Flatfishes

Biology and Exploitation

Second Edition

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Chapter 6

The planktonic stages of flatfishes: physical and biological interactions in transport processes

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Abstract

Flatfish address the problem of connecting between spatially distinct adult spawning areas and juvenile nursery areas through a planktonic larval phase. This strategy minimizes interspecific competition, promotes genetic diversity, and offers opportunities to colonize new habitats, but it comes at the significant risk of wayward advection and settlement to unsuitable nursery areas. Flatfishes have maximized their chances of a successful planktonic gamble by timing production of offspring to co-occur with favourable atmospheric conditions and with oceanographic features that favour survival to settlement. Broad-scale changes in climate-ocean teleconnections threaten to modulate the spatio-temporal relationship between the planktonic larvae and their ocean habitat, including physiological shifts (temperature and developmental timing), ecological changes (circulation and influences on transport trajectory), and behavioural affects (feeding and swimming). Renewed effort to understand these changes and others is called for.

Keywords: Plankton; drift; circulation; settlement; connectivity

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6.1 Introduction

Many marine fishes reproduce over spawning grounds that are appropriate for adult mating and breeding, and their young develop in spatially distinct nursery areas that are suitable for growth and development. Utilization of separate habitats for spawning and nursery allows flatfishes to exploit the best habitat for each purpose, which may be uniquely suited to the needs of one life history stage, but not the other. Nevertheless the same spatial separation that promotes specialized habitat utilization also demands connectivity between one site and the other, a feat most often accomplished through a vulnerable planktonic life stage. The planktonic phase is replete with physical and biological hazards, both for adults that spawn planktonic offspring and for the progeny themselves. Spawning adults risk increased predation due to heightened activity and visibility, as well as poor fertilization success of externally fertilized propagules. Planktonic eggs and larvae are vulnerable to predation by piscivorous species, they are exposed to adverse advective processes that can take them far from suitable nursery areas, and they have limited yolk reserves which make finding and consuming food temporally critical. Indeed, the high mortality during the planktonic phase may underlie the extreme fecundity of fishes that demonstrate this type of life strategy. However, in the long run, advantages must outweigh risks for the planktonic strategy to persist, and flatfishes with a dispersive stage must do better than maintaining a replacement population if stocks are to expand and grow. Certainly planktonic stages experience a reduction in intra-specific competition and cannibalism, which contributes to better survival of young. Likewise, species with a planktonic form benefit from the potential to colonize new areas (Strathmann 1974), as well as advance gene flow and promote genetic diversity. Yet risks remain high; during planktonic stages there is a remarkable culling of individuals (Figure 6.1) to leave the fittest for the given set of environmental conditions. However, surviving the larval stage is no guarantee of living long enough to reproduce. Thus, drift in the plankton has another critical consequence; larvae have to end their drift period in an area that is suitable as a nursery for the juvenile stage.

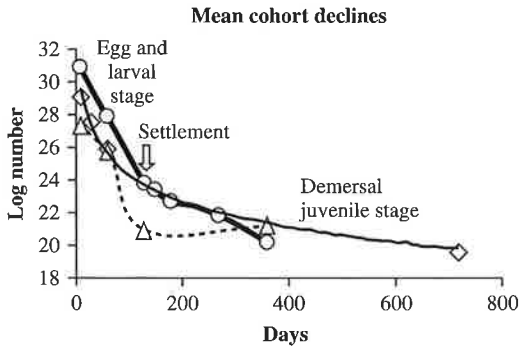


Figure 6.1 Cohort declines for European plaice over the first two years of life. Data plotted from Van der Veer (1986) diamonds, Beverton & Iles (1992) circles, and Nash (1998) triangles. The strength of the year class may be regulated during the early pelagic and postlarval demersal stage and mortality rates may vary on a geographic and interannual basis.

The question is whether they do anything to maximize their probability of arriving there, or whether it is a random process.

Year-class strength may be largely determined by the end of the larval stage (Figure 6.1; Horwood *et al.* 2000, Wilderbuer *et al.* 2002) but can be modified (Van der Veer *et al.* 2000) or even controlled in the juvenile stages (Bailey 2000). According to competing concepts about what controls the recruitment of marine fishes, several involve larval drift. According to the 'supply-side hypothesis' (e.g. Connell 1985; Milicich *et al.* 1992), it is the abundance of larvae that arrive in their nursery areas that controls the abundance of fishes at a later stage. Likewise the 'nursery size hypothesis' (e.g. Rijnsdorp *et al.* 1992; Van der Veer *et al.* 2000) states that each nursery sustains a population in proportion to the size of the nursery area, but that supply to the nurseries or sometimes retention (Iles & Sinclair 1982; Sinclair 1988) is often a limiting factor. In the 'match-mismatch' hypothesis (Cushing 1972), fish spawning times and survival may be related to the zooplankton production cycle but spatial aspects are also important, as Heath (1996) states: 'interactions between dispersal patterns and the spatial and temporal dynamics of plankton biomass are of critical importance for survival, and that the timing of larval production is closely coupled to these factors, implying a degree of adaptation in fish spawning strategies.'

The problem of larval drift and finding a nurturing environment for later stages is particularly acute for flatfishes. Flatfishes generally spawn in water deeper than their juvenile nurseries and most species have a juvenile stage with fairly specific habitat (such as sediment grain size and temperature preferences) and prey requirements. Different flatfish populations may have different strategies to arrive at, and/or maintain themselves in, suitable nurseries. Thus nearshore spawners may take advantage of retention features to maintain themselves in an appropriate habitat, whereas offshore spawners that utilize onshore habitats must be dispersed to inshore areas, or even into specific estuaries. Depending on the relative locations of spawning and nursery habitats, there may be local adaptations to spawn in areas where there are retention features to maintain larvae in favourable habitats; or, alternatively, they may spawn in areas where there are transport steering features such as local bathymetry or prevalent winds that accomplish a goal of targeted movement.

The goal in this chapter is to outline the natural variability in how different species, or even subpopulations within species of flatfishes, have adapted to transport conditions, to discuss the physical mechanisms and habitat specific variability in transport, and to outline the consequences to flatfish populations. Dispersal of eggs and larvae of flatfishes depend on such things as release time, location, stage duration and hydrographic conditions (Van der Molen *et al.* 2007).

6.2 Variations in time and space in the plankton

Are spawning times and locations of flatfish species distributed such that the arrival of offspring in their juvenile nurseries is maximized? Spawning in some species is adapted to supply larvae to persistent hydrodynamic features such as fronts, eddies, or currents, which transport or retain larvae near suitable juvenile habitat. In the case of European

plaice (*Pleuronectes platessa*) in the Irish Sea the spawning grounds are close to the nursery in areas where currents are weak or nondirectional (Nash & Geffen 1999; Fox *et al.* 2006). In the Bering Sea, spawning of northern rock sole (*Lepidopsetta polyxystra*) is spatio-temporally associated with the seasonally developed Bering Coastal Current (Lanksbury *et al.* 2007; Cooper *et al.* 2013), a current of moderate strength which retains larvae in proximity to favourable habitat along the coast. Release of eggs in strong currents where direction and distance of dispersal are optimized maximizes chances of successful settlement (Gibson 1999). This is an essential criterion for most flatfishes, because juveniles have specific nursery and resource requirements that support optimal growth and survival, including food, temperature and avoidance of predation. These factors are strongly influenced by depth, sediment type, exposure and predator abundance. Predation after settlement is believed to be critical, and is strongly influenced by the growth-dependent predator-prey size ratio (Bailey 1994).

Since juveniles have fairly specific habitat and prey requirements, the target for larval transport is not necessarily geographically narrow, but is restricted in terms of habitat-defining parameters. Juvenile habitat is discussed more thoroughly in Chapter 10, but specifically, different species groups tend to have specific feeding patterns as they settle (e.g. Minami & Tanaka 1992). Sediment type, depth, and temperature are important to settlement and must meet relatively narrow species-specific criteria (Norcross *et al.* 1999).

The timing of spawning and rate of egg development in the plankton is likely to be an adaptation in part to the timing of prey production, seasonal and geographic abundance of predators, and seasonal changes in transport conditions. Spawning time may be variable for some species (e.g. common sole *Solea solea* in the North Sea, Bolle *et al.* 1999, or along the Northeast Atlantic coast (Vinagre *et al.* 2008); English sole *Parophrys vetulus* off the Oregon coast, Boehlert & Mundy 1987), and could signal a change in currents, or be related to the plankton production cycle, or even be a purely physiological response to temperature, i.e. through gonadal development. Other species may have constant spawning time, for example European plaice in the North Sea have a mean spawning date of January 19 with a standard error of 2 days (Cushing 1990).

Deep-water species spawn earlier in the year, generally in winter, and tend to have larger larvae (Minami & Tanaka 1992). The offshore spawning species tend to spend a longer length of time in the plankton, and metamorphose at a larger size (Minami & Tanaka 1992). Larvae with a metamorphic size >25 mm may spend more than 3 months in the plankton. In fact, Dover sole (*Microstomus pacificus*) and rex sole (*Glyptocephalus zachirus*) larvae may spend a year or longer in the plankton (Pearcy *et al.* 1977). Larvae with a long planktonic life have a more variable size-at-settling (Minami & Tanaka 1992). This variation in size-at-settling reflects the variability in transport and time needed to find a successful cue for settlement to a suitable habitat. Larvae originating from warm water, as well as nearshore spawners, tend to be smaller and undergo metamorphosis at a smaller size. Species with a metamorphic length <10 mm often have a pelagic duration <1 month.

In general, flatfishes move to shallow water to spawn, and nursery grounds for juveniles are shallower than the spawning grounds (Minami & Tanaka 1992). Many

species show remarkable consistency from year to year in the location of spawning (Nash & Geffen 1999; Fox *et al.* 2000; Hunter *et al.* 2003; Loots *et al.* 2010). Modelling studies have shown that the specific location of spawning, as well as depth and directed swimming, play an important role in retention of fish larvae over offshore banks (Werner *et al.* 1993).

Almost all flatfishes have pelagic eggs or eggs that are deep in the water column offshore. However, five species in the Pacific Ocean (marbled flounder *Pseudopleuronectes yokohamae*, rock sole *Lepidopsetta bilineata*, northern rock sole *Lepidopsetta polyxystra* (Orr & Matarese 2000), dusky sole *Lepidopsetta mochigarei* and kurogarei *Pseudopleuronectes obscurus*), and one in the Atlantic (winter flounder *Pseudopleuronectes americanus*) have demersal eggs. These species spawn in late winter and spring in shallow coastal waters <20 m depth. Demersal eggs in these waters may be an adaptation to prevent their offshore dispersal by surface currents (Pearcy 1962a, 1962b). European flounder (*Platichthys flesus)* in the Baltic Sea were found to have two distinct spawning strategies: demersal eggs in shallow waters in the northern Baltic, and pelagic eggs in deeper water in the southern Baltic area and west coast of Sweden (Florin & Höglund 2008).

6.3 Physical mechanisms of transport and retention

The dispersal process describes a suite of influences that begin with large-scale forcing mechanisms and end with fine-scale temporal-spatial modifications (Bradbury & Snelgrove 2001). For ichthyoplankton with poor swimming abilities, large-scale processes dominate the distribution process, and dispersal of early stages is primarily passive, though buoyancy changes during egg development can influence drift in depth-discrete currents (Haug *et al.* 1986; Duffy-Anderson *et al.* 2011; Domínguez-Petit *et al.* 2013; Duffy-Anderson *et al.* 2013). Near the end of the dispersive phase, behavioural shifts can occur that mitigate the influence of large-scale forcing parameters, making the process of dispersal under more active control of the settling larva. Here several key physical mechanisms that regulate early flatfish larval dispersal are addressed, with comments on small-scale factors that affect settlement-ready flatfish in the water column near the conclusion of the planktonic phase.

6.3.1 Wind-forcing & Ekman transport

Wind conditions during larval development for European plaice showed significant correlations with the 0-group abundance along the Danish coast (Nielsen *et al.* 1998) and with year-class strength on the Swedish west coast (Pihl 1990), implicating the role of wind-induced transport for recruitment. Van der Veer *et al.* (1998) also showed that wind-induced variability in circulation and larval dispersal patterns might be a key factor in determining subsequent year-class strength. In addition to the winter temperature at the spawning grounds, which has an inverse relationship with year-class strength of the European plaice (Van der Veer 1986), residual currents induced by persistent westward winds in cold winters could also have an effect on recruitment in a specific year (Van der Veer & Witte 1999). This was confirmed in a study by

Bolle *et al.* (2009) showing meteorologically-driven variability in the hydrodynamics of the southern North Sea greatly affects the transport patterns of European plaice eggs and larvae, suggesting an important role in determining recruitment variability and spatial connectivity.

Many flatfish species have their major spawning period in winter-early spring, when strong storm-related winds predominate, so there could be adaptations to wind-induced circulation. In this regard, it is noteworthy that onshore/offshore wind-induced currents often produce vertical shear structure in water circulation of shallow coastal seas. In Sendai Bay, Japan, wind-induced circulation could be most responsible for transport of stone flounder (*Platichthys bicoloratus*) eggs and larvae from the spawning site to the vicinity of estuarine nurseries. The spawning site located at the northernmost part of this bay is apparently adapted to southward Ekman transport induced by westerly winds (Nakata *et al.* 1999a). In a shelf region of the Sea of Japan, on the other hand, strong westerly winds predominate during the main spawning period of yellow striped flounder (*Pseudopleuronectes herzensteini*), and larval retention and settlement could be reduced by strong westerly winds, which enhance offshore drift near the bottom. In fact, a significant negative correlation was found between the frequency of strong westerly blows and fishery catch 2 years afterward (Nakata *et al.* 2000).

English sole, an estuarine-dependent species with eggs and larvae spawned offshore on the US Pacific coast, may have a dual strategy for immigrating to estuarine nurseries: onshore Ekman transport for newly metamorphosing larvae and selective tidal stream transport for older larvae once they have settled on nearshore nurseries outside the estuary (Boehlert & Mundy 1987). This strategy may enhance the ability of this species to use the relatively small, isolated Pacific coast estuaries as juvenile nursery areas.

The recruitment of three winter-spawning flatfish species (flathead sole *Hippoglossoides elassodon*, northern rock sole *Lepidopsetta polyxystra* and arrowtooth flounder *Reinhardtius*, as *Atheresthes stomias*) in the eastern Bering Sea was hypothesized to be influenced by wind-driven advection of larvae, associated with the location of the springtime signature of the Aleutian Low (Wilderbuer *et al.* 2002). Intensified downwelling favourable winds during autumn may benefit inshore advection of Dover sole *Microstomus pacificus* and rex sole *Glyptocephalus zachirus* larvae in the Gulf of Alaska (Bailey *et al.* 2008). Doyle *et al.* (2009) investigated relationships of larval abundance of multiple species in the Gulf of Alaska to basin- and local-scale environmental variables. They found that the deepwater species (arrowtooth flounder and Pacific halibut) and northern rock sole were associated with wind-driven transport in spring. Off of the Atlantic coast of United States, annual juvenile abundance of southern flounder *Paralichthys lethostigma* was related to wind intensity during the peak months of larval ingress (Taylor *et al.* 2010).

6.3.2 Estuarine circulation

Another physical process establishing a two-layered circulation system is freshwater discharge into estuaries. As with Ekman transport, complex interactions between vertical migration/movement and horizontal advection often greatly contribute to the

transport/retention of pelagic eggs and larvae. Vertical migration is used by larvae to select either the seaward outflow at the surface or the inflow near the bottom for the purposes of entering, leaving or remaining in estuaries (e.g. Epifanio 1988). This may be a behavioural adaptation to avoid the effect of high flushing rates of the estuaries and to maintain horizontal position (Heath 1992). Ontogenic changes in vertical migration behaviour possibly lead to longitudinal gradients in larval size, age and species composition within the estuary. In the two-layered Cape Fear River estuary, the behavioural responses of the larvae of flounder (*Paralichthys* sp.), primarily to tide and photoperiod, facilitate their transport to appropriate habitats (Weinstein *et al.* 1980). In a small temperate estuary along the Portuguese coast, Primo *et al.* (2012) showed that larvae of Senegalese sole (*Solea senegalensis)* seem to take advantage of spring tides to enter the estuary.

6.3.3 Fronts and eddies

Reproduction of migratory species is often concentrated in geographic areas with relatively stable, long-term, hydrographic characteristics, such as fronts and eddies (Norcross & Shaw 1984). These features can facilitate transport towards suitable nursery areas, or can affect larval retention mitigating dispersal to unfavourable habitat. Examples include: Atlantic herring (*Clupea harengus*) (Iles & Sinclair 1982), Atlantic cod (*Gadus morhua*) (Ellertsen *et al.* 1990; Taggart *et al.* 1996), Japanese anchovy (*Engraulis japonicus*) (Nakata 1996) and others (see Vestfals *et al.* 2013).

In the case of flatfishes, the main spawning grounds of the yellow striped flounder are consistently found in a shelf region near the Sado Strait in the Sea of Japan. This location is characterized by a depth range of 50–100 m at the most upstream region of a relatively wide shelf, where current speeds are appreciably low and coastal eddies are often observed (Nakata *et al.* 2000), suggesting that yellow striped flounder may be adapted to the current system of this region. Chant *et al.* (2000) indicated that a small-scale eddy generated during flood tides appeared to contribute to advection of winter flounder (*Pseudopleuronectes americanus*) larvae to a cove in a southern New Jersey estuary, resulting in high numbers of the settled juveniles in the cove. On the other hand, Dover sole larvae may be prevented from inshore transport at the time of settling and kept in suitable outer continental shelf water by oceanic fronts associated with winter convergence (Hayman & Tyler 1980).

In addition to providing a possible mechanism of egg and larval retention within the coastal nurseries, fronts and eddies potentially play significant roles in accumulation and production of prey organisms, thus contributing to survival and subsequent recruitment of the larvae retained in their vicinity (Nakata 1996). Munk *et al.* (1999) demonstrated the variability in frontal zone formation at the shelf break in relation to the distribution and abundance of five species of gadoid larvae, and pointed out that frontal zone variability had a diverse influence on the larval populations.

6.3.4 Influence of climate and oceanographic shifts

Projections of the effect of climate change on the marine physical environment primarily focus on increase in sea level due to global thermal expansion and freshwater-driven

shifts in ocean mass. In the North Pacific, atmospheric warming is hypothesized to decrease the existing north–south thermal gradient, decreasing the intensity of winter storms in the Gulf of Alaska while increasing their intensity in the Bering Sea. Coastal rainfall is expected to increase in the region, contributing to the melting of land-based ice masses and the stratification of the water column. Reductions in sea ice extent and ice thickness influence ocean density, in turn shifting stable ocean currents. The North Atlantic is expected to experience significant freshwater input from the melting Greenland ice sheet as well as increasing wind speeds which affect direction and flow of surface ocean layers.

These climate shifts can influence hydrodynamic features, ultimately affecting dispersal of northern hemisphere flatfish eggs and larvae. Such shifts can be a cause of year class variation, and several studies have demonstrated that climate-induced variations in the predominant flow fields that advect larvae towards known nursery grounds are correlated with improved recruitment (Hinrichsen *et al.* 2001; Bailey & Picquelle 2002). Alternatively, disruption of stable drift patterns through climate variation can also occur. Wilderbuer *et al.* (2002) postulated that decadal shifts in wind strength and direction away from known nursery grounds were responsible for poor recruitment of several flatfish species in the Bering Sea.

The duration of the dispersal period is likely a significant modulator of the effects of climate-mediated changes in ocean circulation on larval transport. Impacts on flatfishes with long larval periods are expected to be greater than those with short planktonic stages due to the longer times for itinerant advection, although Shanks (2009) has argued that larval duration is not necessarily a strong indicator of dispersal potential. Overall however, effects of faster rates of development and earlier settlement competency are likely to lessen the dispersal scale of planktonic particles (Lett *et al.* 2010). Beyond latitudinal variations in spawning periods (Vinagre *et al.* 2008), warming sea temperatures are also linked to shifts in the timing of spawning for some species, for example common sole (Fincham *et al.* 2013). Shifts in timing of spawning as well as the rate of larval development may influence how the planktonic stages interact with seasonal currents and tides. Nursery ground suitability can also vary with climate shifts. For example, juvenile northern rock sole were abundant in a nursery area in the Bering Sea during a warm climate period, but were almost completely absent during a cold period (Cooper *et al.* 2014), leading to the hypothesis that climate variability limits the utility of the nursery area during cold regimes (Figure 6.2).

Increased temperature resulting from climate change has been associated with the decrease in abundance of European flounder at its southern limit of distribution (Cabral *et al.* 2001). This has been attributed to egg mortality in water temperatures higher than 12 °C. In contrast the southern affinity species Senegalese sole has been expanding its distribution further north (Désaunay *et al.* 2006). Nevertheless, in both cases it remains to be clarified which life stage is most affected by environmental changes and limits or regulates population dynamics.

Theoretically, species that have broad habitat and dietary preferences should be more able to cope with the effects of climate-mediated variable dispersal (Rijnsdorp *et al.* 2009). Generalists that exploit a diversity of prey resources are capable of utilizing a wide variety of substrata, or those species that are flexible in their thermal

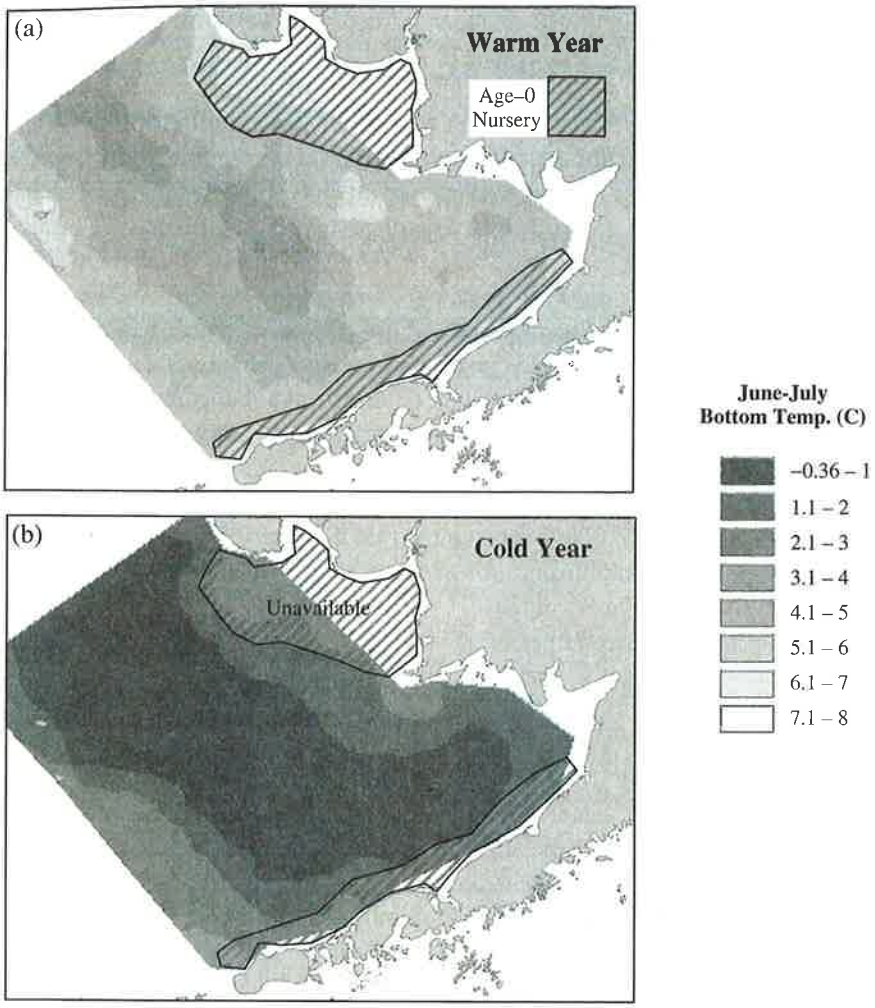


Figure 6.2 Nursery habitat for age-0 northern rock sole during warm (top panel) and cold (bottom panel) regimes. Greyscale ramp indicates bottom temperature (°C). (*Source*: Adapted from Cooper *et al.* 2014). (See plate section for colour version.)

requirements, should experience lower mortality than specialists due to flexible settlement requirements. However, as a group, flatfishes tend to exploit a narrower ecological niche than pelagic fishes, suggesting that this group may be particularly vulnerable to the effects of climate-mediated variations in dispersal that potentially advect them far from nurseries that support thermal and dietary preferences. That said, deep-water flatfishes may be less affected than their coastal counterparts, as thermal modifications are less likely to be manifested at depth. Nevertheless, climate-associated variations in mixing, stratification, and circulation have been shown to impact the dispersal trajectories of deep water species (Duffy-Anderson *et al.* 2013), though effects on recruitment variation remain unresolved.

6.3.5 Behaviour

Behaviour of flatfishes is more completely addressed later in this volume (see Chapter 12), but a brief discussion of the role of behaviour as it is related to the planktonic dispersive phase is presented here. As flatfish larvae approach settlement competency in the plankton, they acquire developmental attributes and swimming abilities that allow them finer control over their distribution, mitigating the effects of large-scale forcing on dispersal. For example, common sole undergo a complex suite of metamorphic changes in the plankton, including fin development and the presence of a swim bladder, that alters their vertical distribution and favours accumulation near juvenile nursery grounds (Lagardère *et al.* 1999).

Tidal currents are important for larval transport in tidal inlets and estuaries if associated with vertical migration behaviour (selective tidal-stream transport, STST), and there is convincing evidence that flatfish larvae can actively control their vertical position with tides to regulate their drift (Rijnsdorp *et al.* 1985; Burke *et al.* 1998; Yamashita *et al.* 1996; Jager 1999). Premetamorphoic and metamorphosing larvae benefit from improved locomotor abilities, a more advanced lateral line system, and increased visual acuity which permits increasing sensitivity and responsiveness to subtle tidal cues. Abiotic variables such as pressure changes associated with tidally induced differences in sea-surface height, vertical shear, salinity gradients, turbulence, temperature changes, or even light levels (Hill 1991; Luettich *et al.* 1998) can all serve as cues to taxis. Similarly, biotic cues such as biochemical gradients and zooplankton concentration may also stimulate kinesis. Regarding marine migrant species, freshwater has been suggested as an important chemical cue to facilitate and drive the orientation of migrating larvae. Interannual variation in river flow has been significantly and positively related with variation in densities and area covered by 0-group common and Senegalese soles and European flounder (Le Pape *et al.* 2003; Vinagre *et al.* 2007; Martinho *et al.* 2009).

Regardless of which cues competent flatfish larvae utilize to initiate behavioural response, planktonic flatfishes can reduce their dispersal distance by moving into near-bottom currents that are slowed by frictional drag. Active maintenance in eddies, convergence zones, or closed-circulation features could also mitigate effects of the broader dispersal process.

6.3.6 Models

Numerical models of water circulation are useful to explore egg and larval transport mechanisms because of the complicated dynamic interactions between physical and biological processes, such as coupling of water circulation and larval vertical migration (Bartsch *et al.* 1989; Werner *et al.* 1993; Lough *et al.* 1994; Bolle *et al.* 2009). Van der Veer *et al.* (1998) applied a 2D circulation model of the southern North Sea to simulate the interannual variability in dispersal of European plaice eggs and larvae from the spawning area in the Southern Bight towards the Dutch coastal nursery areas. An interesting finding from the model simulations was that interannual variability in transport is quite large and of the same order of magnitude as that in larval abundance observed

near the nursery areas, suggesting that the variability in circulation patterns during the early pelagic stages in the open sea might be a key factor in determining year-class strength of European plaice. Meteorologically-driven variability in the hydrodynamics of the southern North Sea appeared to be a key-factor affecting the transport patterns (Bolle *et al.* 2009). However, European plaice larvae could exhibit some active behaviour such as settling on the bottom by late larvae, increasing the role of currents near the bottom in their transport.

Transport of yellow striped flounder (*Pseudopleuronectes herzensteini*) eggs and larvae has been modelled in a shelf region of the Sea of Japan using a 3D Euler-Lagrangian model, with special focus on the effect of wind on inshore retention (Nakata *et al.* 1999b, 2000). The general pattern of egg and larval transport from the spawning habitat on the shelf to adjacent coastal nurseries was reproduced under a constant westerly wind, assuming vertical movement of the eggs and larvae (upward in the earlier phase and downward in the later phase of the drift period), and, using this model, the effect of the westerly wind speed on the egg and larval retention in the inner shelf was evaluated (Figure 6.3). It was shown that the retention rate could be rapidly reduced when the wind speed exceeded a critical value (Figure 6.4). Supporting the model results, the number of juveniles collected in the nursery area (1991–98) showed a significant negative correlation with the frequency of strong westerlies in April. Although field data on the vertical distribution and movement of yellow striped flounder eggs and larvae are limited, the most realistic pattern of transport was obtained only in the case where sequential upward and downward movement was assumed (Nakata *et al.* 1999b). This may indicate that upward movement in the earlier phase could be an adaptation to avoiding wind-induced offshore drift at the spawning

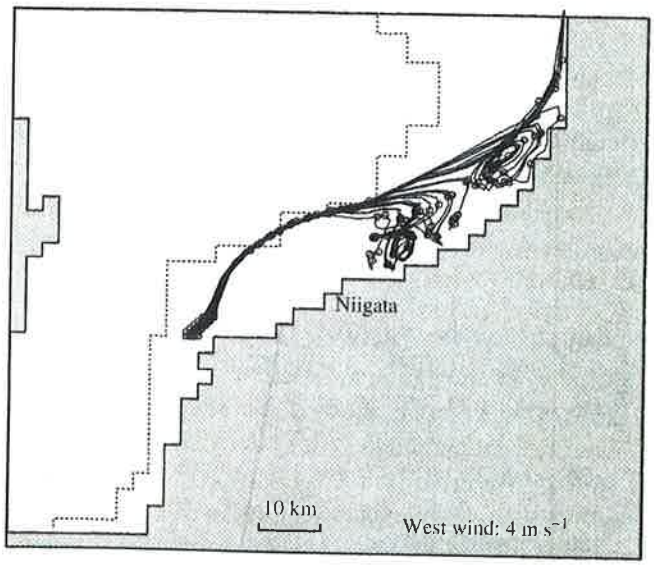


Figure 6.3 Computer trajectories of particles, simulating yellow striped flounder eggs and larvae, released from the spawning location for 30 days under the condition of constant westerly winds. The broken line is the 100 m depth contour. (*Source*: Nakata *et al.* 2000. Reproduced with permission of Elsevier.)

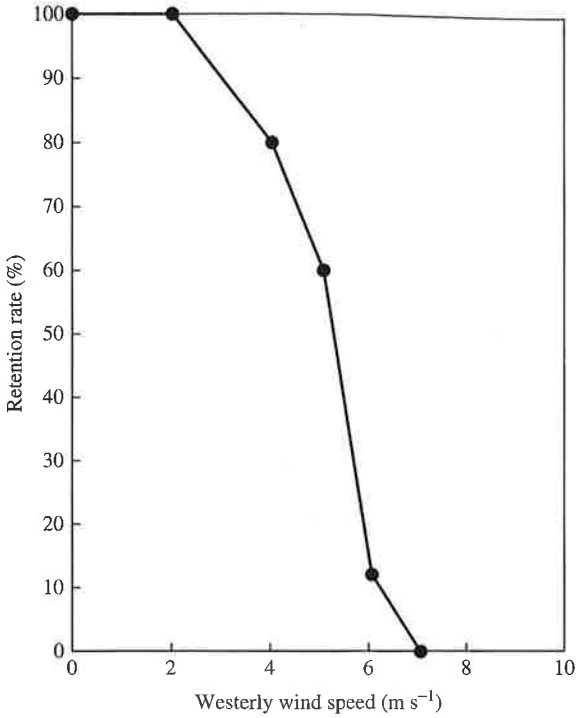


Figure 6.4 From a 3D model simulating transport of yellow striped flounder eggs, the estimated retention rates (%) of particles released from the spawning grid after a 30-day shift under various westerly wind speeds. (*Source*: Nakata *et al.* 2000. Reproduced with permission of Elsevier.)

depth (below 30 m), and to facilitate entrainment into coastal eddies observed in the shelf region.

Hydrodynamic and particle-tracking models have become common and powerful tools in recent years for elucidating transport of flatfish larvae as well as their responses to varying physical and biological factors (see Table 6.1). The majority of recent modelling studies incorporate several types of vertical migratory behaviour of larvae. Larval transport of European plaice and European flounder in the North Sea was simulated with and without STST, and the transport to a nursery area (namely, the Wadden Sea) was found to be enhanced by the active vertical movement of larvae (de Graaf *et al.* 2004). Sentchev & Korotenko (2007) simulated larval transport with several types of vertical behaviour for European flounder in the eastern English Channel, and suggested that the vertical movement synchronized with tidal height is likely to occur, comparing the model results with the observed distribution and migration of larvae. Fox *et al.* (2009) modelled transport of European plaice eggs and larvae from the eastern and western spawning grounds in the Irish Sea, estimating that dominant winds and tidally synchronized vertical swimming behaviour supplied larvae from both sides of the Irish Sea to the eastern nursery grounds. Savina *et al.* (2010) also modelled the larval transport of common sole in the southern North Sea, employing several types of vertical behaviour, and their results suggested that the effect of larval behaviour on

Table 6.1 Differences in spawning and transport-related characteristics of flatfishes

Species	Area	Spawning	Pelagic duration (days)	Nursery	Transport characteristics	Authors
Family Pleuronectidae						
Pleuronectes platessa	North Sea	30–60 km offshore		Nearshore, inland seas	Transport with bottom currents, then STST	Van der Veer *et al.* (1998); Cushing (1990); Rjinsdorp *et al.* (1985)
	Irish Sea	Nearshore		Nearshore	Retention	Nash & Geffen (1999)
	Kattegat/Belt Sea	Offshore		Shallow water ~5 m	Wind-driven currents, selective transport	Neilsen *et al.* (1998)
P. quadrituberculatus	Gulf of Alaska	Nearshore		Nearshore	Retention and selective transport	Bailey, unpubl. data; Norcross, pers. comm.
Pseudopleuronectes herzensteini	Coastal Japan	Coastal waters ~50 m		Nearshore, coastal	Drift north and inshore retention	Nakata (1996)
P. americanus	NW Atlantic	Estuaries	28–42	Estuaries, coves	Tidal accumulation, retention	Chant *et al.* (2000)
P. yokohamae	Japan				STST	Takahashi *et al.* (1986), cited in Tanaka *et al.* (1989)
Limanda aspera	Gulf of Alaska	Inshore	30–60	Inshore, inner bays	Apparent retention	Bailey *et al.* (2008)
L. ferruginea	Grand Banks, Newfoundland	Offshore banks	90–120	Offshore banks	Retention	Neilson *et al.* (1998); Walsh (1992)
L. limanda	North Sea	Offshore		Inshore	Offshore settlement, inshore migration	Bolle *et al.* (1994)
Glyptocephalus cynoglossus	Newfoundland	Offshore banks	120–360	Offshore	Retention	Neilson *et al.* (1998)
G. zachirus	Oregon , USA	Offshore	100–300	Offshore	Long larval life, Ekman onshore transport	Pearcy *et al.* (1977)
Platichthys flesus	East English Channel		30–60	Coastal estuares	Drift north, then after flexion STST towards coast	Grioche *et al.* (2000)
	SE North Sea			Coastal estuaries	STST	Campos *et al.* (1994)
	North Sea	Offshore		Coastal estuaries, tidal flats	STST	Jager (1998, 1999)
P. bicoloratus	Sendai Bay Coastal Japan	Nearshore	60	Estuaries	Ekman	Nakata *et al.* (1999); Yamashita *et al.* (1996); Tsuruta (1978)

	SE North Sea North Sea	Offshore		coast Coastal estuaries Coastal estuaries, tidal flats	STST STST	Campos *et al.* (1994) Jager (1998, 1999)
P. bicoloratus	Sendai Bay Coastal Japan	Nearshore	60	Estuaries	Ekman	Nakata *et al.* (1999); Yamashita *et al.* (1996); Tsuruta (1978)
Parophrys vetula	Oregon, USA	Offshore		Estuaries	Onshore Ekman	Boehlert & Mundy (1987)
Hippoglossoides platessoides	North Atlantic	Offshore banks	30–120	Offshore banks	Retention	Walsh (1994); Neilson *et al.* (1998)
Microstomus pacificus	Oregon, USA	Offshore >400 m	365–550	Offshore, outer shelf	Ekman onshore and postsettlement migration	Pearcy *et al.* (1977); Toole *et al.* (1977)
Eopsetta jordani	Oregon, USA	Offshore, deep water	180	Inner shelf	Ekman onshore	Pearcy *et al.* (1977)
Hippoglossus stenolepsis	Gulf of Alaska	Continental slope	>200	Inshore bays	Directed transport	Bailey & Picquelle (2002)
Reinhardtius, (as Atheresthes) stomias	Gulf of Alaska	Continental slope		Inshore bays	Directed transport	Bailey & Picquelle (2002)
Reinhardtius hippoglossoides	Norway	Continental slope	600–900	Slope, banks, coastal waters	Transport northwards onto banks and coastal waters	Haug *et al.* (1986)
	Bering Sea	Continental slope	>600	Outer, middle shelf	Transport northwards and over continental shelf	Sohn *et al.* (2012)
Family Achiridae						
Trinectes maculatus	Atlantic coast	Estuaries		Estuaries	Presumed retention, movement up estuaries	Miller *et al.* (1991)
Family Paralichthyidae						
Paralichthys dentatus	Onslow Bay, North Carolina USA	Shelf, offshore	30–70	Nearshore, estuaries	Cross shelf, STST	Burke *et al.* (1998)
P. olivaceus	Wakasa Bay, Japan	Wakasa Bay	30–60	Nearshore	Nearshore bottom retention	Burke *et al.* (1998)
	Shijiki Bay, Japan	Offshore		Nearshore	STST	Tanaka *et al.* (1989)
Family Soldeidae						
Solea solea	Bay of Biscay, France	40–80 km offshore	30–60	Inshore bays, estuaries	STST?	Amara *et al.* (1998)
					Retention offshore, then Ekman transport, diffusion inshore	Koutsikopoulos *et al.* (1991)
	Eastern English Channel	Nearshore		Inshore coastal	Retention, tidal	Grioche *et al.* (2000)

Note: Authors for most information are cited, some information also obtained from Miller *et al.* (1991).

their retention above the nursery areas is not consistent through space. Moreover, they showed that the influence of varying hydrodynamic conditions on the variability of larval retention is greater than the variability caused by different larval behaviours.

Models have also been used to determine connectivity of flatfish species between spawning and nursery areas. In the Bering Sea, a biophysical model was used to examine relative importance of selected spawning and nursery habitats for northern rock sole (Cooper *et al.* 2013). Model output was used to identify principal corridors of transport, and to develop connectivity matrices that quantified the contribution of larvae originating from any one spawning area to any nursery habitat. Rochette *et al.* (2012) developed an individual-based model coupled to a hydrodynamic model to simulate common sole larval supply from spawning to estuarine and coastal nursery grounds for the eastern English Channel over a 14-year time series. Larval supply was more sensitive to the duration of larval drift than to the volume of spawning, providing an explanation for lack of significant stock-recruit relationships. Ådlandsvik *et al.* (2004) modelled larval transport of north-east Arctic Greenland halibut (*Reinhardtius hippoglossoides*), and their model indicated that the important nursery habitats for juveniles were the areas north and north-east of Spitzbergen. Studies such as these can offer important insights into which areas constitute critical production areas, and by extension, which might be most important to consider when developing management scenarios. When coupled to climate projection models they may be useful for management strategy evaluations that will guide future fishing practices if the current mechanisms are altered.

A common problem with the widespread use of the larval transport models is the paucity of model validations, both physical and biological. Rigorous oceanographic and biological comparisons with field data, such as the type used to validate the much-employed Regional Ocean Model System (ROMS) are particularly constructive (ex: Danielson *et al.* 2011). However, when our knowledge of biological information, such as ontogenetic changes in vertical distribution of larvae, is limited and not sufficiently incorporated into the model, the model results may not fully explain the observed field distribution, although passive larval transport has been argued to be plausible for juveniles of English sole *Pleuronectes vetulus* found in the northwest estuaries of the U.S. (Rooper *et al.* 2006). Needless to say, well-designed field surveys and laboratory experiments are encouraged in order to provide the best information with which to inform future biophysical models, and vigorous comparisons of model output with field-derived observational data is critical.

6.4 Adaptations to transport conditions: geographical and species comparisons

Across the taxonomic range, flatfishes have a variety of transport requirements during the larval to juvenile stage (Miller *et al.* 1991; Figure 6.5). As noted earlier, they are relatively feeble swimmers, so they must have other adaptations to reach nearshore

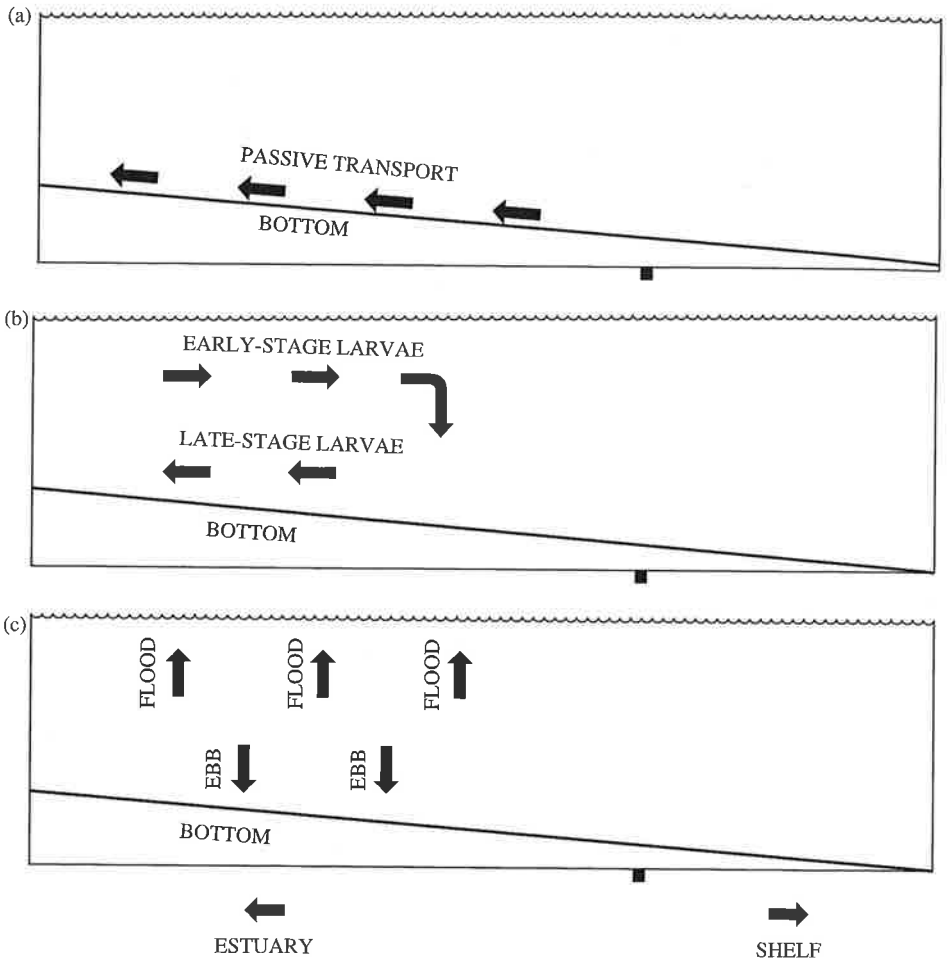


Figure 6.5 Comparison of mechanisms for dispersal and recruitment of estuarine larvae. (a) Spawning occurs offshore and larvae are transported inshore by residual bottom flow. (b) Spawning occurs inshore and larvae are transported downstream by surface flows; older larvae sink and are transported upstream in the residual bottom flow. (c) Spawning occurs near the estuary mouth; larvae migrate up in the water column on flood tides and sink on ebb tides, resulting in net upstream transport. (*Source*: Epifanio 1988. Reproduced with permission from (Epifanio 1988).)

targets. Spawners in estuaries generally have their nurseries in estuaries, so retention is critical. Species that spawn on the coastal shelf/slope with coastal shelf/slope nurseries also depend on retention mechanisms. These species may spawn in areas where fronts, eddies or other retention features may prevail. On the other hand, many species depend on cross-shelf migration into shallow water, into estuaries or even transport up estuaries into freshwater. In this case, spawning in areas that favour directed transport, or behaviours that take advantage of currents, such as STST, are common. This section presents examples of adaptations that flatfishes have developed to get to their nurseries.

6.4.1 Comparisons among species within a geographic region

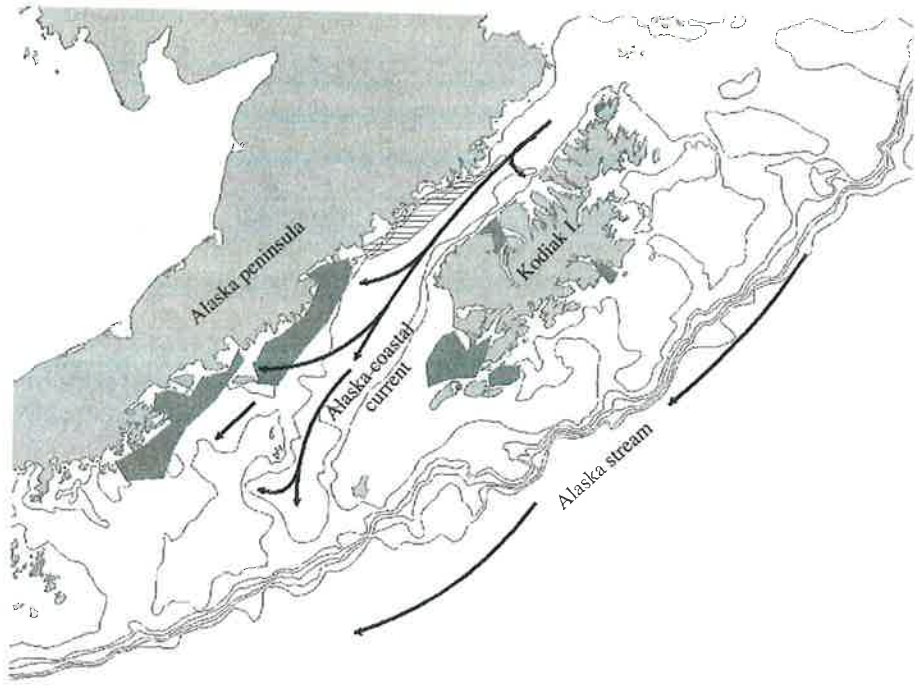
Within a relatively small geographic area, species may be transported in different directions based on their distribution and behaviour in the local current system. In Shelikof Strait, located in the Gulf of Alaska between Kodiak Island and the Aleutian Peninsula (Figure 6.6) there is an estuarine type circulation with the surface Alaska Coastal Current (ACC) flowing towards the southwest, countered by a deep current flowing up the strait. A weak nearshore current flows down the strait hugging the coastline. At about the same time and within the same region, different species of larvae are moving in different directions and at different rates. For example, Pacific halibut (*Hippoglossus stenolepsis*) larvae (eggs 300–400 m deep, larvae in the upper 50–100 m) are transported from the slope region at the exit of the strait in an up-strait direction northward to their nursery grounds in shallow water. Flathead sole (*Hippoglossoides elassodon*) (eggs spawned at 150–250 m, later stage eggs and larvae in the upper 40 m) are spawned near the centre of the strait and are transported southwestward in the ACC, while Alaska plaice (*Pleuronectes quadrituberculatus*) (eggs spawned in shallow water 50–100 m and larvae above 20 m depth) are transported downstream and are retained in the shallow coastal waters in the vicinity of their nurseries in coastal bays. Yellowfin sole (*Limanda aspera*) are spawned on offshore banks, are retained nearby and recruit inshore to bays.

Species in the same vicinity may demonstrate different transport characteristics through variations in vertical migration behaviour within a system of currents. In the eastern English Channel, Grioche *et al.* (2000) showed that European flounder larvae drift northward until they approach metamorphosis. During their drift, flounder larvae do not migrate vertically and are not retained until the flexion stage, when they migrate to near the bottom on the ebb flow, which advects them towards the coast. On the other hand, the common sole remains in the nearshore coastal waters and its retention can be attributed to tidal and diurnal vertical migrations undertaken by the larvae.

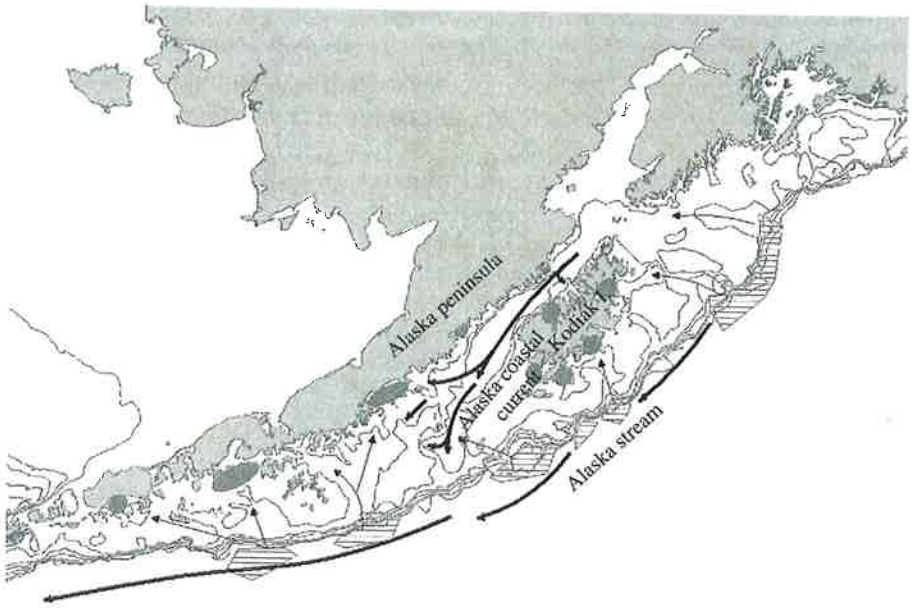
Different colonization strategies were observed in an estuarine nursery ground by several marine flatfish species (Primo *et al.* 2013). For Senegalese sole, though larvae were present throughout the year at downstream areas, evidencing a protracted spawning season, there was low settlement success and juvenile densities within the Mondego estuary. In comparison, European flounder and common sole attained high juvenile densities within the estuary despite low larval abundance, as these species seem to settle mainly in the nearby coastal areas and later move into the estuary (indirect settlement). Studies in another closely located estuary further corroborate different colonization strategies for an area (Ramos *et al.* 2010).

Amara *et al.* (1998) compared the transport characteristics of common sole with the thickback sole (*Microchirus variegatus*) in the Bay of Biscay. In this case, both species spawn 40–80 km offshore. Late-stage common sole larvae and early-stage juveniles are transported to their nurseries in bays and estuaries after about 60 days, possibly using STST. On the other hand, thickback sole larvae have no swimbladder, show limited vertical migration and settle in the offshore habitat. Their larvae are not caught above 40 m depth in the water column and may make an early shift to near bottom, where currents are weaker, effectively retaining them in the offshore habitat. Using the development

Figure 6.6 Potential schematic for different transport patterns of four species of flatfish larvae in the Shelikof Strait, Alaska. Hatched areas indicate spawning areas; grey areas indicate presumed and known nurseries; thick arrows indicate currents, and thin arrows indicate presumed transport routes. (a) Yellowfin sole are spawned in shallow water over banks on the outer side of Kodiak Island. Their eggs and larvae are retained in the current system and juveniles recruit inshore to local bays. (b) Alaska plaice are spawned in shallow water on either side of the sea valley, are transported downstream and are retained near nursery areas in bays.



(c)



(d)

Figure 6.6 (c) Flathead sole are spawned over deep water in the sea valley and are transported downstream in the Alaska Coastal Current towards nursery areas over the continental shelf. (d) Pacific halibut are spawned offshore over deep water and are carried inshore by topographically steered currents up the sea valley; halibut nurseries are in coastal bays. Information on larval flathead provided by S. Porter (Alaska Fisheries Science Center, Seattle, WA, USA) and information on juvenile flatfishes provided by B. Norcross (University of Alaska, Fairbanks, AK, USA) and in Norcross *et al.* (1999).

of accessory primordia in otoliths, the authors inferred that thickback sole shift to lateral swimming orientation associated with settling before metamorphosis, whereas common sole show orientation to the bottom in late metamorphosis.

6.4.2 Congeneric comparisons in different regions

There are differences in the spawning location and transport characteristics of closely related species in different areas. For example, Burke *et al.* (1998) compared transport characteristics of two species of *Paralichthys* in different oceans. In Wakasa Bay, Japan the Japanese flounder (*P. olivaceus)* stays near the bottom throughout the tidal cycle. The tidal currents in this region of coastal Japan are weak and estuarine habitat is limited by a narrow and steep continental shelf. In contrast, the Atlantic coast of the United States has a strong tide, a wide shallow continental shelf and extensive estuarine habitat. In Beaufort Inlet, the summer flounder (*P. dentatus*) abundance varied with the tidal stage; high densities of flounder were sampled at the bottom during ebb tide and in the water column during the flood. Late-stage larvae appear to use vertical migration and tidal streams to migrate from offshore into the estuarine nursery, and settlement occurs in the intertidal. By comparison, in Wakasa Bay, Japanese flounder larvae may be passively transported into the bay. However, in another area of Japan where the tides are stronger, Japanese flounder larvae seem to be using STST to migrate inshore (Tanaka *et al.* 1989). Burke *et al.* (1998) showed from laboratory experiments with wild-caught and laboratory-reared larvae that the degree of development of an endogenous tidal rhythm in the larvae appears to depend on the regional coherence and strength of tidal variation, suggesting some behavioural flexibility in paralichthyids in different areas.

Other congeneric species in different oceanic systems show remarkable differences in transport characteristics (Table 6.1). Species in the genus *Limanda* show a great variety of mechanisms for reaching their shallow nurseries. Yellowfin sole in the Gulf of Alaska spawn in shallow water where currents are weak and larvae are retained. Yellowfin flounder (*L. ferruginea*) that spawn on offshore banks in the western North Atlantic are apparently retained there. Dab (*L. limanda*) in the North Sea spawn offshore, and settlement occurs offshore followed by an inshore migration of juveniles. Finally, marbled flounder (*Pseudopleuronectes yokohamae*) are believed to use STST to reach their nearshore nurseries.

Two species in the genus *Glytocephalus* also demonstrate remarkable differences in transport strategies. Rex sole off Oregon has an extremely long planktonic life, believed to be about a year (Butler *et al.* 1996). Spawning is in late winter. Presumably larvae take advantage of the high production associated with prevalent spring and summer upwelling, and utilize wintertime onshore Ekman currents nearly a year later to reach nurseries over the shelf. Witch flounder (*G. cynoglosus*) in the north Atlantic also has a long planktonic life (Scott & Scott 1988) but is spawned on offshore banks and retained there.

6.4.3 Conspecific comparisons in different geographic areas

Within the family Pleuronectidae there are also some remarkable differences in transport characteristics varying from retention, to selective transport using Ekman

currents, to STST (Table 6.1). However, different subpopulations of European plaice also have different mechanisms to arrive in nearshore nurseries. In the Irish Sea, European plaice spawn nearshore in close proximity to nursery areas in areas of reduced tidal flow and larvae are apparently retained there (Figure 6.7). In the Kattegat/Belt Sea area of Scandinavia where tidal currents are weak, spawning occurs offshore and larvae ride wind-driven Ekman currents to reach shallow nurseries. Finally in the North Sea, larvae ride bottom currents into near coastal waters and perhaps use STST to reach nearshore and inland sea nurseries. Further research is needed to determine whether these adaptations are inherent characteristics of local

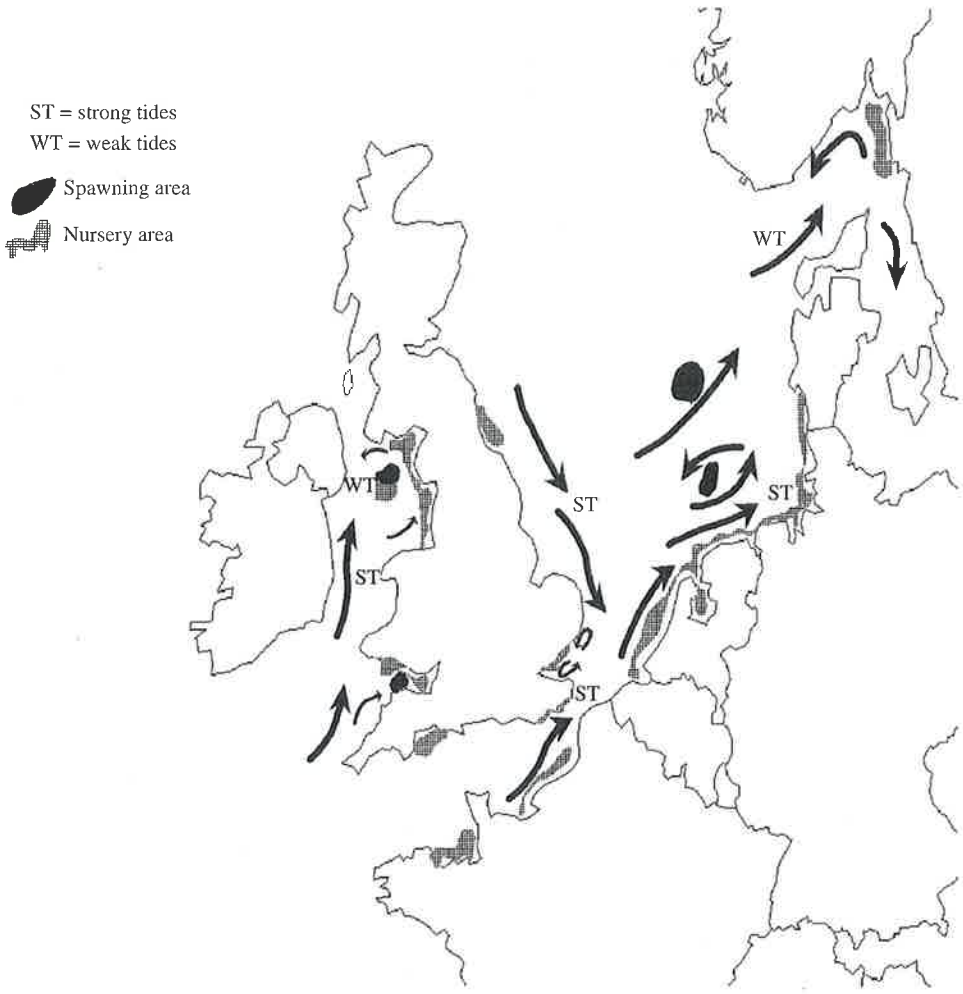


Figure 6.7 Transport conditions for European plaice in three major spawning areas. In the Irish Sea near the Isle of Man, residual tidal currents are weak and plaice spawn near their nursery area. In the English Channel and North Sea, residual currents are strong towards the northeast and tidal currents are strongly shoreward. Larvae drift with residual currents and may use tidal currents to arrive at coastal nurseries. In the Skagerrak-Kattegat area, tidal currents are weak and larvae are transported to the Swedish coastal region by wind-driven currents.

populations or arise from behavioural flexibility and responses to different cues in the different areas.

In the Soleidae family, no evidence of behavioural selection of tidal currents by pelagic common sole larvae was found in the Mondego estuary and Bay of Biscay (Champalbert & Koutsikopoulos 1995; Primo *et al.* 2013) contrary to the findings of Grioche *et al.* (2000) in the English Channel. These differences are likely due to the stronger tidal currents in the English Channel, which trigger vertical migration behaviour. As for Senegalese sole, despite a similar direct settlement strategy in two estuarine nurseries (Mondego and Lima estuaries), the outcome in terms of juvenile densities is quite distinct (low and high densities respectively) (Primo *et al.* 2013; Ramos *et al.* 2010). The lack of suitable intertidal habitat for juveniles in the Mondego is suggested as a possible explanation (Primo *et al.* 2013).

In response to different salinity regimes, European flounder in the Baltic Sea evolved two distinct spawning behaviours, which have led to significant population structure and isolation by distance (Florin & Höglund 2008). These authors suggest that demersal spawners may be descendent from a population that colonized the Baltic earlier than pelagic spawners which adapted to brackish salinity via thicker shelled and more robust eggs. This feature may be essential for survival at low salinity.

6.4.4 *Local adaptations*

Although the above interspecies comparisons show differences in transport mechanisms, species within a common geographic region dominated by different types of currents may share prevailing transport characteristics. For example, in the North Sea where tidal currents are strong, numerous flatfish species use STST to reach inshore nurseries including European plaice, European flounder and common sole. It is recognized that generalizations about tidal currents over broad regions of the shelf are dangerous with regards to life history adaptations of local fish populations, as tidal currents can be strongly affected by local features such as bathymetry. In the California Current system, an upwelling system dominated by Ekman currents, many species either have adaptations to minimize transport offshore, such as spawning demersal eggs or viviparity (Parrish *et al.* 1981). They may spawn during periods of downwelling, or in areas characterized by onshore transport. In addition, some species have an unusually long planktonic period with a flexible age-at-settlement, favouring the eventual finding of suitable nursery habitat. In other areas dominated by specific and predictable current patterns there may be a similar predilection for specific local adaptations. Given the future availability of data on many more species, it will be of interest to discover whether life history patterns are dominated by taxonomic similarities or whether different species in different areas have converged on similar patterns of local adaptation, a trend that the limited amount of available data tend to support.

According to Gibson (1999), with reference to European plaice 'the selection of settlement area is determined by the hydrographic relationship between the spawning ground and the nursery area. In areas where currents are only weakly directional, spawning grounds are situated close to the nursery ground. Where currents are strong, the choice of location of the spawning ground has presumably evolved so that eggs

are released at an optimum direction and distance from the settlement areas. Stocks are thus 'hydrographically contained' (Cushing 1990) within a limited area.' Likewise, according to Boehlert & Mundy (1988) 'behaviours associated with shoreward movement are likely related to distribution in the water column and have evolved to take advantage of mean current conditions in the species habitat.' The above studies, which range from comparisons across the flatfish order, to studies of congeneric species, to studies within a species, support the concept of local adaptation of transport characteristics in different oceanic systems to favour transport towards or retention in nearshore nurseries. Similar observations have been made for invertebrate species (e.g. LeFèvre & Bourget 1992). As those authors summarized, different species have distinct vertical distributions in a given environment and a single species may have different distributions in different environments, affecting how they may be transported or retained.

6.5 Transitioning from the plankton

6.5.1 Criticality of timing

The synchronization of morphological development with the transport process is critical for flatfishes. Theoretically, flatfishes undergo the complex process of metamorphosis in the plankton such that they are competent to assume a demersal existence concurrently with arrival at juvenile nursery areas. However, mismatches between morphological development and delivery to appropriate habitat can occur, potentially leaving vulnerable larvae in the lurch. Available evidence suggests that flatfish larvae undergo metamorphosis within a critical size range, suggesting that metamorphosis cannot be postponed indefinitely. Using European plaice as an example, the larvae of this species cannot delay metamorphosis for long periods, so asynchronies in timing and transport can force settlement in unsuitable habitats (Gibson & Batty 1990). However, there are no indications that the process of metamorphosis results in an increased mortality or that it might affect recruitment in flatfishes (Geffen *et al.* 2007). Larvae arriving to unsuitable nursery areas risk increased predation pressure, exposure to unsuitable prey, or abiotic conditions that do not support growth and development. If settled juveniles survive in substandard areas, the complicated, multi-step process of finding and moving to more suitable habitat ensues (Bailey *et al.* 2008).

Alternatively, larvae may not be competent to settle at the time of arrival at nursery grounds, consigning larvae to continued entrainment in the plankton and potentially missing optimal habitat areas. For example, Greenland halibut in the Bering Sea have a long larval pelagic period (>6 months, Bowering & Nedreaas 2000; Sohn *et al.* 2010) with settlement occurring at very large sizes, 70–100 mm SL. Hydrodynamic modelling results indicate that larvae can be advected to suitable habitat over the continental shelf as early as 3 months after spawning (Duffy-Anderson *et al.* 2013), well before Greenland halibut larvae are competent to settle. Currents with entrained larvae do not remain over the continental shelf long however and eventually return to the Aleutian

Basin, placing settlement-ready Greenland halibut juveniles over the comparatively inhospitable ocean deep.

6.5.2 Fidelity to initial touchdown sites

Metamorphosing flatfish that drop out of the plankton demonstrate remarkable plasticity in their fidelity to initial settlement areas. Some species (or populations) reside within initial settlement zones for long periods (weeks, months) while others continue to make intermittent use of the plankton to move significant distance from initial touchdown sites. In the case of the latter, this 'pseudo-settlement' phase (Tanaka *et al.* 1989) can be a protracted period that precedes final settlement. For example, windowpane flounder (*Scophthalmus aquosus*) postlarvae exhibit a progressive shift from pelagic to demersal habitats (Neuman & Able 2003), occupying a series of transitional habitats over a period of weeks prior to settlement into final nursery areas. During pseudo-settlement, the shift from plankton to benthos is a repeated process; the settlement-ready animal exhibits a cycle of entrainment in the plankton, gradual migration to the bottom of the water column, touchdown, and then a resumption of entrainment in the plankton. This process can be iterative through many cycles, offering significant dispersal potential to metamorphosing flatfish. Mechanisms that control this iterative process are still under investigation, though by migrating only short vertical distances, flatfish may preferentially select their residence in currents moving in different directions, thus influencing the direction of transport in currents whose speeds far exceed their own swimming speeds.

6.5.3 Importance of initial settlement areas

Given that a variety of flatfishes, as well as invertebrates and coral reef species (Johnson & Shanks 2002; Kaufman *et al.* 1992; Miller & Shanks 2004), exhibit repeated transitory exchange between the plankton and the benthos, it is reasonable to ask whether pseudo-settlement areas play a significant ecological role in the life history of benthic species or whether they are merely by-products of idiosyncrasies between a pelagic larval phase and demersal juvenile phase. On the one hand, settlement due to chance disparities between timing of development and planktonic dispersal seem likely, given the stochastic events that exert control over this life phase. On the other hand, prenursery habitat areas may have an important ecological function, offering some advantages to settling fish. Little work has been conducted to determine the significance of the pseudo-settlement process or its associated locations, though some roles may be hypothesized. For example, early presettlement areas may afford some protection to young fish over settlement directly to nursery grounds. In the case of northern rock role in the Bering Sea, it has been speculated that early presettlement in deeper, offshore waters with progressive seasonal movement inshore provides thermal protection from sub-zero bottom temperatures in inshore nursery areas (Cooper *et al.* 2014). Likewise, English sole off the coast of Oregon, USA,

may avoid seasonally-transient near-shore hypoxic conditions (Ciannelli, personal communication, Oregon State University). Alternatively, an iterative settlement process may place small postlarvae away from predators or competitors, allowing them greater opportunity for growth prior to movement into final nursery areas.

6.6 Implications

Variations in transport of flatfish eggs and larvae have important consequences for population connectivity, the dynamics of local populations, the genetic structure of populations, metapopulation dynamics and the recovery of local populations after depletions.

6.6.1 Population genetics

How populations are structured in nature is an important aspect of their management and is a complex process as well as a complicated topic. In theory, species with short larval duration should show more genetic heterogeneity among subpopulations because there would be less gene flow through planktonic dispersal (Doherty *et al.* 1995). However, gene flow can be limited even for species with long pelagic stages as a consequence of larval retention features (Palumbi 1995). For example, geographical differentiation of populations of Dover sole along the continental slope of the northeastern Pacific Ocean is consistent with retention of larvae, despite extended pelagic periods, and is inconsistent with long-distance dispersal of adults (Stepien 1999). Witch flounder also has a long larval stage, but shows significant stock structuring that may be related to larval retention (Fairbairn 1981; Table 6.1). Other species, such as Pacific halibut, have a long planktonic life, and little apparent evidence for subpopulation structure (Grant *et al.* 1984). Species with long planktonic stages may have populations that are differentiated by distance along the flow of ocean currents (Knutsen *et al.* 2007a).

Gene flow should vary inversely with dispersal rates, but even species with potentially high dispersal can show genetic population structure that reflects both the historical demography and present dispersal patterns (Rocha-Olivares & Vetter 1999). Furthermore, present patterns of genetic structure may reflect highly pulsed dispersal that may have occurred in past global climate changes or due to shifts in currents over the last 1–3 million years. Even though present currents may 'connect' them, the persistence of genetic differences indicates a lack of effective contemporary gene exchange (Benzie 1999; Shigenobu *et al.* 2013). In at least one population, that of European plaice in the North Sea, there appears to be evidence of reduced gene flow and inbreeding after a period of high exploitation between 1950 and 1970 (Hoarau *et al.* 2005).

The metapopulation concept may be useful for assessing gene flow, risk of extinction, and potential for recolonization of depleted populations. Given that the major potential for population dispersal is in the planktonic stage, metapopulations for many flatfishes may be organized around larval drift patterns. In support of this concept is the apparent small degree of population structure of several flatfish species in the northeast Atlantic except among major basins like the Mediterranean and North Sea

(Exadactylos *et al.* 1998; Hoarau *et al.* 2004; Was *et al.* 2010). More structure may be found where retention is common (northwest Atlantic: e.g. witch flounder, Norwegian coast: Atlantic cod (Knutsen *et al.* 2007b). There appears to be a high degree of structure in some flatfish populations around the Japan archipelago due to the complex landscape and currents (Shigenobu *et al.* 2007). Cushing (1990) observed that the spawning and feeding grounds of different European plaice stocks are located near different tidal streamlines, and that these pathways may prevent extensive mixing of populations. Exceptions to metapopulations forming around drift patterns may be where long distance migrations occur, for example Pacific halibut.

6.6.2 Recruitment

Many factors have an influence on recruitment (see Chapter 8). However, certain controls may be more important at different latitudes, or among groups of species with similar life history traits (Miller *et al.* 1991). Because of their dependence on transport to nearshore nurseries, variability in this process may be of particular importance to flatfishes.

Numerous studies point out the importance of transport of eggs and larvae for the recruitment process of flatfishes (e.g. Boehlert & Mundy 1987; Nakata *et al.* 2000). Modelling results show that variations in circulation patterns in the North Sea might be a key factor in determining year-class strength of European plaice (Van der Veer *et al.* 1998; Bolle *et al.* 2009). This is further supported by empirical field studies of European plaice recruitment (Van der Veer 1986; Van der Veer *et al.* 1990). Year-class strength of European plaice depends on successful larval delivery, but variability can be dampened on the nursery grounds. Larval transport and sea temperature may both be impacted similarly by wind conditions, and may also interact by the effect of temperature on development rate and therefore the duration of the drift period (Van der Veer & Witte 1999). Winter winds and river discharge, two factors influencing larval transport, were found to explain 83% of the variability in abundance of age-0 southern flounder (*Paralichthys lethostigma*) in the estuarine nursery grounds (Taylor *et al.* 2010). Similarly, river discharge was found to explain 73% and 46% of densities of 0-group European flounder and common sole, respectively, in the Mondego estuary (Martinho *et al.* 2009).

A comparison of European plaice recruitment among stocks has some intriguing implications. In the Kattegat/Skagerrak where tidal currents are weak, wind-driven currents dominate larval transport (Nielsen *et al.* 1998). Pihl (1990) found that variations in onshore winds are related to the abundance of European plaice in their nearshore nursery and Pihl *et al.* (2000) considered that the concentration of larvae in the water column and exchange of water in the nursery ground determine the rate of larval delivery, and may explain some patterns of newly settled European plaice larvae along the coastline of the Swedish Skagerrak archipelago.

In the North Sea, where the larval transport is long distance, larval density near the nursery is correlated with the number of settling age-0s, suggesting that transport is a key factor in the recruitment process. But in the Irish Sea, where the nursery is in close proximity to spawning, the settled numbers are correlated with egg

abundance, suggesting that variability in larval drift is not a critical factor. In fact, year-class strength may be determined in the juvenile nursery (Nash & Geffen 2000).

Rijnsdorp *et al.* (1992) suggested that for common sole, the period in which recruitment level is determined is the pelagic or early juvenile stage based on correlations between age-0 abundance and recruitment levels. The factors determining recruitment vary over a scale of 100–200 km, and similarities in recruitment patterns of 0-group common sole are restricted to nursery areas which have a similar direction of coastline. The authors suggested that hydrographic conditions involved in transport of larvae to coastal nurseries could be important. The coefficient of variation in recruitment was highest in the North Sea (127%), lower in the Irish Sea (97%), and significantly less in the eastern and western English Channel (34% and 55%, respectively). Recruitment variability is interesting to compare with transport characteristics; in the North Sea, postlarval common sole are carried to nursery grounds by residual tidal currents (Berghahn 1984, cited in Rijnsdorp 1992), whereas where sole spawn in the Irish Sea the residual tidal currents are relatively weak therefore successful spawning occurs relatively close to the nursery grounds.

Recruitment of Pacific halibut has been correlated with transport and cross-shelf transport during its 6-month pelagic larval phase. For example, Parker (1989) found that recruitment is density-dependent, but is also influenced by strong winter winds, which favour production of strong year-classes. It was suggested that alongshore and cross-shelf winds generated transport conditions favourable for survival. Parker (1989) and Bailey & Picquelle (2002) also suggested bathymetric steering of currents carrying offshore larvae into coastal nurseries. Accelerated coastal currents could entrain offshore waters into troughs which could be a key avenue for directing larvae in the Gulf of Alaska towards inshore nurseries.

In summary, losses may be substantial when eggs are spawned or larvae are transported beyond typical habitat boundaries. The geographical locations and the times of fish spawning represent evolutionary adaptations to the climatological mean water circulation pattern (Bakun 1985). The deviations from the transport pathway under the mean water circulation may be a cause of recruitment variations. Various physical mechanisms have therefore been proposed to explain the variations in transport pathways as a causal factor for recruitment success/failure. Although it should also be recognized that the relative importance of individual factors may change from year to year (Miller *et al.* 1991), in the case of many flatfishes broad physical processes affecting the transport in the pelagic stages are of great importance to year-class strength determination.

6.6.3 Connectivity

Recruitment of many flatfish populations is constrained by factors influencing connectivity, and for some species the connectivity continuum occurs across several geographic areas. Therefore, disruptions upstream have the potential to impact larval and juvenile ecology over multiple areas downstream. However, the effects of oscillations in larval supply to nursery areas may be mitigated if those habitats receive input from multiple sources. Further, self-recruiting populations with comparatively

closed demographics that rely on oceanographic retention features may be more vulnerable to the effects of transient breakdowns in connectivity than populations with open connections. As an example, winter flounder along the east coast of the United States have a relatively isolated population structure, rely on a complex interaction of larval behaviour and physical oceanography to remain near to adult spawning grounds, and are more vulnerable to fluctuations in local environmental conditions than to broad-scale climate factors (Crawford & Carey 1985; Chant *et al.* 2000; Sogard *et al.* 2001). Breaks in connectivity for these isolated populations could put them at greater risk of local extinctions. The scales of potential disruptions vary in time and space however, and while impacts of local disruptions in connectivity disproportionately impact closed populations, species with open connections, which are facilitated by long pelagic stage durations and large dispersal distance, may be more affected by broad scale shifts in ocean conditions. O'Conner *et al.* (2007) employed the metabolic theory of ecology to predict the effects of increasing ocean temperatures on metabolic rates and pelagic larval duration. These authors estimated that an increase in ocean temperature of 4 °C would decrease larval pelagic stage duration by nearly half. Reductions in dispersal potential have critical implications for flatfish that must disperse to nursery grounds that are scores of kilometres away, as well as for population resistance, resilience and overall biodiversity.

Challenges to direct observation of larval dispersal from spawning area to nursery habitat include the small size of the animals and the complexity of the marine environment (Cowen & Sponaugle 2009). Indirect methods such as population genetics (Stepien 1999), elemental chemical analyses (Tanner *et al.* 2011; Reis-Santos *et al.* 2012), and tagging (Sagarese & Frisk 2011) enable postsettlement discrimination of natal sources from which connectivity can be inferred but direct measurements through the physical oceanographic realm remain challenging. Some progress has been made in the study of flatfishes that utilize nearshore environments but much remains unknown for offshore or deep-water flatfishes where environments are relatively inaccessible or altogether hostile. For these species, biophysical models have proven useful. Vestfals *et al.* (2013) have shown that interannual differences in broad scale circulation may differentially influence dispersal corridors for Pacific and Greenland halibut in the Bering Sea by affecting the timing and location of pathways across the continental slope. For nearshore species, the fronts, eddies, stratification, and winds that all serve as key components of the larval transport process are all vulnerable to local and regional modulation (Munk *et al.* 2009), influencing the dispersal process and potentially connectivity as well.

6.6.4 Management

Historical notions of protracted larval dispersal phases contributing to population panmixia have come under scrutiny (Cowen *et al.* 2000), and management strategies based on views of single, well-mixed populations across large spatial scales are receiving renewed attention (Fogarty & Botsford 2007). Flatfishes are no exception to this re-evaluation. As an example, the International Pacific Halibut Commission, an international US-Canada joint venture, has historically managed Pacific halibut

as a single, well-mixed stock ranging from as far south as northern California to the western Aleutian Islands. However, recent evidence (Seitz *et al.* 2011) suggests that Pacific halibut along the Aleutian chain experience isolating geographic conditions and barriers to oceanographic transport that limit genetic exchange, and the long-standing single-stock management strategy is currently being re-evaluated.

The identification of marine reserves for management of species with specific habitat requirements has also received significant attention in the last decade. However, flatfishes generally have life history characteristics that are conducive to dispersal and connectivity, such as having wide ranging distributions, high fecundity, and protracted pelagic egg and larval phases, and have not been identified having the potential to benefit from the establishment of marine reserves (Shipp 2003). However, if adult spawning occurs in fixed geographic locations, and resultant larvae are subject to oceanographic features that differentially influence the dispersal or settlement process, subdivision could occur within the population, potentially warranting re-evaluation of the utility of reserves for flatfishes. Indeed, Sekino *et al.* (2003) noted just such a confluence of conditions among spotted halibut (*Verasper variegatus*) occurring along the Japanese coast. These authors showed that, despite significant larval vagility, genetic differentiation occurred among fish in all habitats examined. The authors attributed their findings to the settlement of larval 'vagrants' to discrete suitable nursery areas which drove localized recruitment and contributed to discrete population structure. Indeed, successful management of flatfish populations requires concerted, cross-scale efforts that encompass critical production areas, including larval input sources, pseudo-settlement transition areas, and final juvenile nursery habitats.

6.6.5 Research needs

While larvae are generally acknowledged to have a large potential for dispersal, in many species the spawning areas, nursery habitats and connectivity between the two are unknown. This lack of fundamental knowledge represents a major deficit in our understanding of population dynamics of these species, which hinders the development of effective management and conservation strategies. Research should focus on improving baseline knowledge of larval life stages (e.g. mortality, pelagic larval duration, and larval distribution), as well as on other life stages, which are necessary for population dynamics modelling efforts. These basic data will go a long way towards identifying the relative importance of each life stage to population growth and fisheries yield.

Coupled physical and biological models can augment our understanding of population connectivity, and help evaluate the degree to which environmental variables mediate larval dispersal and nursery habitat settlement. Large-scale, broad resolution biophysical models have been employed to determine general drift patterns, but often do not capture the small-scale distribution patterns of settled juveniles. For example, northern rock sole juvenile nurseries are located inshore of a seasonally established hydrographic front, though output from broad-scale settlement models suggest that nursery areas occur offshore of the front (Cooper *et al.* 2013). Much-needed are high-resolution models that can capture the fine-scale oceanographic processes (local

eddies, fronts, tides, etc.) that influence the movement of 'pseudo-settlement' stage postlarvae from initial touchdown sites to final nursery grounds.

Equally useful are additional comparisons among species within the same physical setting, and single-species comparisons between different physical settings. For the former, time-series investigations that can capture mechanisms behind interannual shifts in dispersal pathways are critical. For the latter, studies that examine circumpolar species with geographic ranges that extend over several large marine ecosystems (ex: Greenland halibut) offer excellent platforms for cross-ecosystem investigations of local adaptations and the larval dispersal process. Of course, any single model may not be sufficient to accurately capture the ecology of all phases of early life dispersal, so efforts to develop sequential, linked models over the connectivity continuum are encouraged. The challenge regarding modelling is to obtain realistic depictions of connectivity, namely of source and dispersal linked to oceanographic processes and life history characteristics (Werner *et al.* 2007).

Finally, addressing the temporal stability of connectivity patterns will be an important milestone. Questions that affect the degree to which connectivity might be affected by climate oscillation include: 'Do adults return to the same spawning areas under changing climate conditions? How resilient are larval transport pathways to oceanographic variation? Do larvae adjust their behaviour to mitigate changing circulation?' These questions are particularly important for species living at the limits of their biogeographic ranges. Furthermore, recognizing which spawning sites and settlement habitats effectively maintain adult populations should be prioritized. Such identification is paramount to obtain the highest returns in terms of ecological and economical resources as well as to optimize management and conservation efforts.

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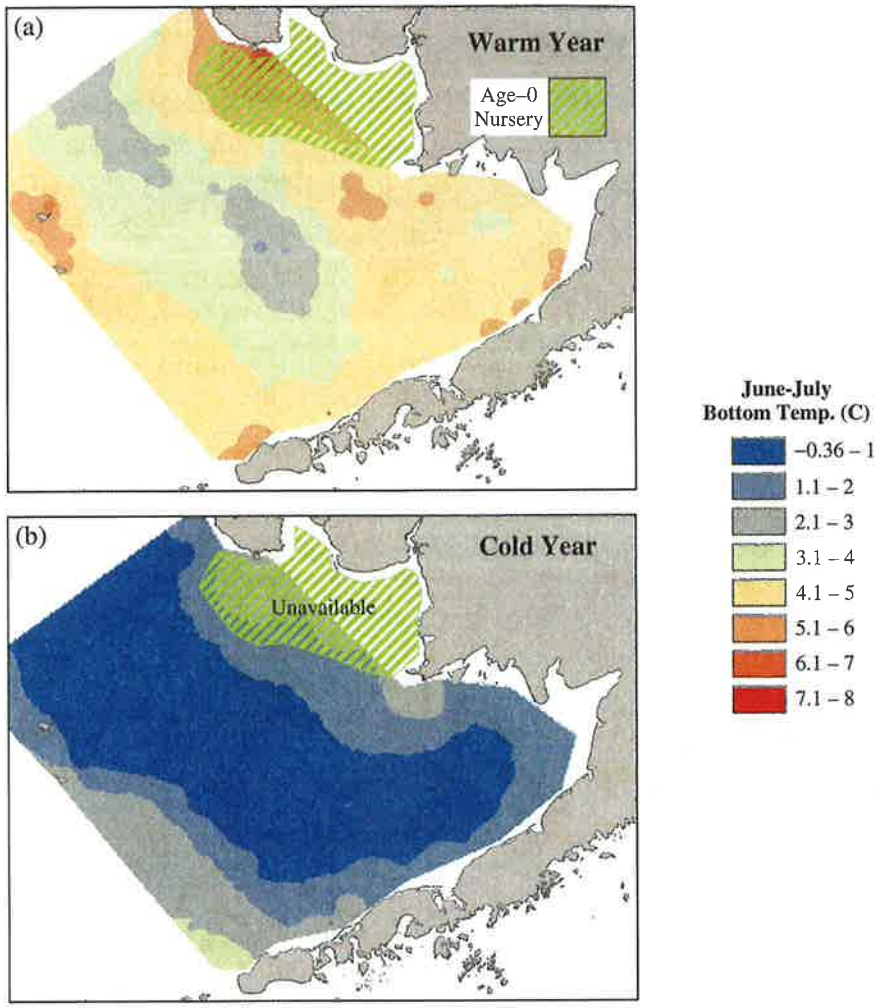

Figure 6.2 Nursery habitat for age-0 northern rock sole during warm (top panel) and cold (bottom panel) regimes. Greyscale ramp indicates bottom temperature (°C). (*Source*: Adapted from Cooper *et al.* 2014).

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