

Flatfishes

Biology and Exploitation

Edited by

Robin N. Gibson

Scottish Association for Marine Science

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Chapter 5

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

Kevin M. Bailey, Hideaki Nakata and Henk W. Van der Veer

5.1 Introduction: the problem

Marine fishes spawn from tens of thousands to millions of eggs per female every year in order to leave sufficient offspring to replace themselves. Temperate species like plaice (*Pleuronectes platessa*) and flounder (*Platichthys flesus*) put up to 44% of their body's energy capital into the spawning process (Rijnsdorp 1994). A strategy of broadcasting many small planktonic eggs to drift in the ocean is a high risk gamble with a low probability of return given that the average survival rate to the age of first reproduction is 0.00001–0.000001%. The obvious risks of this strategy are arriving at an unsuitable habitat, or arriving at the right habitat at the wrong time. Given the natural variability in current speeds and direction, the potential for drift into nursery environments of varying quality might be expected to result in high recruitment variability. There are also some more subtle effects on population genetics caused by the potential mixing of different spawning groups, including outbreeding depression or loss of local adaptive advantage by interbreeding. Surely, however, there must be some overwhelming benefits to a planktonic life stage? One benefit would be the potential for dispersal and colonisation of new habitats (Strathmann 1974). In addition, gene flow between breeding groups might be enhanced, giving rise to the salutary effect of hybrid fitness.

Another advantage of a planktonic stage is to minimise inter-specific competition. Young feeding larvae harvest the numerous prey at the small end of the plankton size spectrum in the sea. Small fish larvae have slow swimming speeds and therefore prey abundance is a critical factor in determining encounter rates and feeding success. As larvae grow and their swimming speeds increase, a shift to larger but less numerous prey becomes possible because speed and improved vision now dominate encounter rates. Prey shifts allowed by ontogenetic development of prowess and by life history changes alleviate competition with other size groups of fish of the same species.

The relative importance of the many causes of mortality of marine fish eggs and larvae varies over a wide range of space and time scales. During planktonic stages there is a remarkable culling of individuals (Fig. 5.1) to leave the most fit for the given set of environmental conditions, or alternatively, the most lucky to have been spawned in the right place at the right time. 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. The question is whether flatfishes do anything to maximise their probability of arriving there, or whether it is a random process.

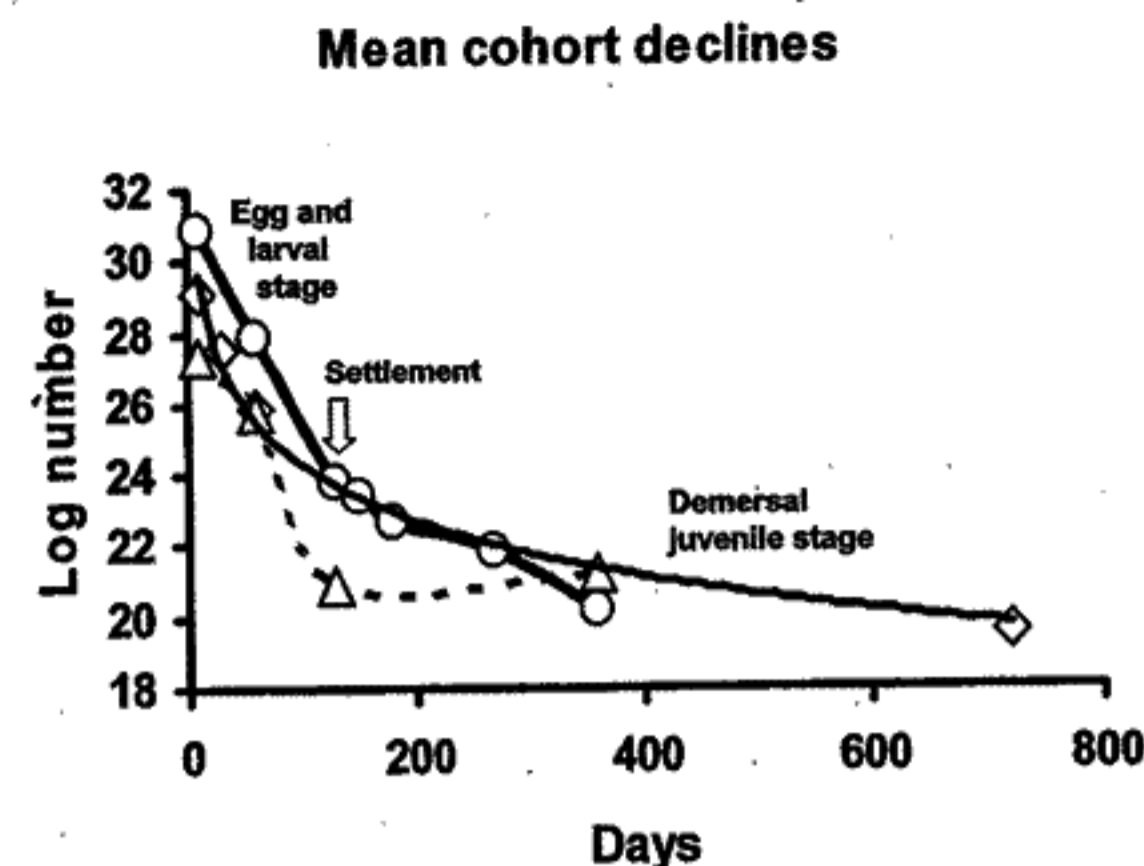


Fig. 5.1 Cohort declines for plaice over the first 2 years of life. Data plotted from Van der Veer (1986) (diamonds), Beverton & Iles (1992) (circles) and Nash (1998) (triangles). The strength of the year-class may be regulated during the early pelagic and post-larval demersal stage and mortality rates may vary on a geographic and inter-annual basis.

Year-class strength may be largely determined by the end of the larval stage (Fig. 5.1; Pihl 1990; Horwood *et al.* 2000) but can be modified (Van der Veer *et al.* 1990) 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) 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 need to get inshore, or even into specific estuaries. Depending on the relative positions of spawning and nursery habitats, they may have 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 topography or prevalent winds that accomplish a goal of targeted movement.

The goal in this chapter is to outline 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 population biology of flatfishes. Other organisms with planktonic life stages, including invertebrates and coral reef fishes, share many of these same problems with flatfishes: eggs and larvae drift in the plankton but juveniles need to recruit to specific habitats. Therefore, comparisons of how quite different organisms have solved similar problems would be illuminating as to how flatfishes have adapted. The cues that may elicit specific behaviours are not discussed in depth here, as there are other excellent reviews of these topics (Boehlert & Mundy 1988; Gibson 1997). This synthesis is largely restricted to a few commercially exploited species from the northern hemisphere, representing a small percentage of the roughly 700 known species of flatfishes, three-quarters of which are tropical (see Chapter 2); unfortunately data on the majority of these other species are sparse.

5.2 Flatfish eggs and larvae in the plankton: variations in form and function, time and space

Various aspects of egg and larval morphology and ontogenetic development affect the process of transport; some of these include size, shape, density and swimming ability. Where and when eggs and larvae are distributed in the plankton will also play a crucial role in the transport process.

5.2.1 Variations in form and function

As a group, flatfish produce a wide variety of egg and larval forms in the plankton. Eggs vary in diameter from 0.5–0.8 mm for the Pacific sand dab (*Citharichthys sordidus*) to 4.0–4.5 mm for the Greenland halibut (*Reinhardtius hippoglossoides*). Variations in egg size may involve adaptations to minimise predation, provide greater maternal investment in individuals, or properties to confer some other benefit to offspring, such as longer egg stage duration whereby hatching larvae are more developmentally advanced. Egg size may vary considerably among congeneric species. For example, for *Pleuronichthys* spp. inhabiting waters off the coast of California, egg size may vary from 1.84–2.08 mm for the curlfin sole (*P. decurrens*) to 0.94–1.08 mm for the spotted turbot (*P. ritteri*) (Sumida *et al.* 1979). Even within a species like plaice, egg size may vary considerably with season (see references in Gibson 1999).

Shell architectures and egg densities also vary considerably. Some flatfishes have intricately sculpted eggs, especially from the genus *Pleuronichthys*. The chorions of different flatfish species have been described as striated, reticulated, rugose, adhesive or covered with a polygonal network (Moser 1996), whereas others are remarkably smooth. Robertson (1981) suggested that egg size of marine fishes and sculpturing of the chorion may influence the ascent rates from depths where eggs are spawned. Based on measuring sinking rates of preserved eggs, he inferred that small eggs and sculpted eggs would have a slower rate of ascent than larger or smooth eggs. Ascent rates will influence the relative duration that eggs spend in bottom and surface currents and affect their ultimate fate.

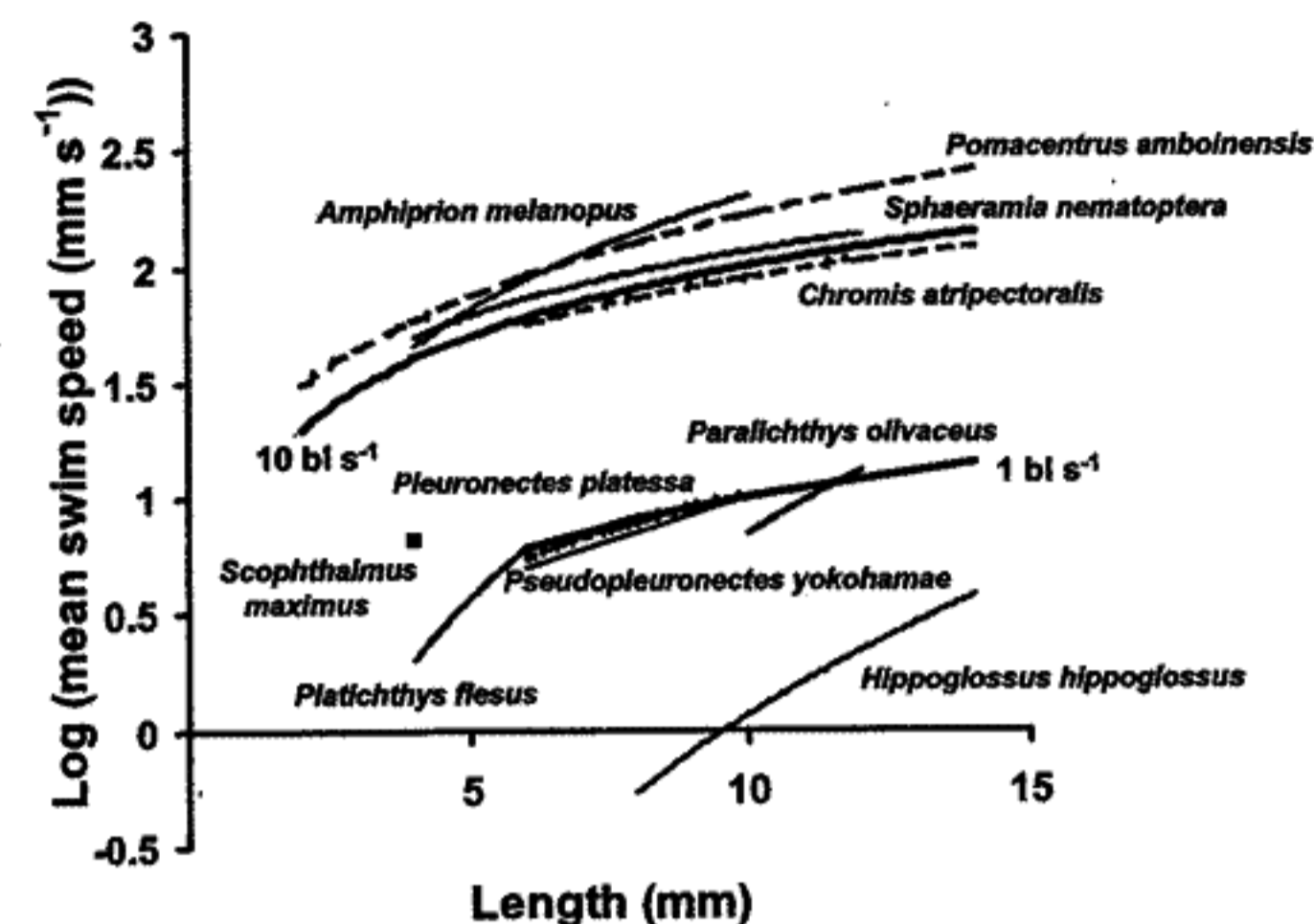


Fig. 5.2 The log of mean swimming speed (mm s^{-1}) plotted against larval length for tropical reef fishes (the species clustering at the top of the graph around 10 BL s^{-1}) and for six temperate flatfish species (clustering around 1 BL s^{-1}). Data are from numerous published sources and use a variety of methods to measure speed over different durations. Differences may be partly due to temperature.

The size of larval flatfishes is also quite diverse. Length-at-hatching can vary from about 2 mm for Pacific sand dab to 10–16 mm for the Greenland halibut. Size-at-transformation varies from about 8 mm for starry flounder (*Platichthys stellatus*) to 49–72 mm for the rex sole (*Glyptocephalus zachirus*). Moser (1996) cites extremes of <5 mm for archirids to >100 mm for *Chascanopsetta*. In general, deeper dwelling species spawn larger eggs and have a longer pelagic life and larger size at metamorphosis than shallower dwelling species (Minami & Tanaka 1992). Some flatfish species are fairly flexible in the size at transformation, whereas others are relatively fixed.

Larval size is closely coupled to swimming speed (Fig. 5.2). Generally, flatfish larvae are weak swimmers in the plankton. Fukuhara (1988) noted that the swimming speeds in body lengths per second (BL s^{-1}) of flatfish larvae are low compared with larvae of other temperate and subarctic pelagic fishes. He suggested that flatfishes have some structural deficiencies of the fin rays that cause them to be feeble. He also noted that swimming speeds of flatfishes decrease at metamorphosis in contrast with speeds for pelagic fishes which tend to increase at metamorphosis.

The decrease in swimming speed at metamorphosis for flatfishes is similar to observations of coral reef fishes, that show decreased swimming speeds after settling onto their reef habitat, but reef fishes also show flexible behaviour (Leis & Carson-Ewart 1997, 1999). In spite of some common traits between flatfishes and coral reef fishes (for example, the necessity of transforming larvae to recruit to specific target habitats), there are some remarkable differences that include swimming abilities of pelagic larvae. Compared with flatfish larvae, many reef fishes have larvae that are notably strong swimmers (Leis & Carson-Ewart 1997; Fisher *et al.* 2000) and thus larvae may play an active role in searching for habitat. Most reef

fishes are perciforms, which have fully developed fins at a small size. Leis & Carson-Ewart found that larvae of the pomacentrid *Chromis tripteralis* only 7 mm in length averaged a sustained swimming speed of 34 bl s^{-1} , and most taxa tested swam at about $10\text{--}15 \text{ BL s}^{-1}$ (Fig. 5.2). By contrast, flatfish larvae swim at a relatively lethargic 1 BL s^{-1} (Blaxter 1986). Leis & Carson-Ewart suggested that swimming performance may be favoured in a coral reef system, as there would be selective pressure on larvae to find a reef 'target'. Current speeds in the area where they made their measurements were $10\text{--}15 \text{ cm s}^{-1}$, so virtually all of the late stage larvae were able to swim faster than currents for sustained periods, and therefore the inference is that they can control their position and distribution. They further suggested that flatfishes may have a larger 'target' for their destination. Alternatively, flatfishes may have adapted to the transport problem in their environment in other ways. For example, by vertically migrating only a short distance, they 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. Where the currents are tidal, such behaviour is called selective tidal stream transport (STST) (Forward & Tankersley 2001).

5.2.2 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 maximised? In the case of plaice, one of the most studied species, the spawning grounds are close to the nursery in areas where currents are weak or nondirectional. In areas where currents are strong, eggs appear to be released in an optimum direction and distance from the settlement areas to guarantee successful colonisation (Gibson 1999). This is an essential criterion for most flatfishes, because juveniles have specific nursery and resource requirements. Using plaice as an example, the larvae of this species cannot delay metamorphosis, so enforced settlement can occur in unsuitable habitats. However, late-stage plaice larvae may demonstrate considerable behavioural flexibility in the settlement process before metamorphosis, such as 'pseudo-settlement' (Tanaka *et al.* 1989) when larvae are transported into shallow areas. Juveniles have specific habitat requirements for optimal growth and survival, including food, temperature and avoidance of predation, as those factors are influenced by depth, sediment type, exposure and predator abundance. While it is not believed that settled juveniles starve, 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 (as compared with a coral reef), but is restricted in terms of habitat-defining parameters. Juvenile habitat is discussed more thoroughly in Chapter 8, but specifically, different species groups tend to have specific feeding patterns as they settle (e.g. Minami & Tanaka 1992). Other fishes with transport 'targets', for example reef fishes, also tend to have specific feeding requirements at settling (Harmelin-Vivien 1989).

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; English sole *Parophrys vetula* off the Oregon coast, Boehlert & Mundy 1987), and could signal a change in currents, or be related to plankton production cycle, or even be a purely physiological

response to temperature, i.e. through gonadal development. Other species may have consistent spawning times; for example, plaice in the North Sea have a mean spawn date of 19 January 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 time in the plankton, and metamorphose at a larger size (Minami & Tanaka 1992). Larvae with a metamorphic size $>25 \text{ mm}$ may spend more than 3 months in the plankton. In fact, Dover sole (*Microstomus pacificus*) and rex sole 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 clue for settlement to a suitable habitat. Larvae originating from warm water and nearshore spawners are smaller and undergo metamorphosis at a smaller size as well. Species with a metamorphic length $<10 \text{ mm}$ have a pelagic duration <1 month.

In general, flatfishes tend to 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). 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*, the newly discovered northern rock sole *L. 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 $<20 \text{ m}$ depth. Demersal eggs in these waters may be an adaptation to prevent their offshore dispersal by surface currents (Pearcy 1962).

5.3 Physical mechanisms of transport and retention

5.3.1 Dispersal/retention mechanisms

Transport and retention are physical processes responsible for moving early pelagic life stages toward an appropriate habitat, or for keeping them within an appropriate habitat (see Norcross & Shaw 1984, for a review). Because Werner *et al.* (1997) have reviewed the physical processes by region on the continental shelf and discussed their effect on pelagic stages of marine species, here the physical mechanisms of larval dispersal/retention are briefly summarised, mainly focusing on flatfish examples.

5.3.1.1 Wind-forcing/Ekman transport

Wind conditions during larval development for 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 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).

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 on/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 littlemouth flounder (*Pseudopleuronectes herzensteini*), and larval retention and settlement could be enhanced by onshore drift at the surface. In fact, a significant negative correlation was found between the frequency of strong westerly blows and fishery catch 2 years after the westerly blows (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 transforming 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.

5.3.1.2 Tidal currents/selective tidal stream transport

Tidal currents are important for larval transport in tidal inlets and estuaries if associated with vertical migration behaviour (active STST). This behaviour usually develops in later-stage larvae as they approach the settlement zone. STST has been shown (whether active or passive) in several species (see Table 5.1). Bergman *et al.* (1989) hypothesised that plaice larvae accumulate in the inshore nursery area of the Dutch Wadden Sea from the coastal zone due to a passive process through tidal water exchange and settlement occurs in suitable nurseries during flood tide (passive STST).

5.3.1.3 Estuarine circulation

Another physical process establishing a two-layered circulation system is freshwater discharge into estuaries. In this case again, 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

Table 5.1 Differences in spawning and transport-related characteristics of flatfishes

Species	Area	Spawning	Pelagic duration (days)	Nursery	Transport characteristics	Authors
Family Pleuronectidae						
<i>Pleuronectes platessa</i>	North Sea	30–60 km offshore	30–90	Nearshore, inland seas	Transport with bottom currents, then STST	Van der Veer <i>et al.</i> 1998; Cushing 1990; Rijnsoorp <i>et al.</i> 1985
	Irish Sea	Nearshore		Nearshore	Retention	Nash & Geffen 1999
	Kattegat/Belt Sea	Offshore		Shallow water ~5 m	Wind-driven currents, selective transport	Neilsen <i>et al.</i> 1998
<i>P. quadrituberculatus</i>	Gulf of Alaska	Nearshore		Nearshore	Retention and selective transport	Bailey, unpubl. data; Norcross, pers. comm.
<i>Pseudopleuronectes herzensteini</i>	Coastal Japan	Coastal waters ~50m		Nearshore, coastal	Drift north and inshore retention	Nakata 1996
<i>P. americanus</i>	NW Atlantic	Estuaries	28–42	Estuaries, coves	Tidal accumulation, retention	Chant <i>et al.</i> 2000
<i>P. yokohamae</i>	Japan			STST		Takahashi <i>et al.</i> 1986, cited in Tanaka <i>et al.</i> 1989
<i>Limanda aspera</i>	Gulf of Alaska	Inshore	30–60	Inshore, inner bays	Apparent retention	Bailey, unpubl. data
<i>L. ferruginea</i>	Grand Banks, Newfoundland	Offshore banks	90–120	Offshore banks	Retention	Neilsen <i>et al.</i> 1988; Walsh 1992
<i>L. limanda</i>	North Sea	Offshore		Inshore	Offshore settlement, inshore migration	Bolle <i>et al.</i> 1994
<i>Glyptocephalus cynoglossus</i>	Newfoundland	Offshore banks	120–360	Offshore banks	Retention	Neilsen <i>et al.</i> 1998;
<i>G. zachirus</i>	Oregon	Offshore 100–300 m	365	Offshore outer shelf	Long larval life, Ekman onshore transport	Pearcy <i>et al.</i> 1977
<i>Platichthys flesus</i>	East English Channel		30–60	Coastal estuaries	Drift north, then after flexion STST towards coast	Grioche <i>et al.</i> 2000
	SE North Sea	Offshore		Coastal estuaries	STST	Campos <i>et al.</i> 1994
	North Sea	Offshore		Coastal estuaries, tidal flats	STST	Jager 1998, 1999
<i>Parophrys vetulus</i>	Oregon	Offshore		Estuaries	Onshore Ekman	Boehlert and Mundy 1987

Table 5.1 (Continued.)

Species	Area	Spawning	Pelagic duration (days)	Nursery	Transport characteristics	Authors
<i>Hippoglossoides platessoides</i>	North Atlantic	Offshore banks	30-120	Offshore banks	Retention	Walsh 1994; Neilson <i>et al.</i> 1988
<i>Microstomus pacificus</i>	Oregon	Offshore >400 m	365-550	Offshore, outer shelf	Ekman onshore and post settlement migration	Pearcy <i>et al.</i> 1977; Toole <i>et al.</i> 1997
<i>Eopsetta jordani</i>	Oregon	Offshore, deep water	180	Inner shelf	Ekman onshore	Pearcy <i>et al.</i> 1977
<i>Hippoglossus stenolepis</i>	Gulf of Alaska	Continental slope >200 m	90-180	Inshore bays	Directed transport	Bailey & Picquelle 2002
<i>Rheinhardtius stomias</i>	Gulf of Alaska	Continental slope	90-180	Inshore bays	Directed transport	Bailey & Picquelle 2002
<i>R. hippoglossoides</i>	Norway	Continental slope 600-900 m	150	Slope, banks, coastal waters	Transport northwards onto banks and coastal waters	Haug <i>et al.</i> 1986
Family Achiridae						
<i>Trinectes maculatus</i>	NW Atlantic coast	Estuaries		Estuaries	Presumed retention, movement up estuaries	Miller <i>et al.</i> 1991
Family Parallichthyidae						
<i>Paralichthys dentatus</i>	Onslow Bay, North Carolina	Shelf, offshore	30-70	Nearshore, estuaries	Cross shelf, STST	Burke <i>et al.</i> 1998
<i>P. olivaceus</i>	Wakasa Bay, Japan	Nearshore, near nursery	30-60	Nearshore	Near bottom retention	Burke <i>et al.</i> 1998
<i>P. olivaceus</i>	Shijiki Bay, Japan	Offshore		Nearshore	STST	Tanaka <i>et al.</i> 1989
Family Soleidae						
<i>Solea solea</i>	Bay of Biscay, France	40-80 km offshore	30-60	Inshore bays, estuaries	STST?	Amara <i>et al.</i> 1998
	Eastern English Channel	Nearshore		Inshore coastal	Retention offshore, then Ekman transport, diffusion inshore	Koutsikopoulos <i>et al.</i> 1991
					Retention, tidal migrations	Grieco <i>et al.</i> 2000

Authors for most information are cited, some information was also obtained from Miller *et al.* 1991.

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 Fare River estuary, it was demonstrated that behavioural responses of the larvae of flounder (*Paralichthys* sp.), primarily to tide and photoperiod, facilitates their transport to appropriate habitats (Weinstein *et al.* 1980).

5.3.1.4 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). Recent examples include: Atlantic herring *Clupea harengus* (Iles & Sinclair 1982), Atlantic cod *Gadus morhua* (Ellertsen *et al.* 1990; Taggart *et al.* 1996), Alaska pollock *Theragra chalcogramma* (Bailey *et al.* 1997), Japanese anchovy *Engraulis japonicus* (Nakata 1996) and others (see Heath 1992).

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

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) recently 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.

5.3.2 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 which are inherent in transport mechanisms (Bartsch *et al.* 1989; Werner *et al.* 1993; Lough *et al.* 1994). Van der Veer *et al.* (1998) applied a 2D circulation model of the southern North Sea to simulate the inter-annual variability in dispersal of 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 inter-annual 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

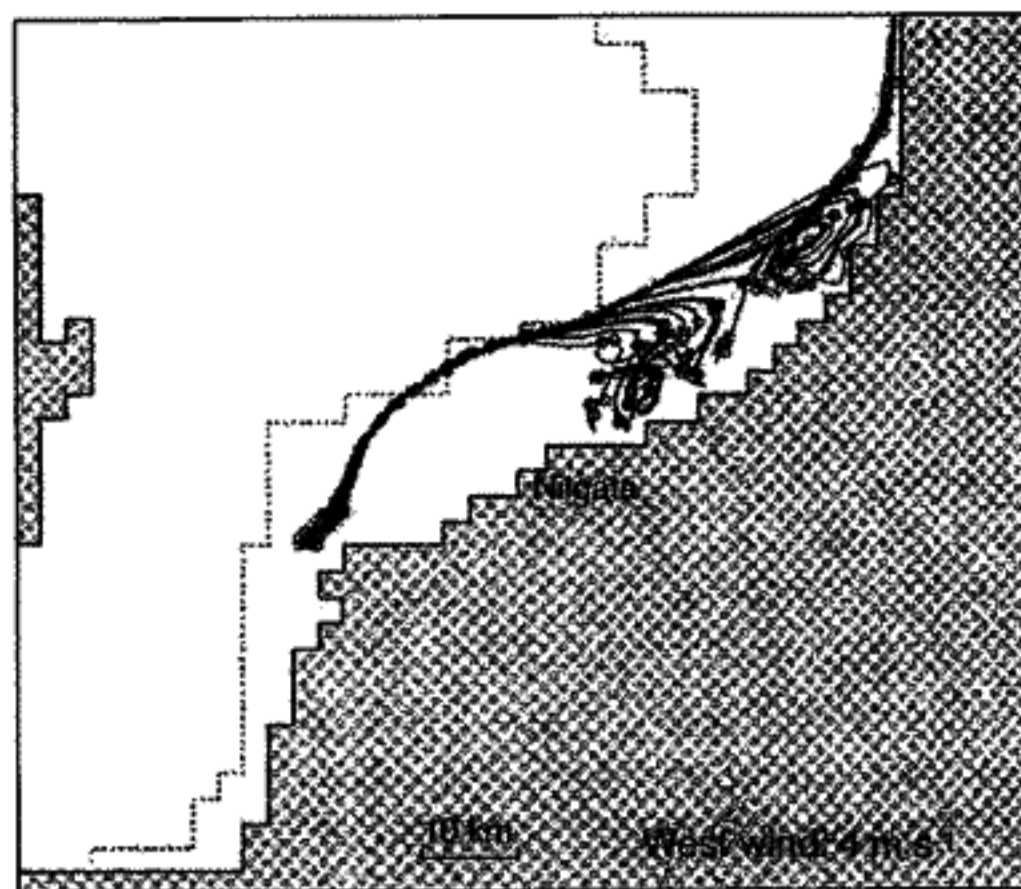


Fig. 5.3 Computed trajectories of particles, simulating littlemouth flounder eggs and larvae, released from the spawning location for 30 days under the condition of constant westerly winds. The broken line is the 100-m contour (from Nakata *et al.* 2000).

be a key factor in determining year-class strength of plaice. However, 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 littlemouth flounder eggs and larvae has been modelled in a shelf region of the Sea of Japan using a 3D Euler-Lagrangian model, with special interest in 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 the effect of the westerly wind speed on the egg and larval retention in the inner shelf was evaluated (Fig. 5.3). It was shown that the retention rate could be rapidly reduced when the wind speed exceeded a critical value (Fig. 5.4). Supporting the model results, the number of juveniles collected in the nursery area (1991–1998) showed a significant negative correlation with the frequency of strong westerlies in April. Although field data on the vertical distribution and movement of littlemouth 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 avoid wind-induced offshore drift at the spawning depth (below 30 m), and to facilitate entrainment into coastal eddies observed in the shelf region.

Considerable advances in the ability to explore the couplings of physics and biology in the models are very encouraging. The examples of flatfish species are still limited, but more research should be encouraged in combination with well-designed field surveys and laboratory experiments. Comparison between species under the same physical setting, or a comparison between different physical settings for the same species using models, would also be useful. Some of these types of comparisons are presented below, but it should be noted that usually

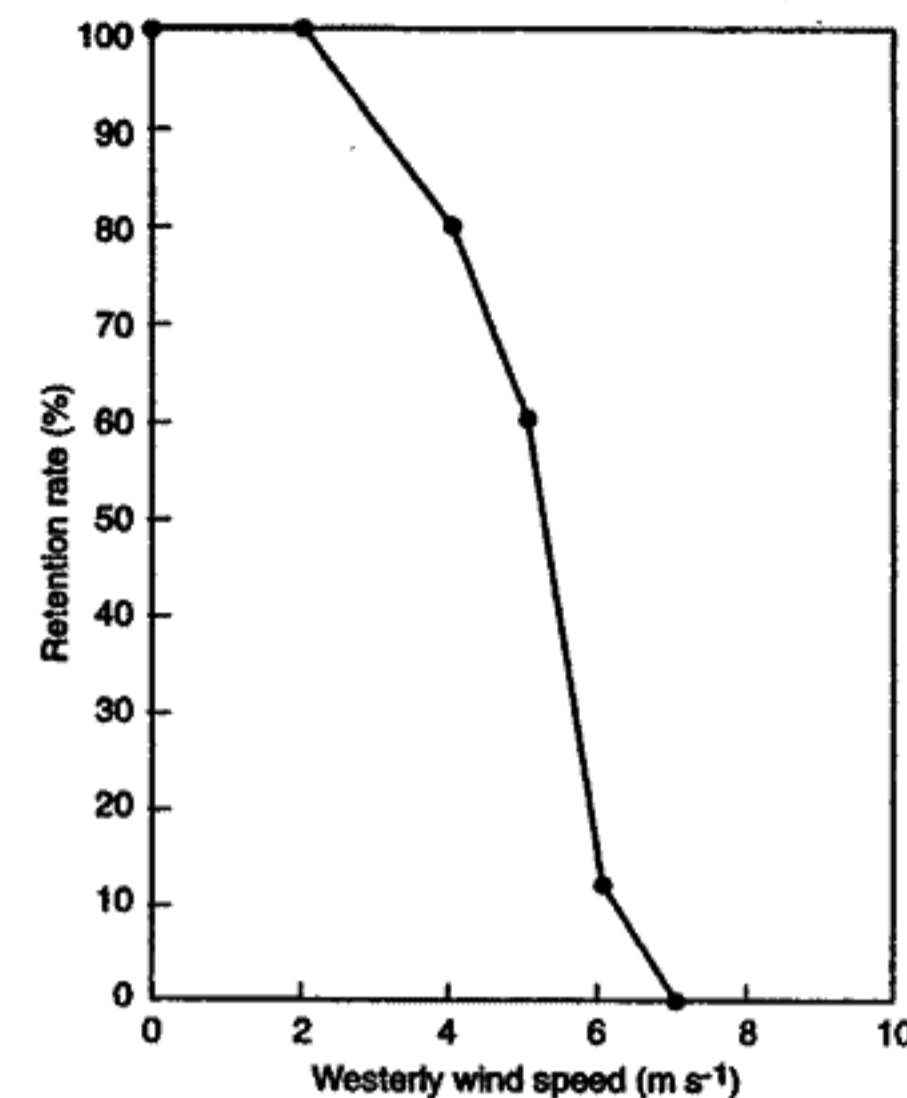


Fig. 5.4 From a 3D model simulating transport of littlemouth flounder eggs, the estimated retention rates (%) of particles released from the spawning grid after a 30-day drift under various westerly wind speeds (from Nakata *et al.* 2000).

the knowledge of the physical or biological parameters is incomplete. For this purpose, precise field data on the behaviour of target species—especially in the vertical water column—are indispensable, as well as data on circulation in the spawning and nursery habitats.

5.4 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; Fig. 5.5). As noted earlier, they are relatively feeble swimmers, so they must have other adaptations to reach nearshore targets. Spawners in estuaries generally have their nurseries in estuaries, so retention is necessary. Species that spawn on the coastal shelf/slope with coastal shelf/slope nurseries also require retention. These species may spawn in areas where fronts, eddies or other retention features may prevail. On the other hand, many species require 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 more detailed examples of potential adaptations that flatfishes have developed in order to get to their nurseries.

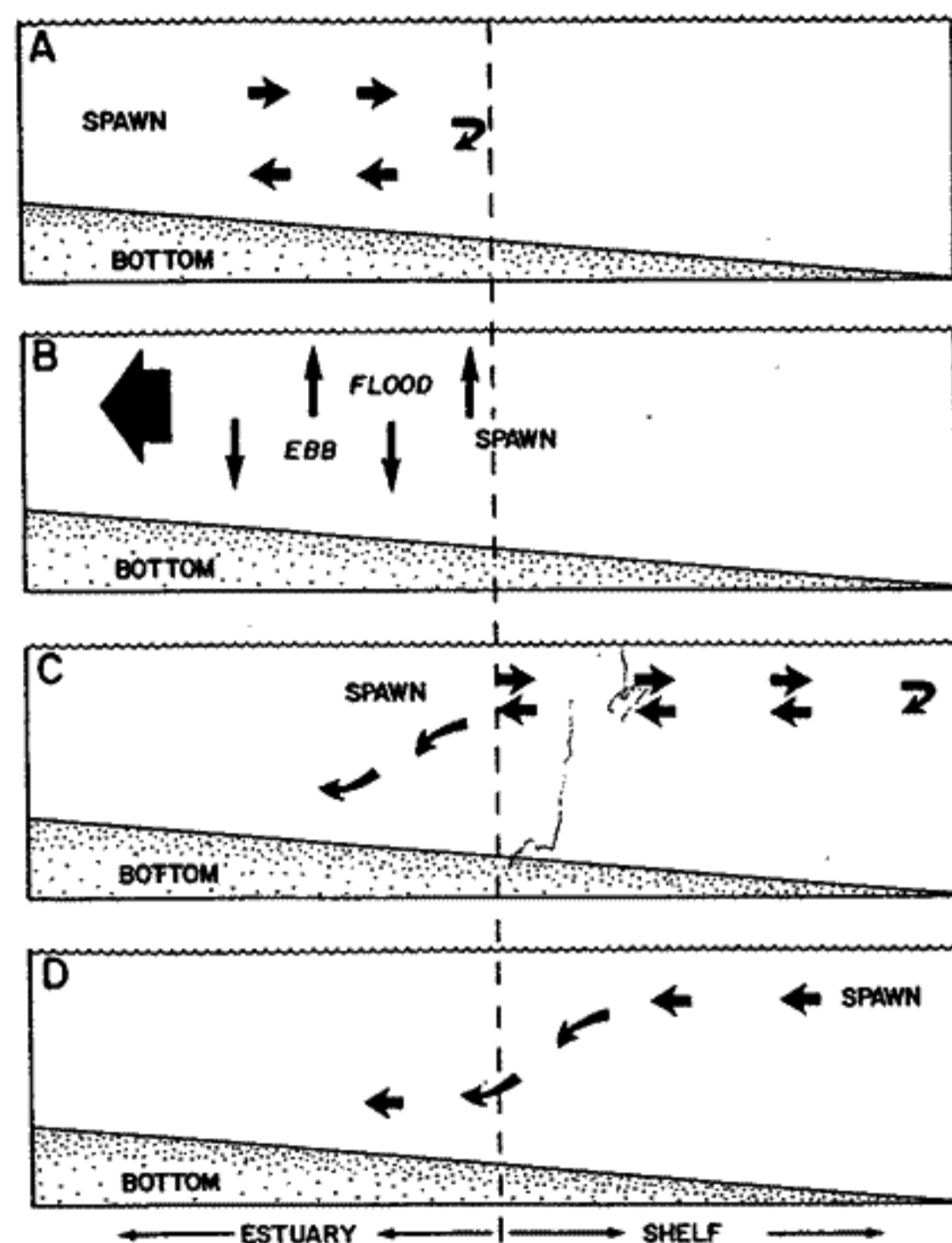


Fig. 5.5 Comparison of four mechanisms for dispersal and recruitment of estuarine larvae. A. Spawning occurs in the estuary and young larvae are transported downstream by surface flows; older larvae sink and are transported upstream in the residual bottom flow. B. Spawning occurs near the estuary mouth; larvae migrate up in the water column on flood tides and sink on ebb tides, resulting in net upstream transport. C. Larvae are spawned near the estuary mouth and are flushed onto the shelf; larvae are retained near the estuary mouth by current patterns. D. Larvae are spawned on the shelf and are transported onshore by current; post-larvae sink and are transported into the estuary by residual bottom flow (from Epifanio 1988).

5.4.1 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 Alaska Peninsula (Fig. 5.6), 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 stenolepis*) 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

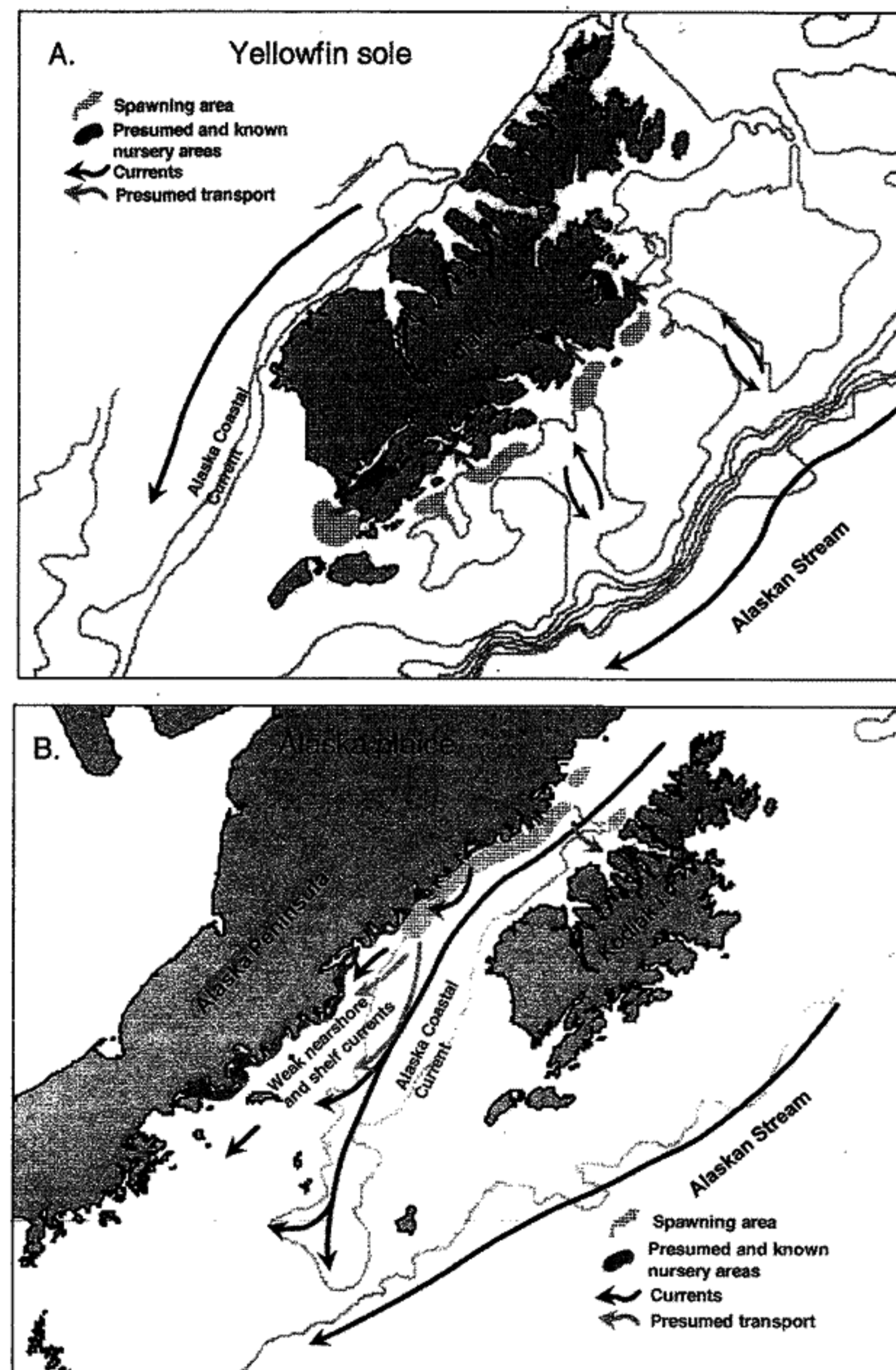


Fig. 5.6 Potential schematic for different transport patterns of four species of flatfish larvae in the Shelikof Strait, Alaska. A. Yellowfin sole are spawned in shallow water over banks on the outer side of Kodiak Island. Their eggs and larvae are retained in the current system and juveniles recruit 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.

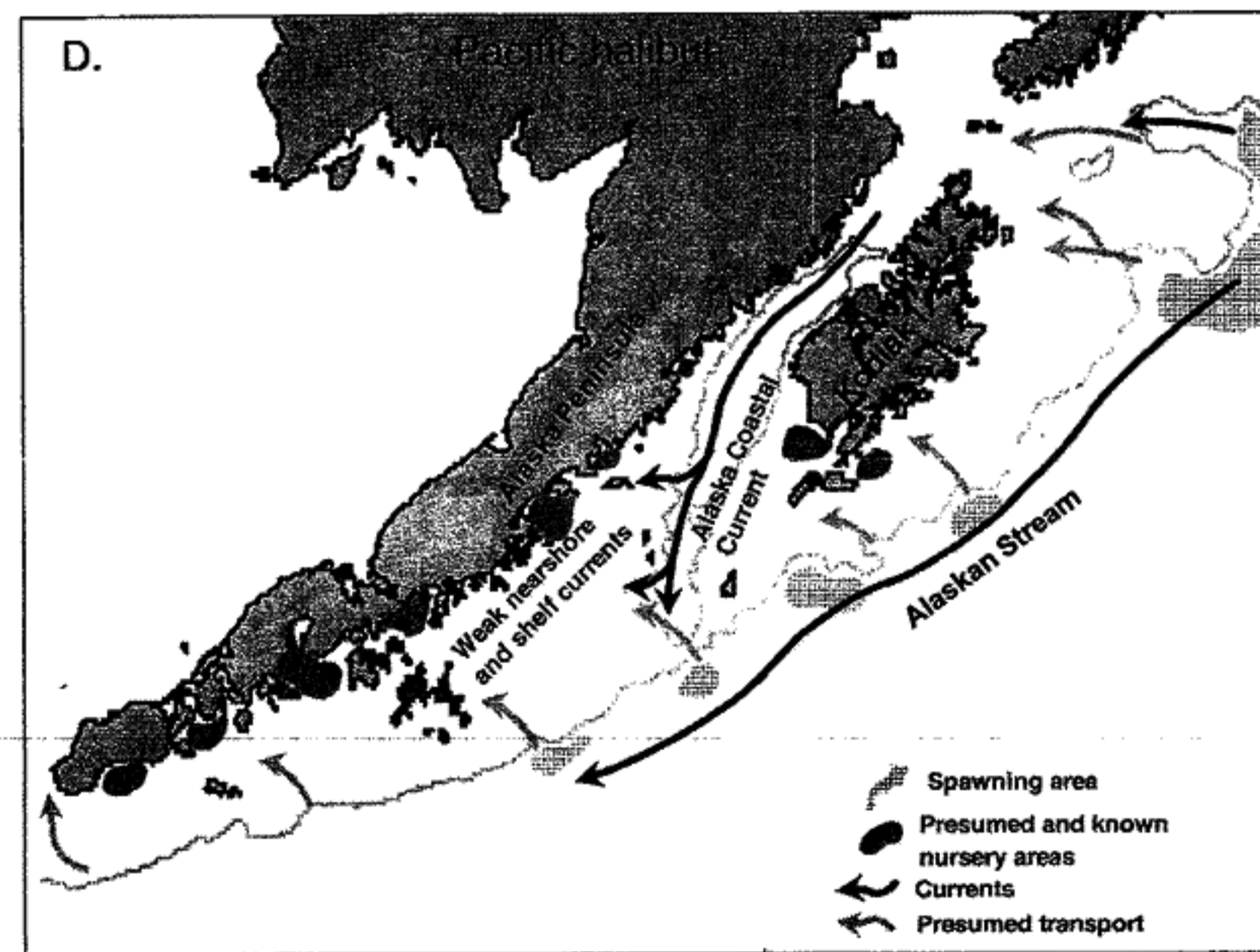
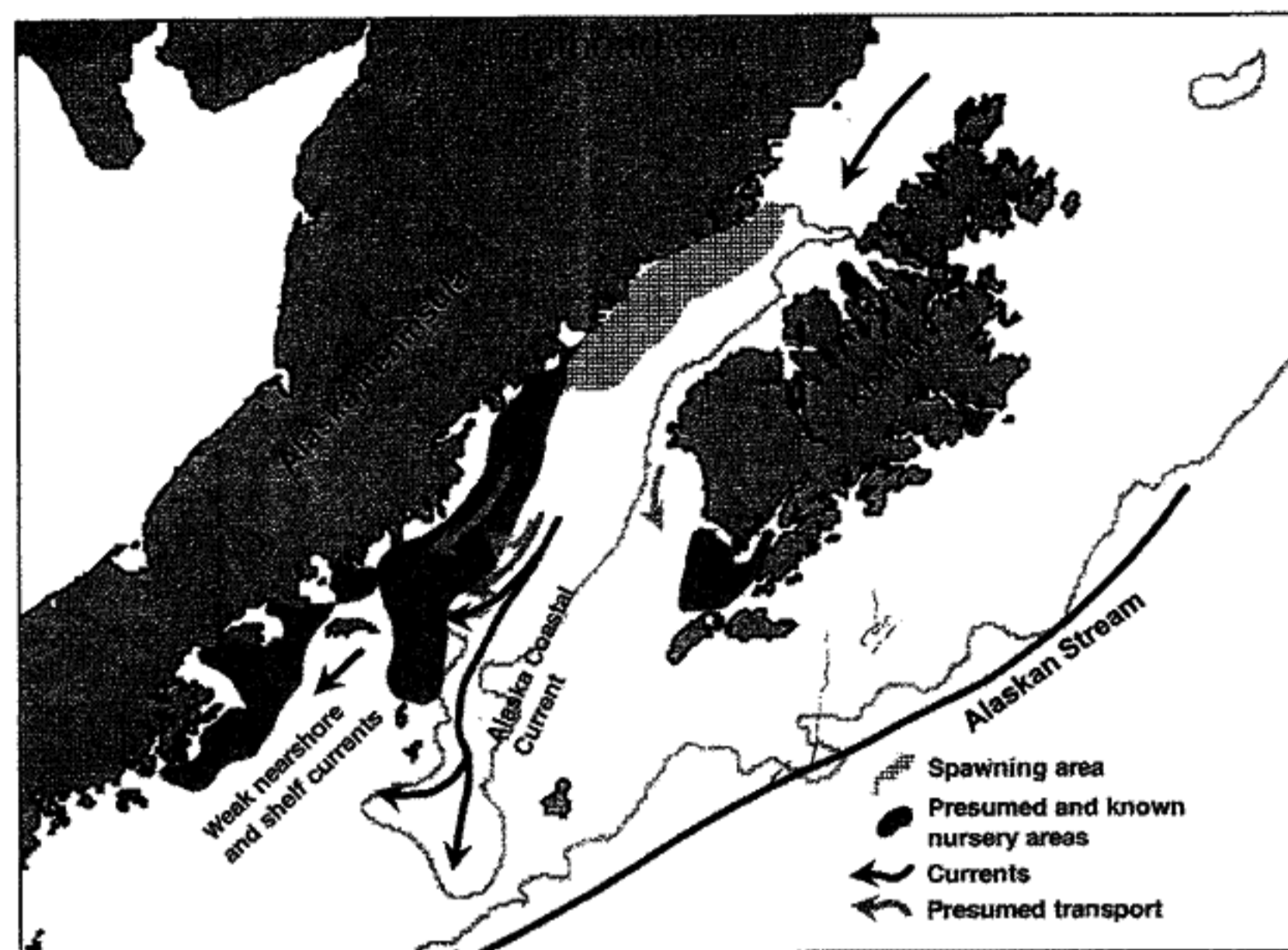


Fig. 5.6 (Continued) C. Flathead sole are spawned over deep water in the sea valley and are transported downstream in the Alaska Coastal Current towards nursery areas on the continental shelf. D. Pacific halibut are spawned offshore over deep water and are carried inshore by topographically steered currents up the sea valley; halibut nurseries are in coastal bays. Information on larval flathead sole was provided by S. Porter (Alaska Fisheries Science Center, Seattle, WA, USA) and information on juvenile flatfishes by B. Norcross (University of Alaska, Fairbanks, AK, USA) and in Norcross *et al.* (1999).

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 shallow) 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 flounder larvae drifted northward until they neared transformation. During their drift, flounder larvae did not migrate vertically and were not retained until flexion when they migrated to near bottom on ebb flow, which advected them towards the coast. On the other hand, common sole remained in the nearshore coastal waters and its retention was attributed to tidal and diurnal vertical migrations undertaken by the larvae.

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

5.4.2 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 bottom in spite of 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 USA 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 5.1). Species in the genus *Limanda* show a great variety of mechanisms for reaching their shallow nurseries. Yellowfin sole (*L. aspera*) 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 Limandayokohamae*) are believed to use STST to reach their nearshore nurseries.

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

5.4.3 Conspicuous 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 5.1). However, different subpopulations of plaice also have different mechanisms to arrive in nearshore nurseries (Fig. 5.7). In the Irish Sea, plaice spawn nearshore in close proximity to nursery areas in areas of reduced tidal flow and larvae are apparently retained there. In the Kattegat/Belt Sea area of Scandinavia where tidal currents are weak, spawning occurs

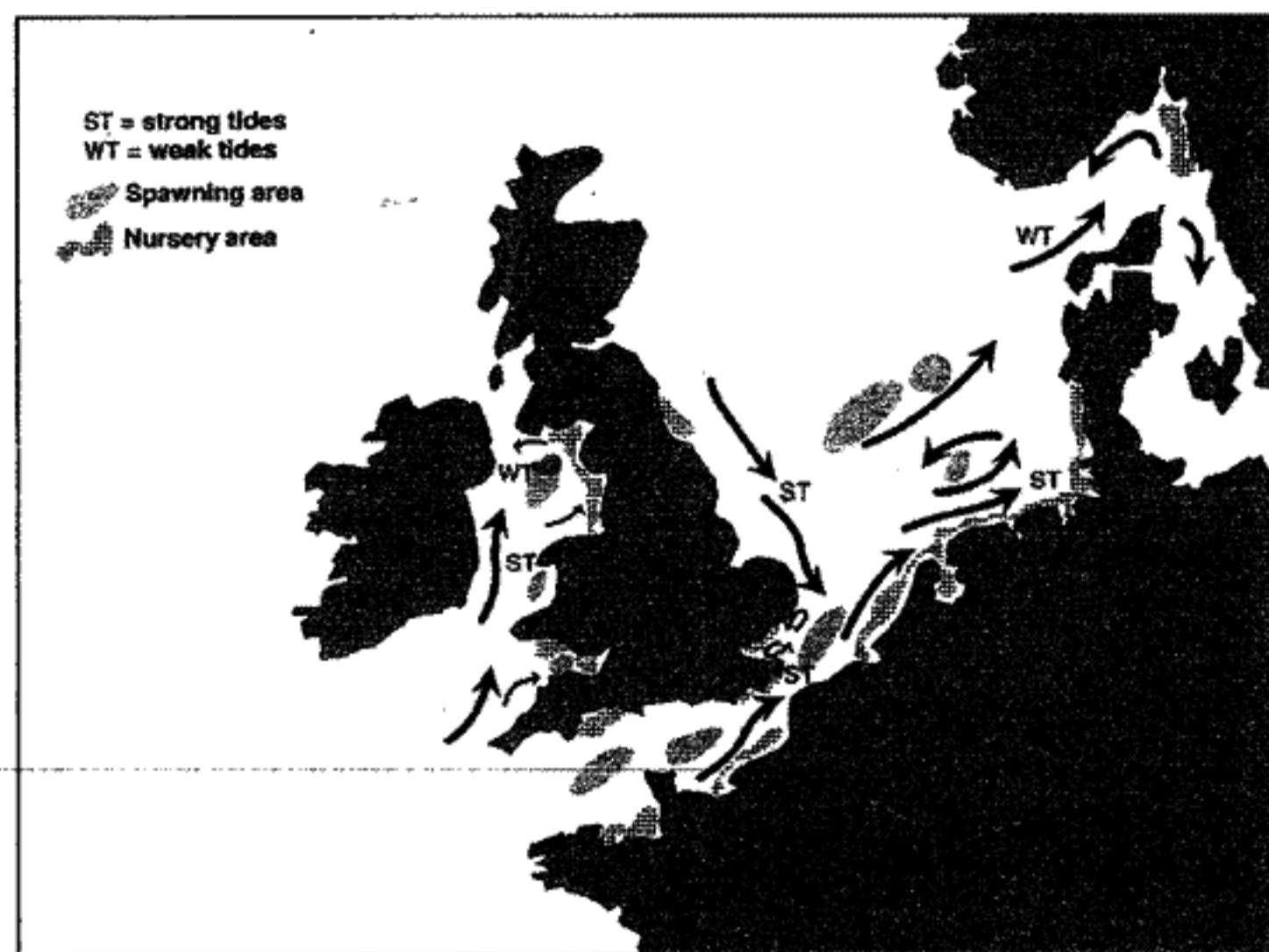


Fig. 5.7 Transport conditions for the plaice in three major spawning areas. In the Irish Sea near the Isle of Man, tidal and residual currents are weak and plaice spawn near their nursery area. In the English Channel and North Sea, residual currents are strong towards the northeast and tidal currents 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.

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

5.4.4 Local adaptations

Although the above inter-species comparisons show differences in transport mechanisms, species within a common geographic region dominated by different types of currents may have prevailing transport characteristics. For example, in the North Sea where tidal currents are strong, numerous flatfish species use STST to reach inshore nurseries including plaice, flounder and common sole. It is recognised that generalisations about tidal currents over broad regions of the shelf are dangerous with regard to life history adaptations of local fish populations, as tidal currents can be strongly affected by local features, such as topography. In the California Current system, an upwelling system dominated by Ekman currents, many species either have adaptations to minimise transport offshore, such as spawning demersal eggs or viviparity (Parrish *et al.* 1981). They may spawn during periods of downwelling, or in areas characterised 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 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 that there is 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. LeFevre & Bourget 1992). As those authors summarised, 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.

5.5 Transport and population biology

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

5.5.1 Population genetics

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 also has a long larval stage, but shows significant stock structuring that may be related to larval retention (Fairbairn 1981; Table 5.1). Other species, such as Pacific halibut, have a long planktonic life, and little apparent evidence for subpopulation structure (Grant *et al.* 1984).

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 patterns 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).

The metapopulation concept may be useful for assessing gene flow, risk of extinction, and potential for recolonisation of depleted populations. Given that the major potential for population dispersal is in the planktonic stage, metapopulations for many flatfishes may be organised around larval drift patterns (Bailey 1997). 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). More structure may be found where retention is common (northwest Atlantic: e.g. witch, Atlantic cod). Cushing (1990) observed that the spawning and feeding grounds of different 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.

5.5.2 Recruitment

Many factors have an influence on recruitment (see Chapter 6). 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 to 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 plaice (Van der Veer *et al.* 1998). This is further supported by empirical field studies of plaice recruitment (Van der Veer 1986; Van der Veer *et al.* 1990). Year-class strength of 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).

A comparison of plaice recruitment among stocks has some intriguing implications. In the Kattegat/Skagerrak where tidal currents are weak, wind-driven currents dominate larval transport (Neilson *et al.* 1998). Pihl (1990) found that variations in onshore winds are related to the abundance of plaice in their nearshore nursery and Pihl *et al.* (2000) considered that 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 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, post-larval common sole are carried to nursery ground by tides (Berghahn 1984, cited in Rijnsdorp 1992), whereas tidal currents in the Irish Sea are relatively weak and common sole may spawn near nurseries to minimise transport distance.

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 up 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 been proposed

to explain the variations in transport pathways as a causal factor for recruitment success/failure. It should also be recognised that the relative importance of individual factors may change from year to year and may also vary over the range of a species because species life history traits vary over their ranges (Miller *et al.* 1991). In the case of many flatfishes and estuarine-dependent species whose juvenile nursery habitats are spatially distinct from spawning locations, physical processes affecting the transport in the pelagic stages are of great importance to the formation of year-class strength.

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