Chapter 6

Environmental processes and recruitment variability

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Abstract: This chapter examines some of the physical processes associated with the regions where life stages of *Illex* species have been identified. Various mechanisms, seen in other OSLR (Ocean Sciences in Relation to Living Resources) studies, for enrichment, concentrating food and paralarvae, transporting eggs and juveniles, and facilitating adult spawning migrations are hypothesized to be acting. In some cases these are substantiated by existing information and in others the additional evidence required is outlined. In general, the greatest variety of processes with the greatest stability is associated with the habitats of *Illex argentinus*, while *Illex illecebrosus* is dominated by a single powerful, but variable current system. *Illex coindetii*'s habitats tend to support only weak and relatively unpredictable processes. These trends appear to be reflected in stock size and stability.

1 Introduction

The combined habitat of the several species of the genus *Illex* found in the Atlantic includes major portions of the subtropical and subpolar regions of the Atlantic Ocean. A comprehensive chapter on all major aspects of ocean variability in such a diverse area would be a large undertaking and its very bulk would probably limit its usefulness. In the context of the near lack of present scientific insight into the mechanisms involved in squid recruitment variability, a major need is to find rational frameworks for limiting the field of view so as to be able to focus effectively on some specific "tangible" issues.

The volume in which this 'paper appears is produced as a response to an initiative of the IOC-FAO Programme of Ocean Sciences in Relation to Living Resources (OSLR). OSLR has now been in existence for more than a decade and certain generalizations and insights are beginning to emerge. It appears that, in the case of coastal pelagic fishes at least, favourable reproductive habitat tends to be associated with a combination of three classes of environmental factors:

1) enrichment of the food web by physical processes (upwelling, mixing, etc.);
2) opportunity for concentrated patch structure of food particles to accumulate (stable structure, convergent flow patterns, frontal formations, etc.); and
3) flow mechanisms that enable a population to maintain itself, through adaptive responses, in a continually moving fluid medium.

Illex squid are in some ways similar to small coastal pelagics. They are nektonic, pelagic, schooling organisms capable of rapid population responses, and as paralarvae and early juveniles they drift and feed within the upper ocean planktonic community. It seems therefore reasonable, at least as a hypothetical framework, to attempt to build upon the other OSLR results.

2 A conceptual framework for the *Illex* recruitment problem

A natural first step is to analyse the life style of the organism. Much still remains to be known on the behaviour and distribution of *Illex* spawners and early life-history stages, but evidently this animal leads a very "high energy" life style. *Illex* squids are thought to have a life span of one year (Dawe *et al.* 1985, Hatanaka *et* *al.* 1985a), and post-recruit stages have shown a very rapid linear growth (Radtke 1983, Koronkiewicz 1986, Rodhouse and Hatfield 1990). Clearly, they need to grow very rapidly to grow to substantial size and to sexual maturity in less than a year.

For rapid growth, *Illex* squids need a highly positive balance between the caloric value of the food ingested and the energy expended to fmd and capture food organisms. Early life stages may have particular problems in that the laws of hydrodynamics bestow distinct size-related advantages on larger organisms. Small organisms are forced to expend relatively greater energy in swimming through the liquid ocean medium than do larger organisms, and so the cost of getting from one "meal" to the next may be such as to impede significantly the rate of growth. And since larger predators can use their hydrodynamic advantages to capture smaller prey, rapid growth through the various size-dependent predation fields is crucial. Thus, access to concentrated sources of food would seem to be a great advantage.

If one considers the habitats of the particular ornrnastrephid squid populations that achieve very large concentrations of biomass, it is clear that they tend to be associated with major permanent current systems (Coelho 1985, Hatanaka *et al.* 1985b). *Illex illecebrosus* is associated with the Gulf Stream system in the northwestern Atlantic. *Illex argentinus* is associated with the Falkland (Malvinas) Current system in the southwestern Atlantic. *Todarodes pacificus* is associated with the Kuroshio-Oyashio Current system in the northwestern Pacific. Other substantial populations appear to inhabit the vicinities of the eastward current filaments which are linked to the subpolar convergences (Roper *et al.* 1984).

High velocity geostrophic currents (such as the Gulf Stream, Kuroshio, etc.) are possible only at interfaces of major water masses of differing density characteristics, where sharp horizontal density gradients support the baroclinic pressure forces that can balance the large Coriolis accelerations generated in a high velocity ocean current. The dynamic forces involved when two water masses of differing densities and relative motion come into proximity create a tendency for flow convergence towards the zone of intersection. Frictional dissipation in the zone of current shear near the water mass interface perturbs the geostrophic balance. Gravitational and pressure forces then cause the water type of greater density to sink beneath the water type of lesser density, which in turn tends to overflow the more dense water type. Mixing processes near the interface act to produce water of intermediate density, which tends to flow under the less dense surface water type. Thus both surface water types are feeding the formation of a mass of mixed water that slowly sinks at the interface between them (Fig. 6.1). The buoyancy-driven flows that supply this mixed water formation are directed from each of the water types towards the interface, resulting in a zone of convergence that acts to sustain the distinct frontal character of the boundary.

Tiny, weakly swimming organisms that may be unable to resist being passively swept along in the horizontal ocean flow field, may be well able to control their depth level in the much less energetic vertical field of motion in the ocean. Such organisms will thus accumulate in the slowly sinking waters of the convergent frontal zone (Fig. 6.1). Thus the distribution of food particles will be highly concentrated, and small predatory organisms such as squid paralarvae may realize a dramatically increased caloric intake per unit energy expenditure. This process would work its way upward through the trophic levels, with each successive level being released from the "minimal net gain" situation (Bakun 1996) that may characterize the large-scale average for the habitat. This would tend to produce "blooming" in individual growth, in reproductive output, and finally in local population growth at each trophic level, ultimately attracting larger nektonic predators to the locally enriched trophic pyramid.

The interface between the water masses is not vertical, except perhaps within the surface mixed layer. Rather, it is highly tilted towards the horizontal, with the less dense water mass tending to lie above the more dense water mass. Thus the interface becomes continuous with the pycnocline of the lighter water mass (which, when facing in the direction of current flow, is to one's right ill the northern hemisphere and to one's left in the southern hemisphere). This allows an omrnastrephid egg mass to find a depth of neutral buoyancy within the

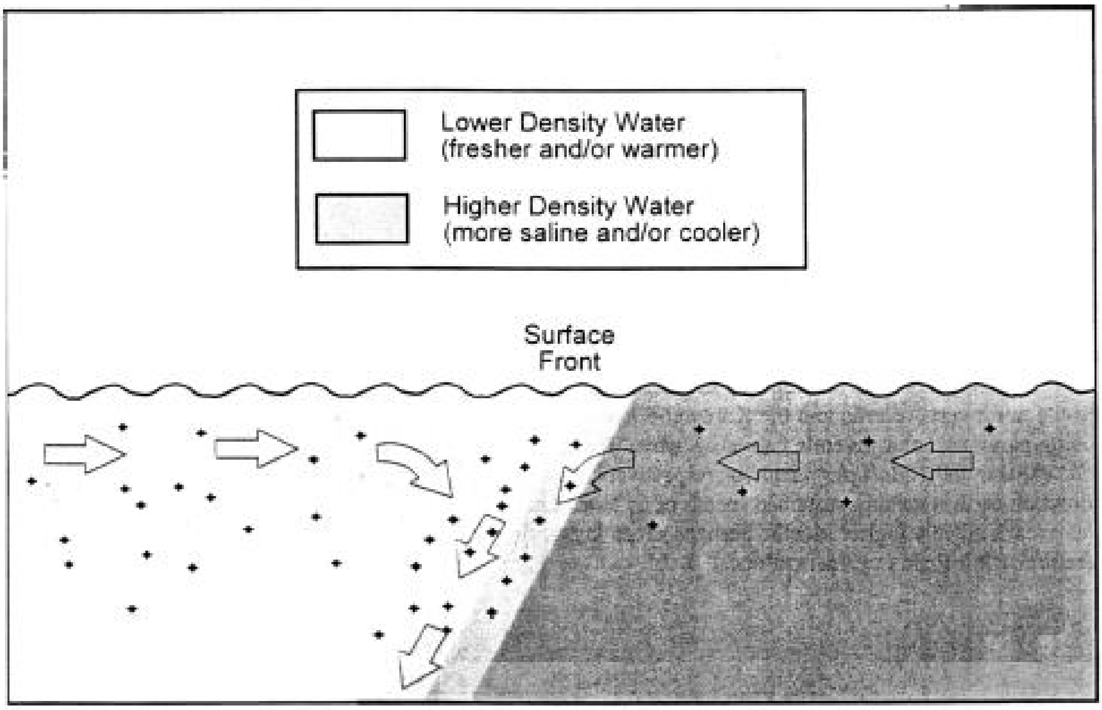

Figure 6.1. Schematic diagram of a front between water of differing density; arrows indicate density-driven flows associated with the front. "Particle" symbols indicate planktonic organisms capable of resisting vertical displacement. (Scales are distorted, vertical scale greatly expanded relative to horizontal; particles greatly magnified, surface waves not to scale, etc.) Redrawn from Bakun (1996)

pycnocline (Fig. 6.2), where it may be relatively safe from predation (O'Dor and Balch 1985) and from mechanical damage that might occur at the sea surface. Clearly, there is no need to expose the eggs to the heavy predation pf the surface frontal zone before the time arrives for feeding to be initiated and for the "life or death" race between rapid growth and high predation mortality to actually get under way.

When the time arrives for hatching, the paralarvae swim vertically (O'Dor 1985) to the sea surface, whereupon the density-driven circulation associated with the frontal processes will tend to carry the paralarvae (Fig. 6.2) directly into the zone of food concentration in the surface frontal zone. Here they may be able to experience the rapid growth that is imperative for successful execution of their life-cycle strategy, as well as being necessary for even short-term survival given the particular vulnerability to predation that the circumstances imply.

Such a high-energy early life-history strategy appears to imply also a high-energy adult strategy. Any zone of intense convergence that is reasonably large-scale is associated with an intense geostrophic current. This is a necessary result of geophysical-scale hydrodynamics. The density-driven converging and sinking water motion near the sea surface required for the concentration mechanism cannot exist without the baroclinic contrasts that invariably imply a swiftly flowing geostrophic current. Thus population maintenance becomes a particular problem. These rapid western boundary currents are essentially a "one-way train" for surfaceliving, temperate zone organisms, and the "train" travels a long way in a short time. Thus long adult migrations may be necessary to close the habitat "loop". Adult *Illex* appear to migrate in dense schools, where cannibalism (Koronkiewicz 1980, Amaratunga 1980, 1983, Maurer and Bowman 1985, Q'Dor 1988) may help to maintain energy reserves of those destined to survive to reproduce. This could be particularly useful in reducing the losses due to starvation when food availability is low. (Clearly, the migration cannot be via the zones of high food concentration in the frontal interface; in these zones the current is very strong and in the opposite direction to the path of migration needed to maintain population in the habitat situation.) The dense schools probably also help to satiate the heavy predation pressures undoubtedly encountered on the journey. In any case, many adults would tend to be lost during migration to predation, cannibalism, possible starvation, and other natural causes. Thus the one-year basic life cycle may in many ways be the "economical" response to this particular "high-energy" life-style design.

3 The northwest Atlantic

The strongest slopes of isopycnal surfaces in the world's oceans are connected with the Gulf Stream flow in the northwest Atlantic and the Kuroshio Flow in the northwest Pacific (Neuman and Pierson 1966), both being paralarval and juvenile habitats for two of the largest ommastrephid squid populations on earth (*Illex illecebrosus* and *Todarodes pacificus*, respectively). Correspondingly, these are the swiftest permanent current flows on earth, reaching sustained speeds of up to six knots. (The Somali Current in the western Indian Ocean may reach slightly higher speeds, perhaps seven knots, during the southwest monsoon; but this is a seasonal feature rather than a permanent one.)

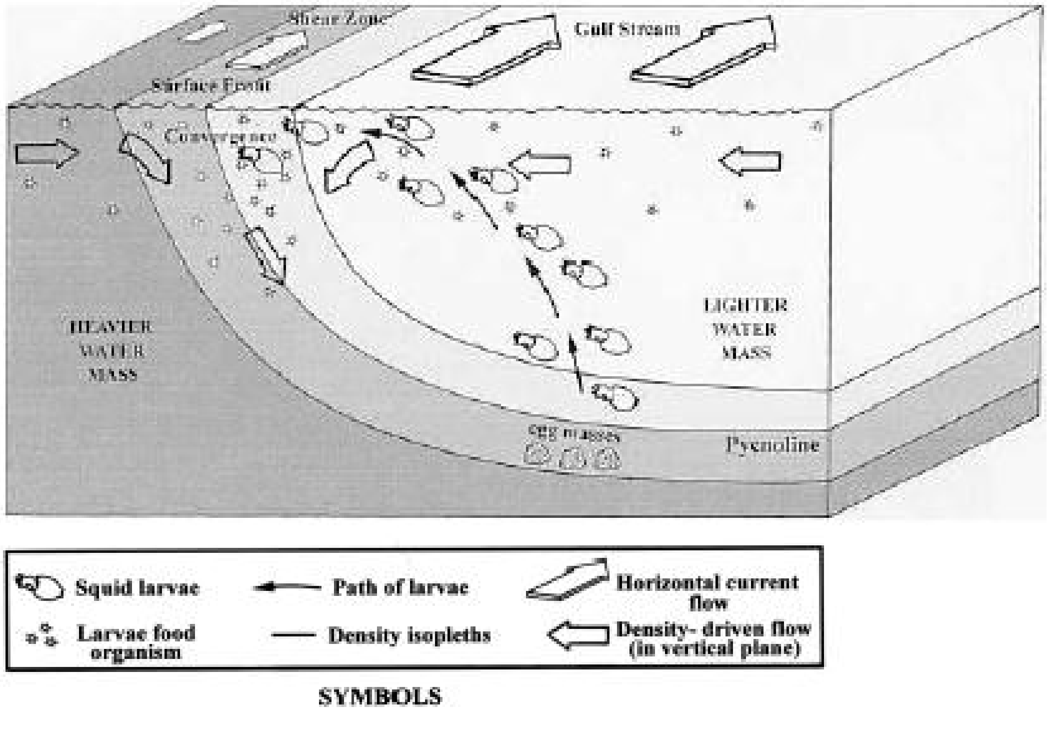

Figure 6.2. Schematic diagram: Within the pycnocline, squid egg masses find a neutrally buoyant level, where they are suspended at mid-depth at suitable development temperatures and under conditions of reduced predation. Upon hatching, squid paralarvae may rise to the surface layer, where they would be carried into the convergent frontal zone by the density-driven flow

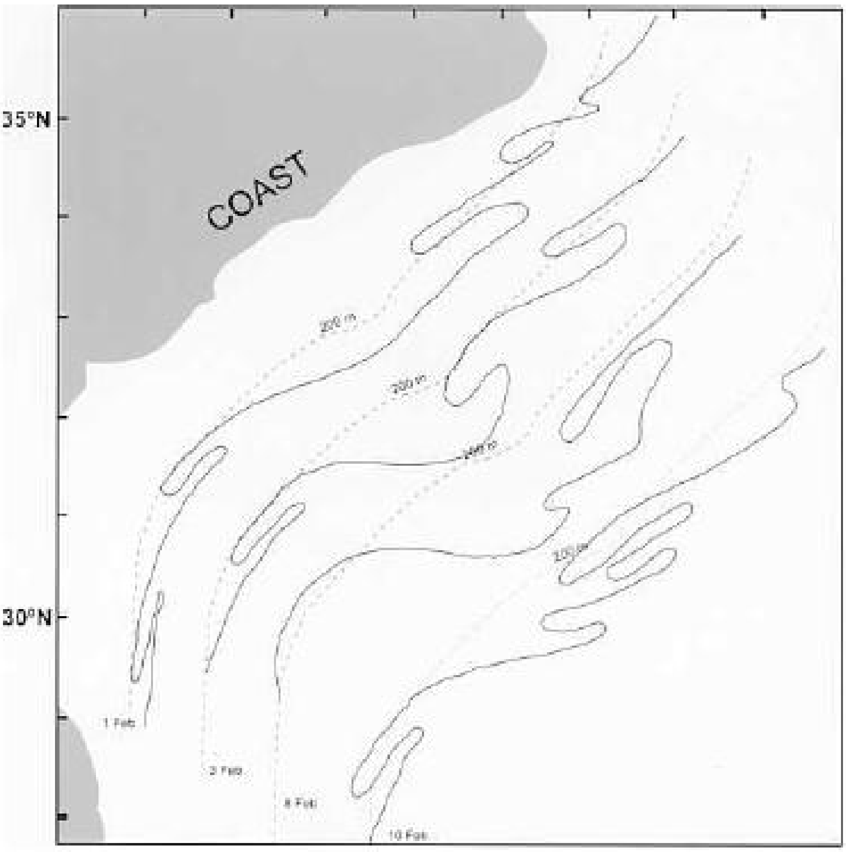

Figure 6.3. Progressively offset locations of the Gulf Stream/slope-water front (redrawn from Rowell *et al.* 1985)

Illex paralarvae have been found mainly along the northern (inshore) edge of the Gulf Stream and particularly in the frontal zone between the Gulf Stream and the "slope water" that lies coastward (Hatanaka *et al.* 1985b, Rowell *et al.* 1985). Spawning is thought to take place within, or adjacent to, the Gulf Stream between the central Florida coast and Cape Hatteras (Rowell *et al.* 1985, Dawe and Warren 1993). This is the zone where the Gulf Stream remains rather confined against the continental slope and does not develop conspicuous meanders. The Gulf Stream separates from the coast near Cape Hatteras. Downstream of the point of separation, meanders develop in the current with amplitudes typically from about 150 km to 450 km (Von Arx 1962).

3.1 Enrichment processes

The horizontal shear in the Gulf Stream is strongest near the frontal zone (Trites 1983). The waters in the Gulf Stream move northwestwardly much faster than does the slope water. Cyclonic (anti-clockwise) shear vortices, called "frontal eddies", develop at the interface in response to the frictional torque of the differential velocities of the adjacent water masses. These give the frontal boundary a "folded wave" or "shingled" appearance (Fig. 6.3) in maps of satellite-sensed sea surface temperature (Rowell *et al.* 1985). The vortices typically are elongated in the direction of the Gulf Stream flow, with the longer axis typically of 100 km or more in length, and appear to have lifetimes of one to three weeks (Trites and Rowell 1985).

In the formation of the cyclonic vortices, part of the response to the applied frictional torque is manifested as the increased local relative vorticity which is evident in the vortices. Another part is manifested as local vortex shrinking, which produces upwelling in the interior of the eddies. Another way to conceptualize this vortex shrinking is that it represents the rearrangement of ocean structure by introduction of water of greater density within the eddy. This is required to produce an inwardly directed pressure force sufficient to oppose the combination of Corio lis and centrifugal forces directed radially outward as a result of the rotary flow pattern, and thereby to produce quasi-geostrophic balance.

As a result of the process of frontal eddy formation, the sea surface in the frontal zone tends to be continually enriched by patches of nutrient-bearing upwelled waters. These patches may generate chlorophyll concentrations one or even two orders of magnitude higher than in the Gulf Stream or resident shelf surface water (e.g. Yoder *et al.* 1981) and clearly are sites of intensified trophic-level interactions (e.g. Haney 1986). The eddy-related upwelling is reported to have a pronounced seasonal pattern (Haney 1986), being strongest in the winter-spring period. And of the several seasonal broods that may be produced, the one resulting from winter spawning (i.e. with a winter-spring paralarval period) usually predominates and is most broadly distributed to the northeast (Lange and Sissenwine 1983).

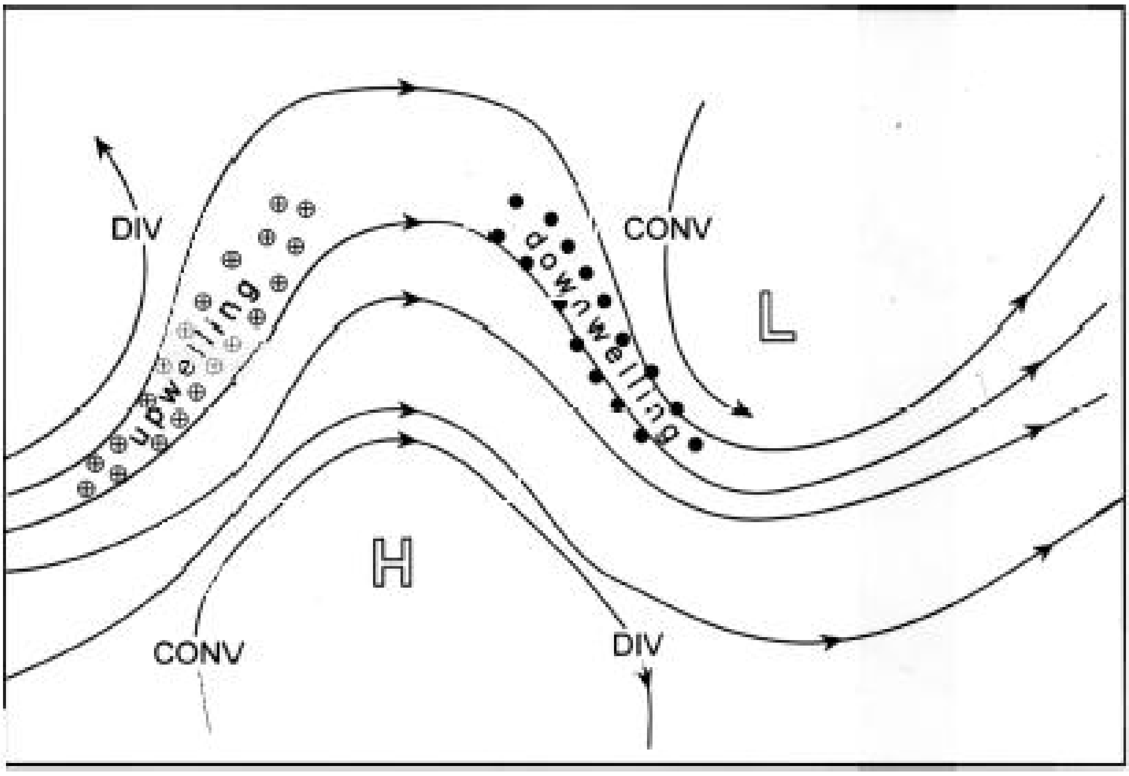

Figure 6.4. Schematic diagram of the convergent and the divergent zones in a Gulf Stream meander pattern; widening distance between streamlines corresponds to divergence; narrowing distance between streamlines corresponds to convergence (redrawn from Arnone *et al.* 1990)

South of Cape Hatteras, where the edge of the Gulf Stream lies near the continental shelf, the familiar type of seasonal coastal upwelling (e.g. Lemming and Mooers 1980, Paffenhöffer *et al.* 1987) and various processes leading to shelf break upwelling (e.g. Hsueh and O'Brien 1971, Paffenhöffer *et al.* 1984, Hamilton 1987; Podestá 1990) also contribute to enrichment of the larval habitat near the inshore edge of the Gulf Stream.

After the Gulf Stream separates from the continental boundary near Cape Hatteras, the "control" on the meander amplitudes is relaxed and another process of enrichment may begin to take effect. The Gulf Stream is narrower in zones of cyclonic (anti-clockwise) curvature of the main current (Von Arx 1962). The geostrophic balance is altered by the increased centrifugal force due to the flow curvature, the centrifugal force acting to augmenthe Coriolis force in a cyclonic meander. This upsets the balance of forces resulting in a deficit of horizontal pressure force. This allows the less dense water associated with the water mass lying to the right of the flow, which is driven by the horizontal pressure force to overflow the mor,e dense water on the left of the flow, to be pushed back. This steepens the inclination of the ocean structure, narrowing the current. There is flow divergence associated with the widening of the current in zones where the curvature of the flow changes from less cyclonic to more anticyclonic. This results in local upwelling (Fig. 6.4) in portions of the meander pattern where the curvature is changing in this sense (Arnone *et al.* 1990, Olson 1990).

3.2 Concentration processes

The major process supporting accumulation of concentrated distributions of food organisms for larval and juvenile stages in the Gulf Stream system is the one described earlier in Section 2. It is also intrinsic to the major enrichment process described in Section 3.1. The effect of turbulent friction (frontal eddies, etc.) in the shear zone between the differentially moving Gulf Stream and slope water masses is such as to locally retard the velocity of the flow. This reduces the Coriolis force which is directed to the right of the Gulf Stream flow. This yields a local excess in pressure force directed towards the front from the Gulf Stream side that pushes the water masses together, continually rebuilding and resharpening the frontal boundary in opposition to the erosion resulting from the frontal eddies and smaller-scale turbulent effects. The local departure from geostrophy implied in this process allows the above-described gravity-driven flow pattern to occur (in an average sense) in the plane normal to the front (Fig. 6.1), which results in concentration of organisms in the frontal zone.

The meander pattern also apparently provides an additional convergence mechanism, albeit an intermittent one, which is the converse of the meander-related upwelling mechanism described in Section 3.1. Just as there is flow divergence associated with the widening of the current in zones where the curvature of the flow becomes less cyclonic (or more anticyclonic), there is flow convergence (Fig. 6.4) associated with the narrowing of the current in zones where the curvature of the flow becomes less anticyclonic (or more cyclonic) (Arnone *et al.* 1990, Olson 1990). This process would tend to concentrate organisms in such zones. As a result, a transit through the meander pattern of the Gulf Stream would appear to be a succession of episodes of upwelling followed by episodes of convergence. Given effective current speeds of around 3 knots (Trites 1983) and typical meander amplitudes of 150 to 450 kIn, the time scale of the alternations would appear to be only of the order of several days. Thus there might not be time for a directly linked sequence of upwelling-production-convergence of food organisms suitable for any but the earliest life stages of *Illex*. Rather the meander-associated processes might be viewed as contributing to an enhanced general level of enrichment and patch formation within the Gulf Stream. This could help support the nutritional requirements of *Illex* paralarvae that may have been ejected from the (hypothetically) more favourable frontal zone into the main body of the Gulf Stream. Moreover, as patches produced in this process are carried into the frontal zone by the convergent flow pattern, they would serve to supplement the more continuous enrichment and concentration linked to the earlier-described processes associated with the frontal zone itself.

3.3 Transport processes

Transport of planktonic stages of squid in the Gulf Stream proper, from south of Cape Hatteras to the Scotian Shelf, would seem only to be a matter of a few weeks. However, the average speed within the frontal shear zone, which appears to be the center of paralarval *Illex* distribution, would be substantially less. Moreover, turbulent diffusion in the frontal eddy system would cause some individuals to move more rapidly than the average speed, and some to move more slowly. For example, an individual that managed to ride the retrograde (southwestward-moving) sides of the frontal eddies, transferring to successive eddies by turbulent diffusion, could conceivably travel substantial distances in the direction opposite to that of the large-scale average flow.

Clearly, the period required to move from the spawning grounds to a given recruitment area would depend on the degree of contortion of the flow path by meanders. More numerous and more eccentric meanders would certainly lengthen the trajectory to be travelled (Dawe and Warren 1993). In addition, meanders sometimes "pinch off" from the main flow and become detached eddies. Those that detach to the right of the main Gulf Stream flow are called" cold-core" eddies because they entrain some of the cooler water that was originally to the left of the flow core. Those that detach to the left (coastward) of the flow core are called "warm-core" eddies. Myers and Drinkwater (1989) produced a time series of warm-core eddy frequencies, based on weekly satellite imagery.

Paralarvae and juvenile *Illex* that happen to be entrained in a cold-core eddy would tend to be carried into the ocean interior and probably lost to the population. Those entrained in a warm-core eddy would, at a minimum, have their trajectories towards the northeast interrupted. Warm-core eddies usually drift to the southwest in the slope current. Thus paralarvae entrained in a warm-core eddy would, even if they managed to successfully recruit, tend to be displaced well to the southwest of the location in which they otherwise might have found themselves.

The other strong ocean boundary flow in the northwest Atlantic is the Labrador Current, which flows southward along the coasts of Labrador and Newfoundland. Much of the flow is deflected eastward to flow across the North Atlantic to the north of and adjacent to the Gulf Stream flow. However, the charts of Defant (1961) and Schumacher (1940) show part of the Labrador Current flow moving westward around the southern coast of Newfoundland to join the westward-flowing Nova Scotian Current and continuous with a general southwestward-flowing movement of water inshore of the Gulf Stream reaching nearly to the point of separation near Cape Hatteras. Average flow along the edge of the continental shelf generally follows the shelf-break trend towards lower latitudes along the entire region from Newfoundland (e.g. Hukada *et al.* 1989), Scotian Shelf/Browns Bank/Georges Bank (Koslow *et al.* 1989) and the mid-Atlantic Bight. This general tendency for flow towards lower latitudes would tend to aid migration of adult *Illex* returning south to the spawning grounds along paths located inshore of the opposing Gulf Stream flow.

3.4 Recruitment hypotheses

Clearly a large number of hypotheses concerning the factors regulating *Illex* recruitment in the northwest Atlantic could be proposed and elaborated. We will mention several of the most obvious according to the analysis and conceptual framework built up in the previous sections. We emphasize however that the material and ideas presented in this particular section should be regarded as hypothetical.

3.4.1 Integrity of the Gulf Stream surface front

The considerations we have presented indicate a particularly favourable situation for paralarval growth and survival within the frontal zone at the inshore edge of the Gulf Stream. The convergent surface flow pattern would tend to help squid paralarvae remain in this zone, and to return them to it if they are ejected by the frontal eddy patterns in the shear zone. However, paralarvae are found to be distributed around the general vicinity of the front (Hatanaka *et al.* 1985b, Rowell *et al.* 1985), not necessarily in the front. Thus there evidently are mechanisms promoting turbulent diffusion or ejection of paralarvae from the front. One certainly is the frontal eddy pattern, which arises as a mechanism for turbulent dispersion of momentum. As such it is a mechanism for turbulent dispersion of other properties, as well as for entrained particles such as paralarvae. Thus, the degree of integrity of the surface frontal zone during the period of paralarval drift might be expected to influence survival and therefore recruitment. Factors promoting such integrity might include the following:

1) an "orderly" frontal eddy pattern, where rather regular eddies would tend to merge waters entrained at the front of the eddy back into the frontal zone at the rear of the eddy (a low frequency of highly eccentric eddies that did not close their circulation and shed large amounts of entrained waters away from the frontal zone);
2) a continuous non-interrupted frontal zone that would carry a large proportion of the surviving paralarvae that managed to remain in the most favourable circumstances (i.e. in the frontal zone) to the recruitment areas; and
3) low frequency of formation of detached eddies during the paralarval drift period.

This hypothesis conforms in some ways to the empirical results of Dawe and Warren (1993), who found that when *Illex* population size in the northwest Atlantic was high, a larger proportion were distributed towards the northern part of the habitat. When the frontal zone has a high degree of integrity, fewer individuals would "falloff the train" early and thereupon recruit further to the south.

3.4.2 Favourable transport from the Gulf Stream zone to the continental shelf

Given a certain number of individuals surviving the period of paralarval drift in the Gulf Stream system, they still have to move long distances through the slope and shelf water masses to feeding grounds near the continental shelf. Thus favourable transport conditions may promote recruitment success. Dawe and Warren (1993) in fact found that warm winter sea-surface temperatures, possibly related to northward transport of Gulf Stream-influenced waters, tend to be empirically associated with improved squid recruitment. The recruitment areas for *Illex* in the northwest Atlantic are within the zone dominated by strong westerly wind flow between the "Icelandic Low" and the "Bermuda-Azores High" atmospheric pressure systems. Westerly winds would produce southward sea surface Ekman drift, which is the opposite direction that the juvenile squids must travel. However, the surface Ekman layer probably does not penetrate substantially below the surface mixed layer, and although juvenile *Illex* do apparently undertake diel vertical migrations, the overwhelming majority appears to stay within or below the pycnocline (Arkhipkm and Pedulov 1986).

Myers and Drinkwater (1988) modelled Ekman transport of larvae of several fish species inhabiting the continental shelf of the northwest Atlantic, but were able to prove little apparent relationship to recruitment (they did not address *Illex* squid). However, in their study of the apparent effect of warm-core eddies in entraining water off the shelf (Myers and Drinkwater 1989), they found evidence that higher warm-core ring frequency did significantly impair recruitment success in a number of continental shelf groundfish species (again, they did not address *Illex*). The species they addressed were ones whose larvae originated on the continental shelf; thus diffusion resulted in offshore loss. In the *Illex* case, diffusion would be from the offshore paralarval source towards the shelf. Thus impact of rings might be favourable (in opposition to the unfavourable effect of rings in hypothesis "3.4.1", above).

3.4.3 Success of the adult "counter"-migration

The other part of the life cycle for which there is little information is the adult migration back to the spawning region. Clearly this is a long and arduous journey, without the aid of a swift boundary current like the Gulf Stream. Although the general trend of the currents inshore of the Gulf Stream is in the direction of the migration path, these currents tend to be weak and variable (Von Arx 1962). As mentioned earlier, it has been suggested that cannibalism within the schools may help to provide part of the necessary energy for the journey.

If the journey goes well, substantial spawning concentrations with significant energy reserves for forming reproductive products would be expected. If particularly high predation pressure is encountered, the squid population may be decimated, or may expend inordinate amounts of energy in evading predation. If unfavourable current patterns are encountered much energy might be lost. If too much energy is lost in the migration, animals may be too weak to effectively evade predation or have little energy reserves to form reproductive products. Alternatively, use of cannibalism to restore energy reserves would contribute to decimation of the population. The net result might be drastically fewer egg masses spawned to begin with, perhaps thereby overriding the effect on recruitment of the other processes we have been discussing.

3.4.4 Other possibilities

Certainly there are a variety of potential "match-mismatch" hypotheses (Cushing 1975) that might be formulated. For example, anomalously low temperature conditions could delay development of needed food organisms beyond the time that arriving squid juveniles may need them as food sources. Lower than normal temperature may also slow down embryonic development and growth of early life-history stages, thus compensating for possible delays in the development of suitable food organisms, but extending the exposure to predation. On the eastern side of a large continent, episodic" outbreaks" of cold, winter continental air masses can exert major effects on conditions in the adjacent ocean (e.g. Husby and Seckel 1980). Dawe and Warren (1993) in fact found that high iceberg counts off Newfoundland, related to cold episodes in the Labrador Current, are empirically associated with an adverse effect on local squid recruitment. Drinkwater and Trites (1991) present a time series of sea-surface temperature conditions in the shelf habitats of the northwest Atlantic from 1971 to 1989 (annual reviews of environmental conditions by these authors are routinely published in the NAFO Scientific Council Studies Series in which the cited study appears). Hamabe (1962), Choe (1966), McMahon and Summers (1971), and Boletzky (1974) show that the rate of embryonic development of cephalopods can be delayed by lower than usual temperatures, and Rodhouse and Hatfield (1990) report that late-hatching squid experiencing a higher average temperature grow faster than the earlyhatching ones.

Variations in predation pressure can presumably affect survival rate at all stages. The Gulf Stream frontal zone may be particularly favourable from the predation standpoint, in that predators of a size to prey heavily on tiny squid paralarvae may have difficulty in maintaining resident populations in the swiftly moving Gulf Stream environment. The Gulf Stream is also a particularly deep flow, which makes countering the advection by vertical migration a very difficult proposition. Even so, whatever predation pressure does exist probably varies with time.

Disease outbreaks are also a possibility for introducing population variability. For example, little is known about parasitic infestations that may take place in natural egg masses. Moreover, enhanced mortalities due to direct physiological stresses associated with non-ideal conditions of temperature, salinity, oxygen level, etc., probably also occur to some extent.

4 The southwest Atlantic

The habitat of *Illex argentinus* in the southwest Atlantic includes one of the most extensive open continental shelf areas in the world. The Patagonian Shelf is well over 400 km wide over most of its 1700-km length off the eastern coastline of southern South America, between 39° and 53°S latitudes. In the vicinity of the Falkland (Malvinas) Islands the shelf width extends to nearly 900 km. Apparently, the habitat of *I. argentinus* also extends northward past the coasts of northeastern Argentina and Uruguay, all the way to southern Brazil (Haimovici *et al.* 1995).

Like the habitat of *Illex illecebrosus* off North America, the habitat of *I. argentinus* is under the influence of strong western ocean boundary currents (albeit somewhat less intense than the Gulf Stream or Kuroshio). The southward-flowing Brazil Current dominates the northern part of the region while the northward-flowing Falkland (Malvinas) Current dominates the southern part. The two currents meet near Rio de la Plata, with the Brazil Current veering offshore and remnants of the Falkland (Malvinas) Current continuing northward near the coast (Figs. 10.5–10.7). These boundary flows are apparently confined to the shelf break and seaward. The flow over the shelf itself appears to be largely decoupled from the oceanic currents (Olson *et al.* 1988, Podestá 1990).

As indicated in Chapter 3 and 10, *I. argentinus* spawning stocks on the Patagonian Shelf area are complex. Our remarks and most of the available observations are focused on the dominant and more abundant winter spawners, which also account for almost all the commercial catches of this species. Most of the *I. argentinus* population spawns during the austral winter (June–August) over the continental slope and outer continental shelf, from about 40° to 50°S latitude (Fig. 3.4). A very small part of the population, only about 1 percent, spawns during the austral summer (January–March) in shallow waters on the Patagonian Shelf (Brunetti 1981, Sato and Hatanaka 1983, Hatanaka *et al.* 1985a, Koronkiewicz 1986, Csirke 1987, Hatanaka 1988).

The main feeding and pre-spawning concentrations of *I. argentinus* take place during the austral autumn (March–June) on the outer Patagonian Shelf and slope, between 42° and 52°S. No direct observations of egg masses or of actually spawning squids have been recorded in the area, but indirect observations indicate that by June–July matured squids undertake short northerly and northeasterly spawning migrations into deep slope waters. Hatanaka *et al.* (1985a) class the spawning migration of *I. argentinus* as being of the "short range" type (as opposed to that of *I. illecebrosus*) in view of the high proportion of mature individuals in the feeding and pre-spawning (fishing) grounds, and Koronkiewicz (1986) reports the capture of recently spawned dead squids without sexual products in July, at 600–700 m depth between 45° and 46°S.

Squid paralarvae then apparently drift northward in the Falkland (Malvinas) Current flow, with concentrations of juveniles appearing on the inner shelf in the spring (Hatanaka 1988). Immature squids then gradually span over most of the continental shelf, while migrating across the wide expanse of continental shelf to the adult feeding and pre-spawning grounds near the outer edge of the shelf, which is also the area of the major multinational fisheries (Csirke 1987). Hatanaka (1988) reports that Japanese trawlers fishing for squids in the Patagonian Shelf area start towing at depths of around 200 m during February to March, and as the newly recruited squids grow and migrate to the feeding and spawning grounds, the towing depth is increased, reaching around 500–700 m by the end of the fishing season in June–July.

4.1 Enrichment processes

Sustained wind-induced coastal upwelling, even on a seasonal basis, occurs only off southeastern Brazil (Bakun and Parrish 1990), which is at the far northern end of the range of reported occurrence of *I. argentinus*. Here the Ekman transport tends to have an offshore component during the austral spring-summer (October–March). To the south (i.e. in the bulk of the *I. argentinus* habitat), seasonal-scale, offshore-directed, wind-driven surface transport that would drive conventional coastal upwelling is largely lacking.

However, shelf-break upwelling is highly evident in vertical hydrographic sections (e.g. Servicio de Hidrograffa Naval, 1969) and in satellite imagery (Podestá 1990, NSF/NASA 1989), even in the area dominated by the northward flowing Falkland (Malvinas) Current. Ekman transport near the sea floor due to bottom drag in such an equatorward western boundary current would be directed offshore, rather than in the onshore direction corresponding to upwelling. Podestá cites several potential mechanisms for shelf break upwelling in such a case. These include upwelling in frontal eddies along the current edge (Paffenhöffer *et al.* 1984) of the type discussed earlier in relation to the Gulf Stream front, interactions between coastal trapped waves and bottom topography (Dickson *et al.* 1980) and effects of interactions of internal tides with the shelf break and wind stress (Mazé *et al.* 1986). In addition, Kinsella *et al.* (1987) describe a mechanism for onshore water movement in response to the Ekman suction caused by curl of the bottom stress in an equatorward western boundary flow.

In addition, tidal mixing over the inner shelf has a similar enrichment effect to upwelling. Hunter and Sharp (1983) identify the Patagonian Shelf as an area of strong tidal mixing. Over shallow shelf regions, tidally generated turbulence may thoroughly mix the water from surface to bottom. In the resulting homogenized water column, nutrients and other properties associated with the denser lower layers of the previously stratified water are mixed into the illuminated upper layers where they are available for photosynthesis. Carreto and Benavides (1989) cite consistently greater availability of nitrates in the euphotic zone of mixed waters on the Patagonian Shelf, compared to nearby stratified waters. They also note the predominance of chain-forming diatoms (such as typify upwelling centres) in the mixed waters and the relative scarcity of phytoplankters (being mostly heterotrophic dinoflagellates) in neighbouring stratified waters. They report the largest phytoplankton concentrations in the transition zone in between. Based on studies of satellite imagery, Podestá (1990) states that the frontal areas of transition between tidally mixed waters and stratified waters, and also the area of the shelf-break front, are the only places on the Patagonian Shelf where nearsurface phytoplankton biomass remains high throughout the summer.

4.2 Concentration processes

The existence of a strong shelf-break front (e.g. Servicio de Hidrografía Naval 1969, Hubold 1980a, 1980b, Podestá, 1990), in conjunction with shelf-break-related emichment processes, provides a paralarval habitat with similar characteristics to that of *I. illecebrosus* at the inner edge of the Gulf Stream (Section 3.2), only in this case the boundary current flow is equatorward rather than poleward. The same type of frontal convergence and associated concentration of drifting organisms (Fig. 6.1) must occur due to similar frictional, gravitational, and pressure-related effects as outlined in Section 3.2. Certainly, comparison of satellite-sensed surface pigment distributions in the two regional situations (NSF/NASA 1989) suggests strong analogies. Likewise, the interactions of the various currents and water masses in the region (Brazil Current, Falkland [Malvinas] Current, shelf waters, etc.) provide the sharp density contrasts supporting the hypothetical favourable mechanism for egg-mass placement and paralarval entrainment outlined in Section 2 (Fig. 6.2).

Towards the northern (terminal) end of the main zone of para larval drift (co 38°S), there exists another habitat configuration that may be particularly conducive to production of concentrated food patch structure (Bakun and Parrish 1991). Major freshwater inputs into the ocean occur due to outflow of the Rio de la Plata and other sources in the vicinity of Rio Grande (southern Brazil). The runoff produces a lens of less saline, and therefore less dense, surface water which tends to override the more dense oceanic waters (Fig. 6.5). The interfaces between the surface waters of contrasting densities are zones of convergence where the waters mixed at the interfaces between the water types, being more dense thall the surface plume waters, slowly slide beneath them in response to gravity. Here, as in other frontal situations, weakly swimming organisms (larval

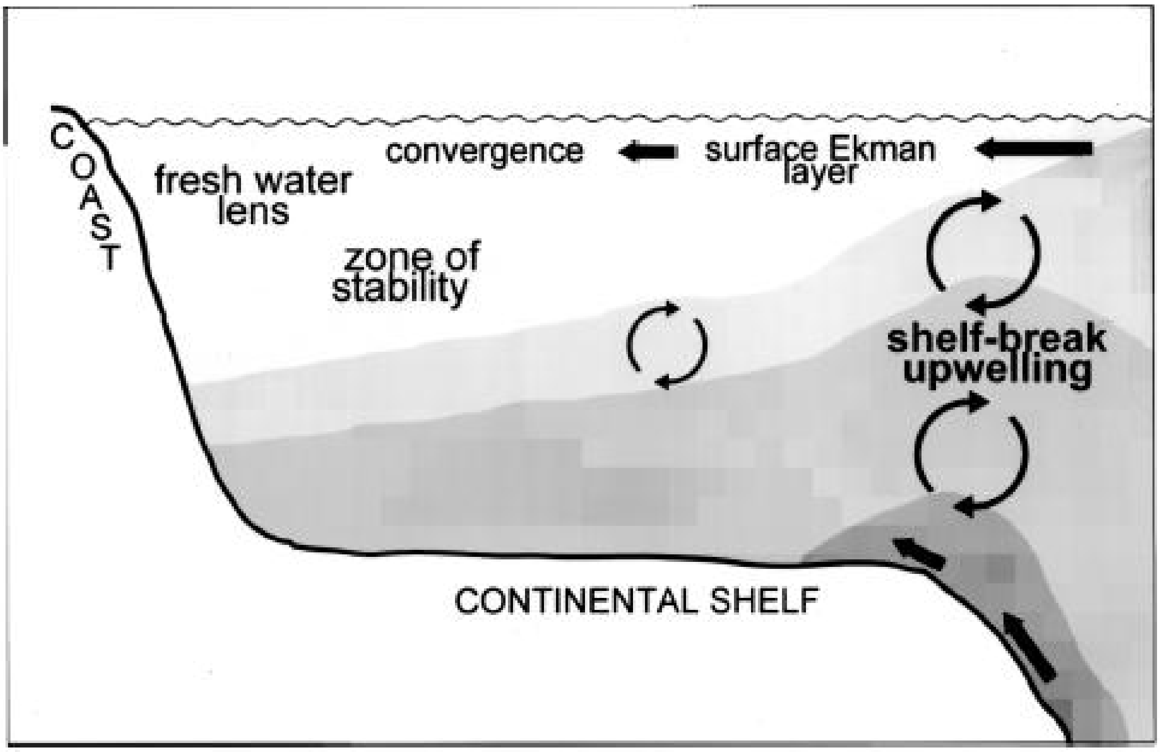

Figure 6.5. Habitat configuration for the extreme north coast of Argentina, coast of Uruguay, and coast of southern Brazil from the southern border to a point somewhat north of the Rio Grande includes: winddriven Ekman transport is toward the coast; enrichment from shelf-break upwelling, supplemented by certain elements in freshwater runoff; and convergent surface fronts and a zone of stability in the subsurface pycnocline associated with a lens of runoff diluted surface water against the coast. Linked circular pairs of arrows represent mixing processes (redrawn from Bakun and Parrish 1991)

food particles, etc.) able to resist sinking tend to be concentrated. In addition, the freshwater inputs may enrich the supply of certain plant nutrients, such as silicates (Hubold 1980b), that may be rare in the oceanic surface waters.

In the juvenile *Illex* habitat of the inner Patagonian Shelf, tidal mixing of the shallower waters results in surface water of greater density and bottom water of lesser density compared to waters at the same depths further offshore (Fig. 6.6). The consequence is that the lighter offshore surface water will tend to override the heavier mixed water, resulting in shoreward surface flow towards a convergent sea surface front. Conversely, heavier offshore deep water will tend to flow under the lighter mixed water at the bottom, resulting in shoreward flow offshore of a convergent front at the sea bottom. Balancing these onshore flows at the surface and at depth, will be an offshore flow of mixed water in a zone of stability within the mid-depth thermocline.

Thus planktonic organisms that are able to maintain their depth level either near the sea surface or near the sea floor may be concentrated in the convergent frontal zones at those levels. Iles and Sinclair (1982) note that observed distributions of herring larvae tend to be contained within boundaries corresponding to the positions of fronts of this type. Enhanced primary production due to the tidal-mixing-based enrichment on the shoreward side of the front would promote a planktonic trophic succession of primary producers, herbivores, primary carnivores, etc., in the water moving, within the mid-depth pycnocline, from the frontal zone towards the open ocean. Thus, small predatory organisms such as juvenile squids may find particularly advantageous feeding conditions in the pycnocline region offshore of the front. At some point, by altering their depth !evel upward or downward, small organisms could enter the surface or bottom flows which are directed towards shallower water and thus avoid removal from access to the enrichment and concentration processes of the inner shelf habitat.

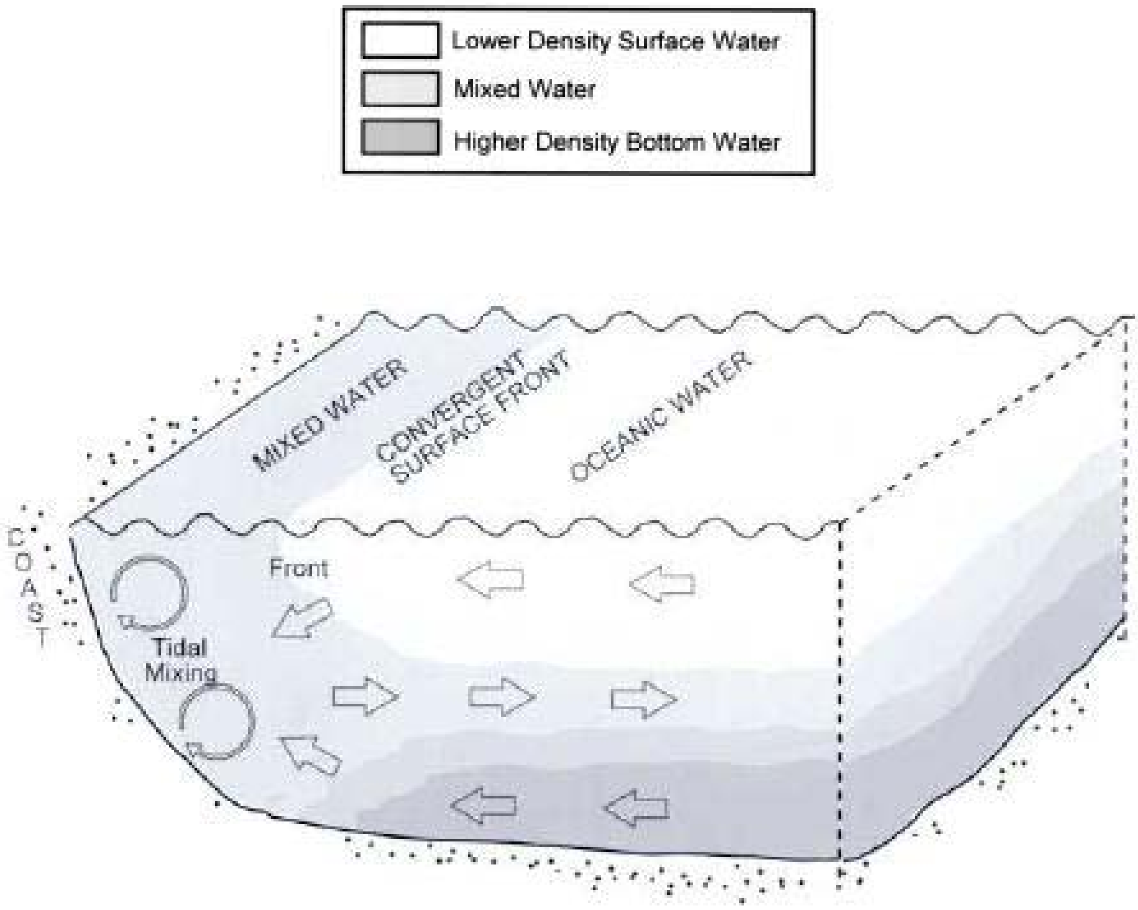

Figure 6.6. Schematic diagram of a shelf-sea front configuration over the Patagonian Shelf (particularly near Peninsula Valdés). Strong tidal mixing results in a homogenized water column near the coast. The result is surface water of greater density, and bottom water of lesser density, in the mixed zone relative to the stratified zone offshore. Thus the lighter offshore surface waters tend to override the heavier mixed waters, resulting in onshore flow towards a convergent surface front. The heavier offshore bottom water likewise flows under the mixed waters, resulting in onshore flow at the bottom. A balancing offshore flow occurs within the mid-depth thermocline (redrawn from Bakun 1996)

4.3 Transport processes

The majority of paralarval drift trajectories are evidently imbedded in the northward Falkland (Malvinas) Current flow (Fig. 10.5). By analogy with the situation of *I. illecebrosus* in the Gulf Stream, paralarvae probably are concentrated, together with larval food organisms, in the frontal zone at the inshore edge of the current which is situated near the shelf break of the very wide continental shelf.

The wind-driven surface Ekman transport pattern tends to be directed towards the coast throughout the region south of the Brazil-Falkland (Malvinas) Current confluence (Bakun and Parrish 1991), particularly during the winter paralarval drift period. The Ekman transport magnitude increases particularly rapidly seaward of the shelf break, as the effect of the "wind shadow" of the South American continent becomes attenuated. Thus, provided they are in the layer above the pycnocline, paralarvae that may be ejected from the shelf-break frontal region by turbulent eddy processes or by their own active adaptive behaviour will tend to be carried towards the juvenile habitat on the inner shelf. Paralarvae that might get ejected to the oceanic side of the frontal region would tend to be rapidly carried by the Ekman transport field, as well as by the convergent flow pattern (Fig. 6.1) associated with the front itself, back into the frontal zone.

As mentioned in the previous section, once the paralarvae or early juveniles reach the vicinity of the tidal mixing fronts (Fig. 6.6), appropriately adapted vertical behaviour could act to keep them in favourable position with respect to the frontal zone. Later, as the animals approached adulthood, behaviour that would keep them mainly in the lower part of the water column over the shelf (which would tend to move offshore to balance the onshore movement of surface waters) would help them on their migration from the juvenile habitat on the inner shelf to the adult habitat near the shelf edge.

4.4 Recruitment hypotheses

In contrast to the Gulf Stream situation (of *I. illecebrosus*), the Falkland (Malvinas) Current does not separate from the shelf break nor tend to develop large meanders and detached eddies. Thus the continuity and integrity of the frontal zone itself does not appear to be as important an issue in the case of *I. argentinus*.

4.4.1 Wind effects

The typical pattern of onshore-directed wind-driven Ekman transport has been identified as particularly favourable to: (1) evident larval recruitment processes, provided the larvae are situated within the upper ocean layer that is under the direct influence of the wind; and (2) pre-adult offshore migration, provided the immature squid exercise an affInity for the sub-pycnocline layers. Thus stronger-than-normal onshore transport conditions (i.e. a stronger-than-normal wind component, but continuing to be directed alongshore and equatorward) might be especially favourable. A variation from this pattern, particularly leading to offshore Ekman transport, might be unfavourable.

Transport-related "match-mismatches" are, however, a possibility. "Too good" transport conditions might result in unfavourably early transfers out of the larval habitat and in early arrivals in juvenile habitat that might not be in proper phase with seasonal development of food resources.

4.4.2 Predation

The Patagonian Shelf is the habitat of large predatory demersal fish populations (Otero *et al.* 1982, Csirke 1987, FAO 1992). It is also the habitat of a large, virtually unexploited anchovy (*Engraulis anchoita*) population

(Ciechomski and Sanchez 1988, Bakun and Parrish 1991) that probably provides a major food source both for *Illex* and for the demersal predatory fish. Anchovy-type fishes are known to undergo very large population fluctuations, even in the absence of significant fishery exploitation (Lluch-Belda *et al.* 1992). A precipitous decline in anchovy biomass might have the affect of shifting the attention of the predators more strongly towards other food sources (towards juvenile squids, for example), as well as remove an imponant food base for the *Illex* population.

4.4.3 Other possibilities

Most of the hypothetical "other possibilities" listed for *I. illecebrosus* in Section 3.4.4 could presumably apply also to *I. argentinus*.

5 Other *Illex* populations

Roper *et al.* (1984) list two additional species of the genus *Illex*. *Illex coindetii* is very widely distributed, particularly in the eastern Atlantic, where it occurs all along the European and African continental boundaries from Norway to Angola and also within the Mediterranean and Black seas; in the western Atlantic it occurs in the Caribbean-Gulf of Mexico region and on the east coast of Florida. *Illex oxygonius* occurs along the coast of the southeastern United States, from Chesapeake Bay to southern Florida and within the Gulf of Mexico to about half way up the west coast of Florida.

We find little information on the ecology of these two species, except that they seem to be less oceanic and more associated with solid ocean bottom than the two species, *I. illecebrosus* and *I. argentinus*, that achieve very large regional biomass concentrations and so are the objects of major directed fisheries. Thus we have little information about their particular larval and juvenile habitat characteristics, drift or migrational paths, etc., that could form the' basis for focused discussion and specific hypotheses.

Certainly, we can assume they are making use of habitat configurations offering appropriate combinationsof: (1) trophic enrichment, (2) concentration processes, and (3) ocean transport conditions and migrational paths, permitting population maintenance and life-cycle closure. The region along the eastern boundary of the Atlantic Ocean from northwestern Spain to southern Africa is dominated by several extensive coastal upwelling systems (Wooster *et al.* 1976, Bakun 1978, Parrish *et al.* 1983). The well-known upwelling-based enrichment (Cushing 1969) makes such ocean regions the most productive, overall, in the world (ICLARM 1992). Because of the incessant wind-induced offshore transport of surface waters, which is the process that drives the coastal upwelling, they also appear to be difficult places for pelagic-spawning coastal organisms to reproduce successfully (Parrish *et al.* 1981). Overly strong winds may also disperse fine-scale food concentrations needed for paralarval nutrition (Lasker 1975, 1978). Thus wind intensity is potentially related to both positive and negative effects. Cury and Roy (1989), for example, found a dome-shaped relationship of wind intensity to recruitment success of coastal pelagic fishes in such regions, such that an intermediate wind speed was optimal and that either too strong or too weak wind levels were detrimental.

Ample opportunity occurs in upwelling regions for convergent frontal formations (Fig. 6.1) between the cooler, more dense, newly upwelled waters and the less dense, resident oceanic surface waters. In addition, major river outflows distributed around the Atlantic continental boundaries provide additional opportunities for frontal formation and enrichment with various nutrient substances. Additional opportunities occur in locations of exchanges of differing water masses between the ocean proper and peripheral seas. Moreover, inside the peripheral seas there are numerous localized regions of upwelling, water mass interfaces, etc. And north of the upwelling zones along the eastern Atlantic boundaries, shelf-sea front formations, such as described for the Patagonian Shelf, are common in the Irish and North seas (Iles and Sinclair 1982, Sinclair 1988). Finally, branches of the Gulf Stream system run through the Caribbean and the Gulf of Mexico (Maul 1977, Richards *et al.* 1989), opening possibilities for similar processes, as discussed in Section 3 in relation to the paralarval habitat of *I. illecebrosus*. Nevertheless, we feel that more specific elaboration of potential environmental mechanisms involved in recruitment variability in *I. coindetii* and *I. oxygonius* must probably await the availability of additional descriptive material, such as that concerning stock delineation, life cycle and habitat characteristics, drift and migrational paths, etc.

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