number of flatfish species (reviewed in Gibson 1994). Lacking, however, are studies that provide direct information on the processes that cause individuals of many species to choose greater depth with increasing size. Most of the information on ontogenetic changes in habitat use comes from descriptive studies, and the associations found with different biotic and abiotic factors are consequently correlative in nature. The abiotic factors commonly manifest themselves in easily distinguishable gradients amenable for correlative studies. There is, however, little evidence to support the proposition that the optimum for these variables changes with ontogeny during the juvenile and adult stages of flatfishes (but see Fonds et al. 1992). A number of abiotic factors, including different combinations of sediment type, turbidity, salinity, depth and temperature, were correlated with species-specific ontogenetic state of the flatfish assemblage in a Louisiana estuary (Allen & Baltz 1997).

Among biotic factors, prey distribution has been suggested to cause ontogenetic changes in habitat use of summer flounder and southern flounder, *Paralicthys lethostigma* (Burke 1995). These two species settled in the same portion of estuaries in North Carolina, USA, and initially relied on the same food types. As the two species developed, their diets became different and the distribution of the species subsequently diverged, reflecting spatial differences in abundance of the major prey species within the estuary. Other studies have suggested that the size spectrum of the prey is important in habitat choice (e.g. Lockwood 1984; Castillo-Rivera et al. 2000). Predation could also be an important part of ontogenetic changes in habitat use. Brown shrimp (*Crangon crangon*) is the major predator on newly settled plaice until plaice reach a size refuge at a length of approximately 30 mm (Van der Veer & Bergman 1987). On tidal flats, plaice initially remain in intertidal pools (Berghahn 1983), minimising the spatial overlap with larger predatory shrimps. On open coasts the early benthic stage of plaice concentrates at depths <1 m (Gibson 1973; Lockwood 1974) reducing the overlap with the shrimps, which are primarily found in deeper waters (Gibson et al. 1996, 2002). By the time the spatial overlap between plaice and this predator starts to increase in both areas, a major portion of the plaice population have reached a size where their susceptibility to shrimp predation is low. The influence of brown shrimp is also evident on the small-scale distribution of flounder, *Platichthys flesus* (Modin & Pihl 1996). Similar predator/prey interactions have been identified in Japanese waters for *Crangon affinis* on stone flounder, *Platichthys bicoloratus* (Yamashita et al. 1996). Other studies of predation risk suggest patterns of size refugia for winter flounder (*Pseudopleuronectes americanus*) relative to predation by fishes (Manderson et al. 1999).
8.3.1 Early juvenile habitat associations

Over 50% of the flatfish papers examined report that juveniles use shallow nearshore areas as habitats. However, because these shallow habitats are logistically easier and less costly to study, and with the recent emphasis on the preservation and conservation of coastal habitats, they have been the emphasis of most of the literature. As methodological advancements are made (e.g. in situ observations with submersibles and/or mounted video camera systems), allowing investigators to broaden the geographic range over which habitat utilisation can be studied, the present-day view of the importance of nearshore nursery habitats to young flatfishes may change (e.g. Sullivan et al. 2000).

Early juvenile habitat characteristics vary among and within flatfish species, and it is no surprise that not all newly settled flatfishes utilise shallow, warm estuaries as nurseries. In some cases these types of nearshore nursery habitats are not available; in others, even if these habitats are available, they may not be used by young flatfishes. An example is provided by juvenile pleuronectid flounders occurring in coastal Alaskan waters (Norcross et al. 1995; Abookire & Norcross 1998). The bays and nearshore habitats off Alaska are considerably deeper (>10 m), at similar distances from shore, than those in other parts of the world. The juvenile nursery areas for these species occur between approximately 10 and 80 m depth, where water temperatures are cold (4–11°C) and salinities vary little (30–32 ppt). Newly settled Pacific halibut (Hippoglossus stenotepis) and rock sole (Lepidopsetta bilineata), arrive in these relatively deep, cold habitats following an inshore migration from even greater depths. The factors controlling such movements remain uncertain. However, even at these depths, fish can experience as much as a 5°C increase in temperature by migrating inshore.

Another example from different populations of a western Atlantic bothid, windowpane (Scophthalmus aquosus), suggests that there may be geographical and cohort-specific variation in juvenile habitats. Juveniles occurring on Georges Bank, approximately 50–75 km from the Massachusetts, USA, coast, presumably do not make the extensive migrations from these relatively deep waters (27–39 m) to nearshore nursery areas (Morse & Able 1995). However, the pattern exhibited by Middle Atlantic Bight windowpane is different in that the spring-spawned cohort of windowpane initially settle in relatively shallow water (<20 m), and then enter nearby estuaries (Neuman & Able 2003). Autumn-spawned windowpane also initially settle in shallow water on the inner continental shelf, but unlike spring-spawned fish, they do not appear to use estuaries during their first few months of life. Factors controlling the passive and active movements of windowpane to their nursery areas on Georges Bank may be quite different from those in the Middle Atlantic Bight, given that the spatial occurrence of newly settled and larger juveniles are highly correlated on Georges Bank, but differ considerably in the Middle Atlantic Bight, especially with respect to the spring cohort (Morse & Able 1995). In addition, this example illustrates that different controlling mechanisms may be responsible for dissimilar patterns of habitat use between distinct cohorts of the same species, an observation that has rarely been noted in the flatfish literature.

Spawning of some species occurs considerably farther offshore (continental shelf and beyond), almost guaranteeing that juvenile stages will not encounter shallow, nearshore habitats. Two species (yellowtail flounder and Gulf Stream flounder, Citharichthys arcticron) occurring in a region of the northwest Atlantic referred to as the New York Bight and one species occurring in the northeast Pacific (Dover sole, Microstomus pacificus) utilise habitats
>40 m depth (Toole et al. 1997; Steves et al. 1999). Two of these species (Gulf Stream flounder and Dover sole) engage in cross-shelf migrations from initial settlement areas to juvenile habitats. Ekman transport has been suggested as the mechanism by which Dover sole are delivered to the juvenile habitat (Toole et al. 1997), but mechanisms of transport for the Gulf Stream flounder are unknown (Steves et al. 1999). Unlike these species, yellowtail juveniles exhibit temporal and spatial stability within the nursery area. This stability is thought to occur because early life stages of yellowtail flounder track a cold cell of remnant winter-bottom water (approx. 6°C), a dominant physical feature that occurs annually on the continental shelf of the New York Bight (Steves et al. 1999; Sullivan et al. 2000).

For a small subset of species, which are resident in estuaries, settlement into juvenile habitat is dynamic. Evidence suggests that for the hogchoker, a western Atlantic soleid, summer spawning occurs in the polyhaline portions of estuaries and that settling larvae follow (or may be transported by the salt wedge transport system) up the salinity gradient to the salt/freshwater interface (0–8 ppt) in a short period of time (Dovel et al. 1969). For this species, congregation in the juvenile habitat may be more dependent on the salinity, and perhaps turbidity, conditions. Preliminary evidence suggests that some populations of the South African black-hand sole, Solea bleekerii, may follow a similar pattern of habitat use (Cyrus 1991). As the preceding examples demonstrate, recently settled flatfishes tend to occupy distinct habitats during discrete time intervals and these spatial and temporal boundaries may be explained, in part, by abiotic characteristics, most commonly depth, salinity and nature of the substratum (Powell & Schwartz 1977; Jager et al. 1993; Le Clus et al. 1994; Norcross et al. 1995; Abookire & Norcross 1998) or extent of river plumes in coastal regions (Le Pape et al. 2003a, b).

On the other hand, a growing body of literature has focused on the role that biotic factors play in governing habitat dynamics. Studies from around the world (MacDonald & Green 1986; Le Clus et al. 1994; Tokranov & Maksimenkov 1994; Toepfer & Fleeger 1995a, b; Aarnio et al. 1996; Gibson et al. 1998) demonstrate that prey availability, predator presence/absence, and species-specific morphology and behaviour may be driving differential patterns of settlement among juvenile flatfishes more than the physical properties of the habitat itself. The majority of these studies suggest that dietary partitioning, along with the staggered, seasonal ingress of different species into the juvenile habitat, may serve to limit predatory and competitive interactions. A series of examples follows.

Spatial, temporal and dietary overlap among the juveniles of five flatfish species (plaice; dab, Limanda limanda; turbot, Scophthalmus maximus; brill, S. rhombus; and common sole, Solea solea) was examined on a sandy beach along the Belgian west coast (Beyst et al. 1999). Even though this habitat is physically dynamic and characterised by low spatial heterogeneity, the species exhibited little dietary overlap and were segregated spatially and temporally during their time of residency. In another example, juvenile summer flounder and southern flounder tended to be spatially segregated within North Carolina, USA estuaries (Powell & Schwartz 1977; Burke 1995). Substratum and salinity were the two most important abiotic factors governing their distributions, with higher southern flounder abundances over clay/silt or organic-rich bottom in areas of low salinity and higher summer flounder abundances over sand bottom in areas of moderate to high salinity. Thus, spatial segregation may have resulted from feeding differences between the species that were related to their habitat preferences. Observations made in southern New Jersey, USA estuaries indicate that age-0
summer flounder make extensive use of salt-marsh creeks. Their movements into and out of the creeks may be aided by tidal stream transport, and residency and movement within the creeks was correlated with specific habitat parameters including temperature, salinity, dissolved oxygen and food availability (Rountree & Able 1992; Szedlmayer & Able 1993). The summer movements of flatfishes and benthic crustaceans in Gullmarsfjord Bay, Sweden were attributed to a combination of foraging activities, predator avoidance and selection of suitable environmental conditions (Gibson et al. 1998).

These studies are some of the few that provide qualitative information regarding the potential impact that predators and competitors may have on the movements of juvenile flatfishes. In related efforts, attempts to calculate mortality estimates due to predation by benthic crustaceans, fishes and birds on juvenile flatfishes in European, South African, US and Japanese waters have been made (Whitfield & Blaber 1979; Van der Veer & Bergman 1987; Tanaka et al. 1989; Bevertong & Iles 1992a, b; Witting 1995; Gibson et al. 1998; Leopold et al. 1998; Manderson et al. 1999). While these studies provide important estimates of predation rates imposed by predators on juvenile flatfishes, they are limited in terms of the study duration, the spatial scale examined, and the assumptions made regarding prey and predator population sizes. With these limitations, it has been very difficult to predict whether mortality due to predation contributes significantly to habitat use and to inter-annual variation in recruitment. The European literature on flatfishes suggests that mortality imposed by benthic crustaceans only dampens inter-annual variability in year-class strength (Van der Veer & Bergman 1987; Pihl 1990; Van der Veer et al. 1997).

8.3.2 Late juvenile and adult habitat associations

Late juvenile and adult flatfishes tend to be distributed over broader spatial and temporal scales than early juveniles. This difference is probably because the known life histories of many species are such that early juveniles congregate in nearshore, protected areas, or other nursery areas, that are spatially limited. Unfortunately, the available information on late juvenile and adult distributions (except perhaps with regard to spawning distributions) is less detailed than those for early juveniles. Of the abiotic factors thought to affect the distribution of late juvenile and adult flatfishes, temperature, depth and substratum type are cited most regularly (Rijnsdorp et al. 1992; Diaz de Astarloa & Munroe 1998; Rogers et al. 1998; Yamashita et al. 2001). Salinity may play a less important role, except perhaps with respect to species that inhabit estuaries throughout their lives, such as certain populations of hognchoker and blackhand sole (Dovel et al. 1969; Cyrus 1991). It has been proposed that turbidity affects the density of at least two species of flatfishes that are known to form aggregations on patches of homogenous substrata in the Sea of Japan (Gomelyuk & Shchetkov 1999). Biotic factors, especially prey availability, also influence the timing of movements (Tokranov & Maksimenkov 1994) and the formation of mixed patchily distributed conspecific and groups of adult flatfishes (Gomelyuk & Shchetkov 1999).

Dispersal of flatfishes from juvenile to adult habitats, whether seasonal or size/age-related, has been attributed to changes in dietary requirements, reduced risk of predation by larger predators and an assortment of abiotic variables, most commonly the avoidance of decreasing temperatures in shallow water with the onset of winter in temperate climates (see Seasonal cycles, p. 172). Correlations between dissolved oxygen levels and abundance of some
flatfishes have been identified. A negative relationship between oxygen concentrations and
the biomass of plaice and dab was found in Scandinavian waters (southeast Kattegat) where
hypoxic (<3 mg l⁻¹) conditions occur during the autumn months (Petersen & Pihl 1995). Other
studies have shown that some flatfishes may be particularly well adapted to withstanding low
dissolved oxygen conditions. For example, the spawning adults of Dover sole occupy a depth
range from 600 to 1000 m where there is an oxygen minimum zone (dissolved oxygen levels
0.7 mg l⁻¹) (Vetter et al. 1994).

While the previous examples illustrate that the information available on factors controlling the
distribution of late juvenile and adult flatfishes is often descriptive and somewhat
speculative, the literature on factors that affect timing and location of spawning in adult flat-
fishes is relatively plentiful. This difference occurs because abundances can be particularly
high during discrete time intervals and in specific locations. In addition, it is relatively easy
to quantify the reproductive state of field-captured adults through a variety of techniques
(e.g. gonadosomatic indices), enabling investigators to identify where and when spawning
adults occur (Wilk et al. 1990). In instances where data are available the spatial boundaries
of spawning in some flatfishes may be related to depth (Zimmermann & Goddard 1996; Tok
& Biryukov 1998), salinity and hydrodynamics (Stoner et al. 1999).

8.3.3 Dynamics of habitat associations

The estuaries and marine habitats of flatfishes can be highly dynamic environments where
biotic and abiotic factors change over a multitude of timescales. The distribution of mobile
animals, such as flatfishes, would therefore be expected to change over time in response to
the changing environment. Some changes are cyclic (e.g. seasonal) and the animals may have
adapted their habitat choices through behaviour or life cycle characteristics relative to the
predictability of the dynamic environment. Other changes may be episodic (e.g. hypoxia)
and a direct response to the changing environment would be expected unless the magnitude
and extent of the change causes mortality. Changes in habitat characteristics could also be
long-term (e.g. climatic) leading to gradual changes in distribution that could be mediated by
an evolutionary response by the population. There are, however, most certainly constraints
on the dynamics of habitat associations that could lead to discrepancies between the spatial
pattern in occurrence of flatfishes in relation to habitat quality. For example, flatfishes might
have limited capabilities to locate the habitat with the highest habitat quality at all times. The
cost of movement/migration may also exceed the benefits of changing habitat.

8.3.3.1 Tidal, diel and seasonal cycles

Tidal and diel cycles. Changes in distribution with the tidal and diel cycles have primarily been
studied in flatfishes utilising shallow areas as feeding areas and little information is available
for deeper waters. The tidal and diel cycles are normally out of phase, which may add to the
complexity of the temporal changes in distribution. However, the difference in frequency
does make it possible to distinguish between the tidal and diel component of the dynamics in
habitat associations through repeated sampling (see Gibson et al. 1996). The spatial scale of
movement would be expected to be small because of the high frequency of tidal and diel cycles.
Ultrasonic tagging has shown that juvenile summer flounder (Szedlmayer & Able 1993) and
adult flounder (Wirjoatmodjo & Pitcher 1984) move on the order of $10^2$–$10^3$ m with each tide. In several examples, tidal migrations, which may be species-specific (Gibson 1973), have been attributed to increased feeding potential in the intertidal zone (Tyler 1971; Berghahn 1987; Raffaelli et al. 1990) and to predator avoidance (Gibson 1973; Ansell & Gibson 1990). The influence of tides can also extend into the subtidal zone. Juvenile summer flounder utilise salt-marsh creeks as feeding grounds during high tide (Rountree & Able 1992) but these areas are characterised by substantial fluctuations in environmental conditions. Movements out of the marsh creeks at low tide may therefore partly result from 'behavioural homeostasis', whereby the fish move to remain at nearly constant physical conditions over the tidal cycle (Szedlmayer & Able 1993).

Diel movements occur both in combination with tidal movements (Burrows et al. 1994) and alone where the tidal amplitude is negligible (Bregneballe 1961; Gibson et al. 1998). In the latter, flatfishes move inshore during the evening and return to deeper waters at dawn, and the movements and feeding rhythms of potential predators are sometimes reported to match the diel cycles. Gadoids can be important predators on flatfishes in tidal (Ellis & Gibson 1995) and non-tidal areas (Pihl 1982; Arnott & Pihl 2000), and these gadoids are most abundant in the deeper parts of the juvenile habitat during the night (Gibson et al. 1996, 1998). Predation by diurnal predators such as birds can also be of significant magnitude (e.g. Summers 1979; Leopold et al. 1998), but it has not been established if this predation risk affects the diel movements of flatfishes or of their fish predators.

For one of the most extensively studied flatfishes, plaice, tidal and diel movements have been studied in several areas within the species range. On the extensive mud flats of the Wadden Sea, newly settled plaice remain in the intertidal zone during the entire tidal cycle and tidal migration patterns gradually develop during the course of approximately 1 month (Berghahn 1983; Van der Veer & Bergman 1986). This change in behaviour corresponds to increasing fluctuations in temperature and oxygen saturation that may force them to leave the tidal pools at low tide. Once the tidal movements have developed, diel comparisons show that the tidal flats are used to the same extent during the day and night (Berghahn 1986). On open coasts with a tidal regime, plaice primarily seem to settle in the subtidal zone and initiate onshore and offshore movements with each tidal cycle (Gibson 1973; Lockwood 1974; Wennhage, personal observations). The distribution in these subtidal areas is modified by a superimposed diel movement pattern with onshore tidal movements being more pronounced during the night (Burrows et al. 1994). On the Swedish west coast, where the tidal amplitude is low (<0.3 m) the diel movements resemble those on open tidal coasts (Gibson et al. 1998).

Seasonal cycles. Descriptive studies of flatfish populations have commonly found changes in the distribution patterns over the season. Seasonal changes in habitat use may, however, be hard to separate from those caused by ontogenetic changes in habitat use. This is especially true for the juvenile stage, as a large proportion of the flatfish species have their life history adjusted to produce offspring at a certain time of the year. We have therefore restricted our comments to a few examples where the seasonal movements persist for a considerable part of the life cycle. A number of flatfish species use estuarine habitats seasonally. Flounder use estuaries as juvenile habitat and the adult fish also use the estuaries as feeding grounds during the summer (Bregneballe 1961). Summer flounder show a similar use of estuaries (Able & Kaiser 1994). Plaice use shallow coastal areas as juvenile habitat during their first summer and a proportion of these fishes return as I and II age-group juveniles the following summers
(Kuipers 1977). Winter flounder may display a latitudinal change in seasonal movements along the east coast of North America (McCracken 1963). During the summer this species leaves the shore zone in areas where the water temperature rises above 15°C to reside in colder waters offshore. In the winter the northern populations move to deeper water when the temperature gradient is reversed (but see Howe & Coates 1975 and Phelan et al. 2000 for different interpretations).

In most flatfish species in temperate regions, seasonal dispersal of late juveniles from nearshore habitats into deeper, oceanic waters is common during the autumn months when water temperatures inshore begin to drop. This temperature decline may serve as a cue to juveniles of some species (e.g. smallmouth flounder, *Eiropus microstomus*, Able & Fahay 1998; summer flounder, Szedl Mayer & Able 1993) that it is time to make seasonal offshore migrations to waters that exhibit more stable temperatures during the winter months. In polar and tropical regions, one might expect water temperature to play less of a role in explaining seasonal movements of flatfishes, but so few studies have been conducted that it remains uncertain how abiotic factors affect flatfish distributions in these regions. Movements of late juveniles and adults in tropical regions may be mediated by seasonal changes in rainfall and the subsequent effect this may have on salinity, rather than by changes in temperature (Manickchand-Heileman 1994; Sánchez-Gil et al. 1994).

Bathymetric shifts to deeper water are not limited to those flatfishes that utilise nearshore areas as juveniles. For example, species that settle in relatively deep, oceanic habitats, such as arrowtooth flounder (*Reinhardtius mirabilis*) and Dover sole (*Hippoglossus hippoglossus*; Hunter et al. 1990; Rickey 1995), undergo seasonal migrations to even deeper habitats, but the reasons for these migrations are not well understood. Field surveys have suggested that late juveniles and adults undergo seasonal offshore migrations to particular depth zones and substratum characteristics (Ford 1965; Vetter et al. 1994; Zimmermann & Goddard 1996; Tok & Biryukov 1998). It has been hypothesised that some flatfishes are fairly immobile, may remain buried in sediments, and grow very little during winter months in temperate regions (Able & Fahay 1998; Hales & Able 2001; Neuman et al. 2001). Following this season of inactivity, adults may migrate inshore to shallower depths during the warmer months to presumably take advantage of warmer waters and enhanced feeding opportunities due to increased productivity (Bregnebøl 1961; Tokranov & Maksimenkov 1994).

Habitat associations change most dramatically, for both juveniles and adults, when they make seasonal or reproductive migrations. A prior, extensive review of the behaviour of flatfishes, including that for juveniles and adults, has covered the topic of migration and the possible cues (Gibson 1997). One of the most intriguing findings in recent decades is the ability of adults to use vertical migrations and thus tidal stream transport during migration. To date, this has only been verified for plaice (Arnold & Metcalfe 1995) and common sole (de Veen 1978; Greer Walker et al. 1980). Tidal stream transport might also occur in the juveniles or adults of other species. For example, summer flounder migrate long distances (Able & Kaiser 1994; Packer & Hoff 1999), are known to move with tidal currents in a selective manner (Szedl Mayer & Able 1993) and are known to move off the bottom regularly (Olla et al. 1972). Other species that might be likely to exhibit tidal stream transport include California flounder (Kramer 1991) and Japanese flounder, *Paralichthys olivaceus* (Tanaka et al. 1989).

During the adult stage most migrations are associated with spawning. As an example, tag/recapture studies have clarified migratory pathways for summer flounder and these help to
explain the difference in the timing of spawning in different parts of the species range (Burke et al. 2000). However, one intriguing tag/recapture study in northern New Jersey waters (Phelan 1992) noted the apparent presence of non-migratory adult winter flounder on the continental shelf during the winter when they are expected to be in the estuary in preparation for spawning there (Bigelow & Schroeder 1953). Alternatively, spawning may occur on the continental shelf during the winter (Howe et al. 1976) or the location of reproduction varies geographically. It would be interesting to confirm if there are non-migratory, spawning winter flounder on the shelf in the winter and to determine whether the same phenomenon occurs in other flatfishes as well.

**Long-term changes.** There are few examples available, beyond those of fishing impacts, but observations over a 7-year period in Narragansett Bay, USA, suggested that a reduction in the abundance of winter flounder was related to climatic changes, i.e. a trend for increasing temperatures, while that for a co-occurring species, windowpane, did not vary (Jeffries & Johnson 1974). In another example, the increasing occurrence and abundance of green macroalgae in recent decades (Pihl et al. 1999) may have influenced vulnerability to predation of plaice (Wennhage 2002).

**Episodic events.** Extremes in abiotic factors such as temperature, salinity and oxygen concentration would be expected to affect the dynamics of flatfish habitat use. Extremely low water temperature during the winter can lead to thermal death. During the severe winter of 1963 in the southern North Sea, large numbers of dead adult common sole were caught by research and fishing vessels (Woodhead 1964). Other flatfish species found dead, but in lower numbers, were dabs, plaice, brill and turbot. It was assumed that most of the mortality was caused by the low temperature per se, even though a skin disease was also observed in a number of the species. In other examples, newly settled plaice that remain in tidal pools during calm conditions and sunshine can, however, be subjected to lethal temperatures and detrimental UV radiation (Berghahn et al. 1993). Also, oxygen concentrations can drop quickly at high rates of respiration or decomposition in estuarine and marine ecosystems. This drop could be especially prominent in stratified water bodies or where water circulation is impaired for other reasons (e.g. vegetated areas). The Kattegat area between Sweden and Denmark is shallow (average depth 23 m) and has a pronounced halocline at 15–20 m depth, leaving a thin layer of poorly mixed bottom water. During the autumn when oxygen concentrations are at their lowest levels, the biomass of flatfishes can be reduced drastically (Pihl 1989; Baden et al. 1990; Petersen & Pihl 1995). Migration of fishes was considered to be the main cause of this change in distribution, as fishermen reported unusually large catches of flatfishes in gill nets at or above the halocline. A similar migratory response of adult summer flounder, away from low dissolved oxygen habitats on the continental shelf and onto ocean beaches and adjacent estuaries, has been reported in the New York Bight (Freeman & Turner 1977; Swanson & Sindermann 1979). In plaice juvenile habitats, proliferation of ephemeral macroalgae can concentrate individuals in the remaining unvegetated parts (Wennhage & Pihl 1994). Cage experiments have shown that growth rate is reduced in the presence of these macroalgae and that the oxygen levels under floating algae at night were lower than in the unvegetated areas (Wennhage, unpublished observations). Other studies have demonstrated that habitat suitability for winter flounder, as demonstrated by variation in growth of caged small juveniles, indicates that multiple environmental variables (temperature, salinity) can change rapidly (Manderson et al. 2002).
Typically, we know little about how biotic interactions (e.g. competition, predation, etc.) influence the dynamics of habitat associations. Perhaps one of the more intriguing possibilities is that social behaviour can play an important role. In one example, habitat use for the Caribbean eyed flounder, Bothus ocellatus, varied on a diel cycle with sexually dimorphic habitat use (Konstantinou & Shen 1995). Both sexes maintained overlapping territories during the day, when reproduction was occurring and dispersed to ‘retirement’ sites at night that were tens of metres away. Similarities in social organisation and habitat use have been suggested for other bothids (Moyer et al. 1985; Carvalho et al. 2003). In another example, two pleuronectids (marbled flounder, Pseudopleuronectes yokohamae and littlemouth flounder, P. herzensteini) formed distinct groups composed of conspecific or congeneric animals in homogenous habitats (Gomelyuk & Shchetkow 1999). It was suggested that these flatfishes form and maintain groups through visual contact.

8.4 Future emphasis

Enhanced understanding of the distribution of flatfishes and the dynamics of their habitat associations can come from a variety of approaches including improved data gathering and modelling (e.g. Boisclair 2001; Stoner et al. 2001), manipulative experiments in the field and numerous technological advances, especially when they can be used in tandem. Some techniques, such as the use of otoliths to back-calculate the life history and ecology, are continuing to improve with the added ability to detect and interpret extreme events (e.g. Berghahn 2000) or natal homing with analyses of microchemistry (e.g. Thorrold et al. 2001). Others have used field manipulation experiments to assess habitat-specific measures of growth to address habitat quality such as growth (Sogard 1992; Duffy-Anderson & Able 1999; Phelan et al. 2000), feeding success (Duffy-Anderson & Able 2001) and predation, e.g. tethering (Haywood & Pendrey 1996, but see Kneib & Scheele 2000).

Tagging techniques have been enhanced in a number of ways, especially by the miniaturisation of the tags themselves (e.g. coded wire tags, Wallin et al. 1997; ultrasonic tags, Boehlert 1997), to environmental data collection with archival tags that dramatically enhances the interpretation of habitat use and movements (Metcalf & Arnold 1997; Kasai et al. 2000). Other approaches, not yet used on flatfishes, include the use of data storage and satellite transmission of that data (Block et al. 1998; Luteavage et al. 2000). Among the most potentially insightful approaches are those that address the habitat and behaviour of flatfishes with in situ techniques such as underwater video (e.g. Gibson et al. 1998) in relatively shallow waters, and ROVs (e.g. Norcross & Muter 1999), submersibles (e.g. Sullivan et al. 2000) or unmanned lander platforms (e.g. Priede & Bagley 2000) in deeper waters.

Despite these possibilities, for juvenile and adult flatfishes we still lack the most basic data on distribution and abundance of many species, especially for species in polar and tropical waters. Thus, one approach that still needs considerable attention is the description of pattern (Underwood et al. 2000) of habitat use in order to improve our ability to ask better questions with the improved techniques available. As a further example, studies reporting ontogenetic changes in habitats are often inferred but not always tested. Accordingly, the reported changes could be caused by differences in size-selective mortality between habitats or along environmental gradients, where mortality may either be natural or caused by fish-
ing, either directly or indirectly (e.g. habitat degradation). Studies that provide estimates of swimming capabilities and mortality rates relative to the magnitude of ontogenetic change, and the spatial and temporal scales at which changes in the distribution occur, would help to clarify the role that ontogeny plays in mediating flatfish distributions. As with most advances in science, conceptual changes in the way we view and evaluate progress can come from a variety of sources including governmental initiatives (e.g. Essential Fish Habitat in the US; NOAA 1996) or conceptual redirection of older paradigms (Beck et al. 2001) and these can apply to juvenile and adult flatfishes as well.

In summary, our review and the conclusions we have drawn may be somewhat biased by the fact that abiotic and biotic factors controlling patterns of flatfish distribution have only been examined for a small subset of the total number of flatfish species known (approximately 20%). Furthermore, the majority of these species represent only six of the 15 recognised flatfish families (see Chapter 2). Even with these limitations, we can still draw some general conclusions about the factors affecting distribution patterns of juvenile and adult flatfishes. Spatial and temporal boundaries on both broad and finer scales are, in part, defined by water temperature, salinity, depth and substratum characteristics. At finer scales, biotic variables such as food availability and predator and competitor avoidance may play important roles. In our view, and those of others (Moyle & Cech 1996; Helfman et al. 1997), these results are not unique to flatfishes. The one exception may be with respect to the significant role that substratum type plays in mediating flatfish distributions (Gibson 1994; see also Chapter 10).

In conclusion, there is convincing evidence that the distribution patterns of many flatfish species change with ontogeny. The change in habitat utilisation could be a response to more than one factor and these factors are likely to vary through ontogeny due to the change in habitat requirements over the life cycle. Experimental studies are therefore needed to evaluate how the effects of single factors and combinations of factors affect habitat use with ontogeny. Tagging experiments are needed to establish the relative importance of migrations and differential mortality in producing these ontogenetic patterns, as well as seasonal, episodic and short-term changes in distribution.

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