ENVIRONMENTAL INFLUENCES ON THE DISTRIBUTION AND TRANSPORT OF ATLANTIC COD, *Gadus morhua*, EGGS AND LARVAE IN COASTAL NEWFOUNDLAND

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Environmental influences on the distribution and transport of Atlantic cod, *Gadus morhua*, eggs and larvae in coastal Newfoundland.

By

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Abstract

This study examines spatial and temporal variability in distribution of Atlantic *cod (Gadus morhua* L.) eggs and larvae in Placentia Bay, Newfoundland, from three directions. The first chapter reviews the literature regarding the roles of transport and behavior in planktonic egg and larval pattern for benthic marine invertebrates and fish. This review suggests that the processes affecting each group are very similar, acknowledging that differences may be found in the capacity to contribute actively to dispersal and habitat selection. The second chapter provides evidence that variation in location and timing of spawning of Atlantic cod has a major impact on occurrence, distribution and development of eggs and larvae in Placentia Bay. Repeated ichthyoplankton surveys of the bay during the spawning and post-spawning periods indicate that eggs spawned early in the year (March - May) are lost from the bay. By contrast, elevated egg production late in summer of 1998 (July) resulted in a dramatic increase in larval densities. The third chapter combines modeling and field examination of the relationships between mortality, transport, and temperature during the egg stage, and demonstrates that consistent transport out of the bay may limit numbers hatching within the bay. Thus, the appearance of larvae is confined to summer months when development times are shortest. This thesis demonstrates the importance of cod spawning timing and location, as well as temperature and hydrographic influences on the transport and development of planktonic eggs and larvae in coastal Newfoundland.

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Introduction and Overview

Historically, the cod stock complex off the coast of Newfoundland and southern Labrador was one of the worlds largest and most valuable groundfish resources (Lear and Parsons 1993; Taggart et al. 1994). Extensive exploitation, possibly compounded by poor environmental conditions, resulted in a collapse of the stocks in the early 1990's. Consequently, a moratorium on commercial fishing was implemented in 1992-93. Since that time, although there has been little or no recovery in the offshore, large spawning aggregations have been documented in coastal areas (Rose 1996; Taggart 1997). Although there have been historic accounts of spawning aggregations in coastal areas (Graham 1922; Thompson 1943), the current proportion relative to the offshore is unprecedented. Therefore, the current health and eventual recovery of the stock complex may be largely influenced by these coastal spawning events.

Despite recent documentation of coastal spawning events (Rose 1996, Lawson and Rose 1999), the degree to which inshore spawning may impact recruitment success remains largely unknown. Smedbol et al. (1998) made a notable contribution to this question in finding no recruitment signal from a large spawning event in Trinity Bay Newfoundland, but few studies have examined the egg and larval ecology of cod in coastal Newfoundland. Given the current status of the stock complex, this information may be critical to the proper management of a recovery. Several studies have suggested that egg and larval distribution may be important to survival and recruitment success in Atlantic cod. High mortality could occur due to starvation resulting from a mismatch with local production (Ellertsen et al. 1989) or through advection away from favorable nursery areas (deYoung and Rose 1993). Nonetheless, the complex topography of Newfoundland bays may facilitate egg and larval retention in areas with high prey densities (Frank and Leggett 1982). As a consequence, coastal Newfoundland may provide ideal nursery conditions.

The main purpose of this study is to examine the processes that influence the presence of eggs and larvae of Atlantic cod in Placentia Bay, Newfoundland. The study can be divided into three components. The first component reviews the literature on factors that influence spatial and temporal pattern in planktonic eggs and larvae. This review is broad in scope, encompassing species of benthic fish and invertebrates that possess a planktonic dispersal stage. The second chapter examines spatial and temporal pattern in cod eggs and larvae in Placentia Bay during the spawning and post-spawning periods using conductivity-temperature-depth (CTD) data, limited data from current moorings, and chlorophyll a data from water sample extractions, *in situ* fluorometers, and SeaWiFs (Sea-viewing Wide Field-of-view Sensor) satellite imagery data. I examine between-year and seasonal variation in the coastal environment and the roles these variables play in egg and larvae spatial and temporal pattern. The third chapter uses a simple model of the influence of temperature on egg and larval pattern in order to develop several hypotheses on the development and dispersal of cod eggs. The suitability of the model is then tested using field data on cod eggs and larvae, temperature, and currents.

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Co-Authorship Statement

All manuscripts in this thesis were co-authored with Paul Snelgrove; and chapters 2 and 3 were also co-authored by Sandy Fraser. In all instances, I was the principle contributor to project design and proposal, implementation of the field research component, analysis of data and manuscript preparation.

Chapter 2 has been submitted to the Canadian Journal of Fisheries and Aquatic Sciences and Chapter 3 to Fisheries Oceanography. Some parts of chapter 2 and 3 have appeared in Canadian Stock Assessment Secretariat Research Documents 99/74, and 00/22 respectively.

Chapter 1. Pattern in Benthic Marine Fish and Invertebrates : the role of transport and behavior.

1.1 Introduction

Attempts to understand the processes that contribute to and maintain temporal and spatial pattern in benthic ecosystems have long been at the forefront of benthic ecology (Snelgrove and Butman 1994). A number of these studies have suggested that pattern in egg and larval distribution has significant consequences for recruitment and population stability (Gaines & Roughgarden 1987; Sinclair 1988; Cowen 1995). Because a large proportion of marine benthic and demersal organisms have a planktonic egg and larval stage, formation of distribution patterns in these species is undoubtedly a combination of biological and physical processes. Disentangling the relative contribution to pattern formation of processes such as advection, locomotion, and active habitat selection has proven to be very difficult (Boicourt 1982).

Organisms that reside in benthic environments face an evolutionary dilemma. On the one hand, they must colonize new habitat in order to avoid intraspecific competition and reduce the risk of extinction through local disturbance, predation, or a host of other threats. Many species of fish and invertebrates have developed a similar life history strategy, wherein planktonic larvae disperse to and colonize non-local habitats. On the other hand, these species face the challenge of placing often weak-swimming propagules into a habitat suitable for survival and growth. Although many larvae have some swimming capacity, limitations in swimming ability can result in transport by currents into unsuitable habitat. Many species of invertebrates and fish have very specific habitat requirements. In fish, post-settlement movement can aid in finding suitable habitat. but in most invertebrates the capacity to move is effectively lost at settlement. This raises the question of whether larvae of fish and invertebrates utilize similar approaches to achieve the sometimes inconsistent goals of dispersing to new areas, but also finding a suitable benthic environment.

The majority of marine fish and up to 70% of all benthic temperate and tropical invertebrate species (Thorson 1950, cited in Scheltema 1986b) display a planktonic larval stage. Invertebrates and fish have therefore evolved early life history strategies in response to the pressures inherent to life in a planktonic environment. The presence of a planktonic stage in the early life history of marine fish and benthic invertebrates suggests that mechanisms regulating spatial and temporal pattern in both groups may be similar, but there have been few attempts to contrast the bio-physical components of planktonic dispersal in these groups. This dichotomy between the scientific study of fish and invertebrates has undoubtedly resulted from problems associated with taxonomy and sampling logistics (Scheltema 1986b), as well as the immense scale involved in examining such a question. But the discontinuity also extends across studies, in that scientists studying invertebrates rarely cite those studying fish and vice versa. Do the findings of one group have significant implications for those studying the other? In other words, should the invertebrate and fish scientists be cross-fertilizing?

The goal of this review is to contrast the relative roles of physical transport and behavior of planktonic stages in the formation of spatial and temporal distribution in benthic marine fish and invertebrates. A taxonomically broad approach comparing species with extremely different life histories and locomotory abilities provides the scope to explore the processes involved in dispersal. This review deals with benthic invertebrates living on sedimentary and hard (corals and bedrock) substrates, and fishes that are associated with these environments. Defining the dispersal stage and habitat are more difficult for species of invertebrates and fish with pelagic adults, and this review is restricted to benthic species with planktonic dispersal stage.

Historical Perspective

Beginning in the early 1900's, evidence pointing to the importance of the early life history to recruitment in marine fish began to accumulate (Hjort 1914). Many studies (e.g., Walford 1938) were subsequently conducted during the 1930's and 40's correlating water currents with the distribution of spawning products. Since these pioneering studies, considerable effort has been put into linking meteorological and oceanographic variation to recruitment success (Cushing 1969; Sinclair 1988; Ellertsen et al. 1989). Oceanographic features such as Ekman, geostrophic, and frontal currents are now known to transport, concentrate, and aid in retention of eggs and larvae (Norcross and Shaw 1984; Shanks 1995). Spatial variation has also been implicated as a cause of recruitment variability in the member-vagrant hypothesis, where vagrants may be lost from the population through transport into unfavorable areas (Sinclair 1988).

Dispersal distances in benthic invertebrates can differ dramatically between species, ranging from centimeters to thousands of kilometers (Scheltema 1986b). The pervasive attitude toward invertebrate dispersal early in this century was that dispersal was, for the most part, a passive process but that a sufficient number of propagules were produced to ensure that some individuals would settle in appropriate environments (e.g., Petersen 1913). Laboratory experiments during the 1920's and 1930's demonstrated that many benthic invertebrates are capable of habitat selection (e.g,Wilson 1937; Mortensen 1938). Speculation on the relative roles of behavior and transport has continued through this century (e.g., Gardiner 1904; Thorson 1961; Scheltema 1974; Butman 1987), and current thinking is that transport and behavior both play major roles but at different spatial scales (Butman 1987).

The dynamics of larval behavior, and in particular the concept of active substrate selection, has received considerable attention in the last 50 years. For some taxa, substrate contact is required (e.g., Morse 1985), whereas for other taxa contact with water-bourne chemicals results in modified behavior in the water column such as cessation of swimming (Scheltema 1986b; Turner et al. 1994). Invertebrate larvae are not usually able to settle throughout the entire planktonic period, will typically spend some period of time in a precompetent phase during which settlement is physiologically impossible. As development progresses, individuals reach a point where they are physiologically capable of settling and metamorphosing. Metamorphosis is defined as a series of morphological and physiological changes associated with settlement (defined as a termination of pelagic life). Topics such as the ability of many species to delay metamorphosis in the absence of suitable habitat have been considered by others (see Young 1996). These concepts have developed primarily from studies of invertebrate meroplankton; however, several authors have applied this terminology to planktonic fish larvae. The use of these terms varies somewhat among fish and invertebrate scientists creates obvious problems. For instance, metamorphosis has been used extensively in the study of reef fish recruitment (see Cowan and Sponaugle 1997), but in most instances the process in question is settlement because the magnitude of morphological or physiological changes observed in fish is considerably less than that observed in invertebrates (flatfish are a notable exception).

Is it a question of swimming ability ?

In a static ocean, dispersal would depend entirely on locomotory ability. Although the range of swim speeds and planktonic durations in fish varies, it is reasonable to assume a maximum sustained swim speed of 1cm/s and a dispersal time of 4-6weeks (Table 1). Swimming at this speed for 24 hours a day for 6 weeks would give larvae a dispersal distance of about 40 km. For an invertebrate larva with a swim speed on the order of ~3mm/s (Butman 1986) for 6 weeks would result in a total travel distance of about 10 km. However, dispersal is never this simple. There are many examples of fish (e.g., Schultz & Cowen 1994) and invertebrate larvae (e.g., Katz et al. 1994) that are transported much greater distances over shorter time periods or remain at spawning grounds despite currents that would be expected to result in greater dispersion.

In contrast to dispersal, the ability to select habitat actively at settlement may also directly influence distribution patterns. This capacity is dependent on swimming ability in relation to boundary flow conditions. We hypothesis that fish larvae have greater swim speeds relative to most invertebrates which may favour active habitat selection under a wider range of flow speeds. Although swimming ability and habitat selection may contribute significantly to adult distributions in both groups, our inability to explain dispersal by swimming capacity and behavior alone suggests the need for interdisciplinary studies that incorporate behavior, larval duration, and physical oceanography.

1.2 Dispersal and Concentration Processes

Currents produced by wind, tides, and thermohaline forces interact to move bodies of water on multiple spatial and temporal scales. These processes concentrate and disperse reproductive propagules. The latter are critical in maintaining habitat associations, and the former allow colonization of new habitat and the extension of distributions. The process of dispersal often begins from the moment that eggs are released into the water. On a small scale, eggs and passive larvae in a static ocean would disperse through eddy diffusion, and diffusion alone could disperse planktonic larvae up to 100 km over a period of a month (Okubo 1994). For colonizing new habitats in particular, these mechanisms can be extremely effective, but many species retain reproductive propagules within a suitable environment. Just as water masses advect eggs and larvae, various circulation features have the potential to concentrate buoyant particles, including eggs and larvae. Retention and concentration of propagules is theoretically possible anywhere eddies (Fig. 1.1a, 1.1b), gyres, or persistent downwelling associated with frontal formation occur (Fig. 1.1c, 1.1d).

Planktonic offspring can be released in or transported to areas favorable to survival. In many cases successful recruitment depends on retention of larvae in these habitats, whereas transport away reduces survival (Hare & Cowen 1993). Harden Jones's (1969) classic model of larval drift from spawning to nursery areas and juvenile migration to adult spawning grounds is unsuitable for many species. Cod and haddock larval distributions off the northeastern United States coast suggest that the spawning and nursery grounds are the same area (Sherman et al. 1984). The vast majority of benthic invertebrates are immobile or have little mobility after settlement. Thus, most invertebrates will metamorphose into juveniles as they settle and remain near their settlement site through maturation. Only in some instances (e.g., Vance 1973; prawns in Australia) are juveniles and adults predictably segregated spatially.

1.3 Passive and active processes : a matter of scale?

In the following sections the literature on the dispersal and concentration of invertebrate and fish eggs and larvae is reviewed, starting first with large-scale processes and moving toward small-scale influences on spatial and temporal distributional patterns. We hypothesize that due to the limited locomotory abilities of most larvae, passive processes will dominate in large-scale pattern formation and active processes dominate at much smaller scales.

Large-Scale Ocean Currents

The importance of large-scale ocean currents to variation in settlement and recruitment has been recognized for over a century. These are currents that have their source in ocean basin dynamics. Haeckal (1892) stressed the importance of these currents in the transport of marine organisms, even referring to them as "zoocurrents". The relatively poor swim speeds of many invertebrate and fish larvae in relation to currents means that rate and direction of advection will depend more on passive transport than on behavior (Butman 1986, Carlon and Olson 1993). Currents such as the Kuroshio (Yamaguchi 1986), and the Leeuwin Current (Morgan and Wells 1991) have been extensively studied with respect to larval transport.

Infestations of *Acanthaster planci* off the coast of Japan have been studied in response to population explosions that have decimated reef-building corals. Yamaguchi (1986) correlated a shift in infestation sites in the mid-seventies with a shift in the Kuroshio, and suggested that removal projects have been unsuccessful to date because the larvae are coming from an upstream source. Since the 1970's, large scale removal projects have been in place to protect the reefs, but with little success. Similar work by Kenchington (1977) suggests that crown-of-thorns starfish outbreaks on the Great Barrier Reef system move in conjunction with the East Australian current, from north to south.

The Leeuwin Current off Western Australia has been correlated with the southward transport of propagules of several species of tropical marine organisms along the west coast of Australia (Maxwell and Cresswell 1981, Cresswell 1986, Hutchins 1991, Morgan and Wells 1991). Hutchins & Pearce (1994) reported that patterns in reef fish larval transport could be explained by the strengthening of the Leeuwin current in the spring.

Regional Currents

On a smaller spatial scale, regional currents such as those formed through continental shelf dynamics may also influence transport eggs and larvae. Atlantic cod eggs and larvae for example, are transported in the Labrador current along the coast of Newfoundland towards the Grand Banks (Pepin and Helbig 1997). Similarly, Jenkins and Black (1994) observed that high interannual variability in the frequency and timing of regional hydrodynamics regulated transport of larvae to juvenile habitats in Port Phillip Bay, Australia. In the Shelikof Strait in Alaska, eggs and larvae of walleye pollock (*Thelagra chalcogramma*) were observed to drift southwest with predominant coastal currents to downstream nursery habitats (Hinckley et al. 1991). Barnacle recruitment has been largely explained by predictions based on the transport of planktonic stages from coastal areas off Rhode Island (Gaines and Bertness 1992) and California (Roughgarden et al. 1988).

Modifications to Large-Scale Currents

Mesoscale Eddies

Eddies are rotary currents, defined here to range in size from centimeters to kilometers in diameter. Eddies often result in the formation of convergences and can therefore concentrate buoyant plankton (Fig. 1.1a). The effect of ocean eddies on larval transport and subsequent recruitment has received limited attention (Wroblewski & Cheney 1984). Based on a modeling study of Gulf Stream ring and larval dynamics, Flierl & Wroblewski (1985) propose a relationship between the frequency of ring interaction and year class strength in cod and haddock on Georges Bank. Wolanksi and Hammer (1988) conclude that topographically-controlled currents such as eddies commonly aggregate buoyant particles and prevent dispersion as would be expected in the open ocean. Coastal and island eddies are better understood than ocean eddies with respect to their influence on recruitment dynamics. Stabeno et al. (1996) observed high larval and egg abundances in association with eddies in the Shelikof Strait of Alaska. Drogues placed in these eddies were entrained for several weeks before they drifted away. The waters off Hawaii are characterized by mesoscale eddies that may have implications for larval transport and retention. Lobel & Robinson (1986) conclude that mesoscale eddy systems can entrain larval fish from reefs over sufficient time periods for many reef fish species to complete their pelagic development phase. Oceanic islands such as Hawaii pose a particularly interesting case given their isolation from other areas of shallow habitat. Are local populations self seeded or are larvae advected from elsewhere? Schultz & Cowen (1994) examined this question for Bermuda fishes. A comparison of planktonic larval duration with predicted transport speeds indicated that populations of reef fish must be replenished mainly by local spawning events because of the great distance from other larval sources, and a local retention mechanism is therefore necessary.

Pattiaratchi (1994) raises the interesting point that most studies of eddies assume negligible wind effects, yet only in rare spawning events is this condition ever met. For example, there are several accounts of coral spawning slicks during CORSPEX (coral spawning experiment) that were broken up within days by strong winds (Wolanski et al. 1989, Willis & Oliver 1990).

Ekman transport and wind forcing

Many studies have shown that wind driven Ekman flow can transport the eggs and larvae of nearshore and offshore spawners towards or away from appropriate nursery grounds (Norcross & Shaw 1984). Wind-induced transport has been associated with recruitment success of a number of marine invertebrates (Roughgarden et al. 1988, Farrell et al. 1991, Miller & Emlet 1997) and marine fish (Riley et al. 1979, Bailey 1981). The presence of a seasonal Ekman upwelling off central California is one example of the effect of Ekman transport on settlement in benthic invertebrates (Farrell et al. 1991). Transport associated with Ekman upwelling resulted in barnacle cyprid larvae dispersal offshore; onshore transport, and thus recruitment, depend on relaxation of dominant winds. The result is that highly variable recruitment is observed, though variation can be offset somewhat by the extended spawning period (Miller and Emlet 1997). Another example is variation in settlement of benthic invertebrates such as the acorn barnacle, *Semibalanus balanoides*. Settlement variation has been linked to local weather conditions through transport of larvae by wind-driven circulation (Bertness et al. 1996) In fact, wind signatures have been observed to affect settlement patterns of many planktonic invertebrate larvae. Settlement on the southern side of Narragansett Bay in 1991 and 1992 was associated with winds from the north, and conversely settlement on the northern side was associated with southerly winds (Bertness et al. 1996). Daily larval settlement and the accumulation of recruits were also correlated with local winds. Similarly, Botsford et al. (1994) matched the distribution of Dungeness crab with empirically-derived predictions of abundance based on the effects of wind forcing.

Wind patterns are perhaps the most temporally variable of the processes that influence larval distributions, and they can have dramatic effects on larval fish survival and settlement (e.g., Bailey 1981). Given that surface current speed produced from wind events is ~3% of the wind speed and decreases with depth, the ability of larvae to move horizontally and vertically may play a major role in transport. Cod larvae on Georges Bank associated with the Ekman layer (upper 10 - 20m) were generally lost to the open ocean and assumed perished where Ekman transport carried them offshore (Lough et al. 1994). Larvae occurring deeper in the water column were less influenced by wind forcing and more likely to remain on the bank.

Seamounts - Taylor Cap Formation

Taylor caps are formed when ocean currents move up and over raised topography such as seamounts; their rotary and convergent properties may retain planktonic eggs and larvae. The vertical current movement at the seamount compresses fluid above and results in the anticyclonic (clockwise in the northern hemisphere, counter clockwise in the southern hemisphere) motion in order to conserve vorticity (Fig 1.1b; Chapman and Haidvogel 1992; Mullineaux and Mills 1997). The extent to which seamounts possess the potential for retention of larvae is unknown. Temporal stability of such structures is dependent on the stability of the current. If the current is relatively stable, then these structures may persist for long periods of time (weeks to months). Small fluctuations in the current direction, however, will cause the column to be shed and larvae will no longer be retained (Bakun 1994). Larval settlement on seamounts has been shown to be partially a function of retention, and larval abundances correlate with tidally rectified circulation in flow generated by interaction with the seamount (Mullineaux and Mills 1997).

As with eddies, the temporal stability of Taylor caps may dictate the extent to which they affect settlement. Parker and Tunnicliffe (1994) examined benthic invertebrate dispersal and Taylor cap stability on Cobb Seamount off the Oregon coast. They estimated the residency time of water over the seamount at 17 days, which may be very significant in this habitat because their survey of benthic invertebrate species showed that the seamount is dominated by species with either short-lived or non-planktonic larval stage. They propose that Taylor cap stability is important for trapping short-lived larvae over the bank, and that species with larval periods greater than the replacement time are advected away from the seamount.

Tidal currents

The utilization of tidal currents by larvae has lead to several theories on selective tidal transport. Many studies have explained transport and retention in estuaries using vertical migration (e.g., Bousfield 1955; Rowe & Epifanio 1994; review by Dame and Allen 1996). Several authors have observed increasing larval size from the offshore to the inshore (Norcross & Shaw 1984), and attributed the pattern to shoreward transport of developing larvae via tides and currents. Larvae can be transported in tidal streams, over internal waves, and within a tidal bore produced by an internal wave (Shanks 1995).

As previously mentioned, wind-driven Ekman forcing often results in a net transport of water and organisms offshore in many coastal areas. Many researchers have suggested tidal currents as a mechanism for onshore transport. Settlement of the megalopae of the rock crab, *Cancer irroratus*, in Block Island Sound, Rhode Island is dependent on tidal advection resulting in a shoreward movement (Clancy & Cobb 1997).

Two mechanisms related to tidal currents have been proposed for shoreward transport of eggs and larvae via internal waves (Shanks 1983, Shanks and Wright 1987, Pineda 1991, Pineda 1994). Internal waves are often formed when the tides ebb and flow over areas of irregular bottom topography such as the shelf break, but the mechanisms of these waves are not well understood (Pond and Pickard 1995). The formation of currents over the wave causes a convergence over the trough and a divergence over the crest (see Fig. 1.1.; Ewing 1950). A number of studies have hypothesized that the onshore movement of a convergence associated with the trough of an internal wave could transport buoyant particles shoreward (Shanks 1983, Jillet and Zeldis 1985, Kingsford and Choat 1986, Shanks and Wright 1987). Evidence that these waves can propagate larvae is seen off southern California (Shanks 1983; Shanks and Wright 1987), where surface drifters and high organism abundance are associated with the convergence zone.

An extension of this mechanism occurs when large internal waves become asymmetrical and break to form a tidal bore. Tidal bores occur near the bottom and propagate towards shore. Settlement of intertidal barnacles has been correlated with temperature anomalies that were probably an indication of an internal tidal bore (Pineda 1991). Pineda (1994) developed this hypothesis in demonstrating that onshore larval transport was dependent on these internal tidal bores.

Although surface slicks and internal tidal bores both provide potential transport mechanisms for larvae, their role may depend on larval position in the water column. Shanks (1995) suggested that larvae suspended near the surface could be aggregated in surface slicks and transported shoreward; however, larvae would have to be near the bottom to be influenced by internal tidal bores (Pineda 1991). Pineda (1999) demonstrated that warm tidal bore fronts can accumulate neustonic larvae and transport them as the fronts propagate shoreward. He suggested that although the surface slicks described by Shanks (see Shanks 1983) may concentrate and accumulate strong swimming larvae, warm bore fronts may better explain the patterns observed.

When the convergences that concentrate and retain eggs and larvae of marine organisms are displaced horizontally (see discussion of internal waves above), organisms trapped in the front will be transported (Pineda 1999). The presence of frontal circulation and its influence on larval transport has been studied by several authors. Larval cod retention and loss on Georges Bank, for example, has been related to frontal formation (Townsend and Pettigrew 1996).

Oceanographic gyres

Oceanographic gyres are large-scale rotary currents and are present in most large ocean basins and over coastal banks (e.g., Georges Bank). Because gyres result in very little net displacement, they can retain eggs and larvae. In addition to the closed nature of a gyre. the formation of convergent fronts at its boundaries can also help retain eggs and larvae. Gagne and O'Boyle (1984) concluded that for the Scotian Shelf, cod larvae do not drift from spawning to nursery grounds, but are retained within the general spawning area. O'Boyle et al. (1984) proposed that this retention mechanism may result from tidally-generated gyres, a mechanism that has been proposed for other species (Sherman et al. 1984., Smith & Morse 1985). Similarly, retention of sea scallop (*Placopecten magellanicus*) larvae over Georges Bank is thought to be entirely dependent on the stability of the gyre that persists over the bank (Silva and O'Dor 1988; Tremblay and Sinclair 1990). One might predict that retention would be greatest when development time is shortest, and that spawning in warm waters would result in reduced time to settlement and less transport off of banks where mortality would presumably be high. Indeed, sea scallops on Georges Bank spawn during the warmest water temperatures, which occur in the fall of the year.

Fronts

Frontal formation occurs near the ocean surface at sharp boundaries between adjacent water masses with different characteristics (Fig 1.1c & 1.1d; Shanks 1995). Within the frontal zone, flow may be convergent on one or both sides. It is this surface flow toward the front and subsequent downward net movement that results in the accumulation of buoyant particles. Front formation is often the product of secondary flow generated in association with complex topography such as islands, reefs, and headlands (Wolanski and Hammer 1988). In these situations, stable wakes generated by topography interact with shallow bottoms to produce secondary circulation that characteristically slopes upward from the center of these eddies. This slope results in bottom flow moving radially toward the center, producing upwelling at the center of the eddy and downwelling at the edges.

As an example of fronts, visible surface slicks formed from larvae of broadcast spawning corals have been observed on the Great Barrier Reef; observations of these features over time have provided insight into the biological importance of topographically generated fronts. Willis and Oliver (1990) reported aggregations of coral larvae in topographically-generated fronts associated with islands, headlands, and reefs. Alexander and Roughgarden (1996) found that the dynamics of central California barnacle populations were determined by the interaction of advection - diffusion and the location of an offshore front. Larvae associated with the front successfully recruited if wind conditions moved the front into the coastline, but larvae were lost and recruitment was unsuccessful if the front remained far from shore.

Many fish species rely on frontal circulation to maintain larvae in the vicinity of suitable nursery habitats. Dover sole, *Microstomus pacificus*, in the North Sea, for example, are retained in suitable offshore waters by fronts associated with a winter convergence (Hayman & Tyler 1980). On the Scotian Shelf, Taggart et al. (1996) found fish larvae and zooplankton were most concentrated in a narrow frontal region generated by a gyre-like water mass. Peak densities of larval cod in the North Sea are also associated with a front, and may be a recurrent phenomenon resulting from the spawning habits of cod and convergence associated with the front (Munk et al. 1995). They speculate that retention in the frontal zone is beneficial through enhancement of food availability and initial cohesion of the population.

Hydrothermal Plumes -"Larval Highways in the Deep Sea"

Perhaps one of the greatest dispersal challenges is observed in species endemic to hydothermal vents. The long-term viability of communities inhabiting vents may well depend on dispersal, given that vent activity is ephemeral on time scales of decades (Mullineaux et al. 1995). As hydrothermal flow slows and stops, colonization of new vent habitat becomes essential to species survival. Mullineaux et al. (1995) sampled plumes associated with the Juan de Fuca Ridge and found a wide variety of vent species with abundances as high as 600 larvae per 1000 cubic meters. This work and others (see Kim et al. 1994) suggest that plumes may facilitate dispersal of larvae into new environments.

1.4 Influences of Planktonic Duration and Behavior on Dispersal

The past tendency has been to treat passive and active transport as mutually exclusive processes despite evidence pointing towards interaction between the two (Boicourt 1982; Butman 1987). Active contributions to transport can come from two mechanisms. First, a mechanism of regulating transport relates to duration in the plankton. For species with broadly-defined habitats, an increase in planktonic duration will lead to an increase in dispersal. For species with very specific habitat requirements, increased precompetent larval duration may decease the likelihood of encountering a suitable habitat unless the competency period is also increased (see Jackson and Strathman 1981). Second, as described earlier, swimming can make a significant contribution to horizontal dispersal (see section 1.5).

Dispersal Potential and Planktonic Duration

Dispersal ability or potential has been equated by many authors with the ability to survive long periods in the plankton (Maragos & Jokiel 1986). For this review, dispersal potential is defined as the length of the planktonic period (Maragos & Jokiel 1986).

The use of development and dispersal terminology is more common in reference to invertebrate larvae than to fish, suggesting either a lack of knowledge regarding the physiological basis of settlement in fish or perhaps a fundamental difference in settlement processes in fish and invertebrates (exceptions occur in coral reef fish studies, see Cowen 1991). An additional problem is that invertebrate planktonic durations are often measured from fertilization, however, marine fish larvae are aged from hatch and egg stage duration is therefore generally not included. Although egg stage duration may be very short (days) in tropical areas, it may be on the order of weeks in temperate latitudes. Unfortunately there are insufficient published data to adjust fish larval durations adequately to include the egg stage, compounding the difficulty in contrasting fish and invertebrates.

Within larvae of benthic invertebrates and fish there are species whose larvae have very short or very long planktonic durations. However, synthesizing the published literature on dispersal distances is challenging because most of the published information is vague, if available at all. With the exceptions of a few tunicate species (Davis and Butler 1989; Olson 1985) there are virtually no data on dispersal distance. Identifying dispersal distance is problematic not only because planktonic durations are highly variable, but also because the exact spawning location for many species of invertebrate and demersal fish varies with biotic and abiotic conditions and is rarely known. Even when planktonic periods are known, most data are based on laboratory experiments. Some authors have pointed out that many of these appear to be overestimates as more field studies are conducted (Levin & Bridges 1995). For these reasons, it is not presently possible to measure dispersal distances for many species.

Despite the limitations on available data, it is possible to summarize the current information on dispersal potential in larval invertebrates and fish, though several generalizations and assumptions are required. The influence of factors such as temperature, salinity, and prey density on larval duration cannot be considered because there is little published information on these effects for fish and invertebrates. Moreover, data on larval duration often represent a single estimate from a range of possible values. Whenever possible, median duration values have been estimated for a given taxon. The majority of published data are from laboratory experiments; however, the degree to which these studies represent what happens in a field setting has yet to be determined (Mann 1988; Young 1996). Although there is increasing interest in studying invertebrate larval development in the field (reviewed by Levin 1990), there are many logistic challenges to overcome. Table 1 presents the data collected from the literature on the PLD (planktonic larval duration) of fish and invertebrate species, as well as data on the distribution and habitat preferences of these species.

One-way analysis of variance comparing larval duration of 100 invertebrate larvae and 112 fish larvae gave a p-value = 0.236 (df = 211, f = 1.414). Thus, from this sample of PLD's, there is no difference in larval duration and therefore the passive dispersal potential between the two groups. The relative percentages of both fish and invertebrate larvae in each of the three groupings of dispersal potential (see Table 1) show similar distributions (see Fig. 1.2). Invertebrates and fish are both composed of a high proportion of actaeplanic species, fewer teleplanic species, and fewest anchiplanic species.

Planktonic Duration and Geographic Range

The assumption that dispersal potential is directly related to PLD can be evaluated through an examination of the biogeography of the species listed in Table 1.1. For this evaluation, the world's coasts were divided up into approximately equal regions of coastline of about 10 degrees latitude based on regions used by Scheltema (1989) with the addition of several others. The number of regions occupied by the species in Table 1.1 for different PLD groupings is shown in Fig. 1.3. Invertebrates and fish both show an increase in the proportion of teleplanic (PLD > 2 months) species that occupy a larger number of regions. The anchiplanic (PLD < 1week) invertebrate occupy far fewer regions, but anchiplanic fish species were too few to draw any generalizations.

The observation of no significant difference in planktonic durations of the two groups and the similarity in geographic pattern seen in Fig. 1.3 suggests that planktonic duration is associated with dispersal, and that dispersal potential between the two groups is similar. A critical assumption here is that differences in evolutionary time scales for invertebrates and fish have not created convergent patterns. The influence of planktonic dispersal on biogeography has been developed by other authors working on fish and invertebrate species (Gardiner 1904; Thorson 1961; Scheltema 1989). Most noticeably, the planktonic duration of species inhabiting isolated islands and reefs has provided insight into barriers to dispersal. Johnston Atoll has been referred to as one of the world's most isolated reefs due to lack of island stepping stones between it and other reef habitat. The lack of favorable currents limits external larval supply to species with a prolonged planktonic stage (Maragos and Jokiel 1986). On a broad geographic scale, Wellington and Victor (1989) found that reef fish genera with a confined regional distribution have a shorter mean larval life than widely-distributed genera.

Similar examples of relationships between geographic range and dispersal mode have been noted for invertebrates. Scheltema (1986a) observed that gastropod species present in coastal Hawaii have longer planktonic durations than species associated with continental masses. Given that Hawaiian species have longer planktonic durations, the low level of endemism is hardly surprising, and this supports the idea of continuous gene flow (Scheltema 1986a) through the entire Indo-Pacific for species with teleplanic larvae. Interestingly, Indo-Pacific species of reef fish with planktonic durations of a week to a month generally have larger ranges than species from other geographic regions, suggesting relatively long transport potential even for non-teleplanic species.

Because planktonic duration can have a strong influence on dispersal, there is considerable potential influence of temperature on dispersal through its effect on stage duration. The effect of temperature on larval stage duration can be seen in Fig. 1.4, which indicates that lower temperatures increase dispersal potential. Given that a rise in temperature may shorten the pelagic larval stage, temperature must be taken into account when considering temporal effects of transport or retention mechanisms. Thus an ocean current that is warmed as it progresses (e.g., currents running from W. Africa to Brazil) may transport propagules shorter distances than currents that are cooled (e.g, the Gulf Stream) as they progress (Thorson 1961), all other things being equal.

Connolly and Roughgarden (1999) document an increase in intertidal barnacle recruitment, which they suggest was due to transport anomalies associated with the presence of El Niño conditions. While their argument is convincing, changes in flow associated with El Niño conditions are also accompanied with a rise in water temperature that may also affect dispersal potential (refer to Fig. 1.4). Scheltema and Williams (1982) examined the effect of temperature on development time of barnacle larvae (*Balanus eburneus)* from nauplii to cyprid stage. They show a decrease in larval stage duration of almost 64% with an increase in temperature of 10°C. A 7°C difference in nearshore temperatures between El Niño and non-El Niño years off California is not unusual (Strub et al. 1991), and the warm temperature during El Niño will have dramatic consequences for dispersal of barnacle larvae and may interact with the transport effects to produce the observed increases in recruitment.

Despite the physiological constraints on planktonic duration the ability to raft on floating matter enables both fish and invertebrates a mechanism to prolong planktonic duration beyond the larval period. The larvae of the ascidian, *Botrylloides* sp., swim for a short time after release (minutes to an hour) before settling and metamorphosing (Worcester 1994). Because of this short planktonic period, long distance dispersal is dependent on rafting on substrate (e.g., eel grass *Zostera marina*) that breaks off and drifts. Rafting colonies generally can travel distances two orders of magnitude greater than by swimming alone. (Worcester 1994), and rafting may therefore be an important mechanism for the colonization of new habitat by some hard substrate benthic invertebrates.

Rafting appears to be a rarity in larval fish perhaps because of the nature of the substrate interaction (i.e., no physical attachment). In an examination of geographic distribution and larval duration in damselfishes Wellington and Victor (1989) observed a link between short planktonic duration and relatively small geographic ranges, with one exception. The genus *Abudefduf* is widely distributed, yet possesses a short planktonic period, perhaps because many species of this genus are capable of metamorphosing while beneath floating debris and drifting for long periods (e.g., Gooding and Magnuson 1967)

Locomotion and Dispersal

In terrestrial systems, animal distributions are most often equated with active mobility and locomotion. Plant seed dispersal may be a better analogy to marine larvae, but even in this case there is no behavior, growth or development during dispersal. In planktonic organisms, understanding dispersal means understanding the hydrodynamics of the parcel of water that contains these organisms, as well as the contribution of active behavior. Larval contributions to pattern formation can come from two sources. Active swimming can significantly affect transport, and prolonged competency periods (see previous section) can also impact dispersal and retention.

For many organisms vertical movement may play a more significant role in transport. Bakun (1994) suggests that the ocean be thought of as a series of stacked conveyor belts moving in opposite directions. Simply by changing vertical position in the water column and making use of various currents, horizontal dispersal can sometimes be controlled (see review by Dame and Allen 1996). The advantage of this strategy is that vertical currents tend to be weaker than horizontal currents and a relatively weak swimmer has a greater chance of regulating its transport through vertical movement than horizontal swimming.

Comparison of Swim Speeds

Generally there is believed to be little, if any, active swimming contribution to horizontal transport from the egg and early larvae stages in fish (Lyne and Thresher 1994) or invertebrate larvae (Boicourt 1982, Levin 1983). As fish and some invertebrate larvae mature, however, there may be an ontogenetic shift in the relative importance of passive and active processes to dispersal.

To compare the potential importance of swimming behavior in fish and invertebrate larvae, data on swim speeds were obtained from published sources. One-way analysis of variance comparing swim speeds of 77 invertebrate larvae and 52 fish larvae gave a p-value < 0.0005 ($df = 138$, $f = 44.364$). Thus, larval fish have significantly faster swim speeds than larval invertebrates, at least for the studies included in this analysis. This difference in swimming speeds, which likely relates to swimming mechanisms, may result in increased horizontal and vertical locomotory ability in fish. Fish swimming relies on muscles to set up inertial forces in the surrounding water. The speed produced in fish is dependent on the length of the fish, as well as the frequency and amplitude of the tail beat and the effect of streamlining. In larval invertebrates, few taxa have evolved such effective swimming capabilities, and many invertebrates swim using cilia and or muscular contraction (Chia et al. 1984). The use of cilia dictates small size. Invertebrates that utilize muscular contraction, such as decapod larvae, must possess a rigid skeleton (e.g., hydrostatic, or exoskelton) and often display greater swim speeds than invertebrates dependent on cilia (Chia et al. 1984). These taxa are more similar to fish larvae in terms of swimming potential. Similarly, several invertebrate groups display a positive relationship between larval swimming speed and dispersal distance, including ascidians (Davis and Butler 1989), coral species (Carlon and Olson 1993), and the American lobster, *Homarus americanus* (Katz et al. 1994). In fact, in the American lobster, directional swimming in the late larval stages accounted for the majority of the horizontal dispersal distance of over 150 km.

Recently, increasing attention has been focused on the horizontal swimming abilities of pre-settlement reef fish. A few studies (Stobutzki and Bellwood 1994; Stobutzki and Bellwood 1997; Leis et al. 1996) have shown coral reef fish larvae to be capable of sustained swim speeds of up to 45 $cm \cdot s^{-1}$. These studies have also observed that larvae can orient themselves with respect to the reef from distances of up to 1 km. Although such swimming capacity may have dramatic consequences for horizontal movement, smaller fish and invertebrate larvae are generally not capable of such swimming speeds. However, where these animals may actively contribute to dispersal, at least on a smaller scale, is in the benthic boundary layer.

Butman (1986) examined the swimming capacity of benthic invertebrate larvae in near-bottom flow and concluded that flows in excess of most larval swim speeds are encountered within a few body lengths off the bottom. In Figure 1.5, the smooth-turbulent velocity profiles from Butman (1986) are presented along with data on invertebrate and fish larval swim speeds. Butman (1986) concluded that through most of the boundary layer the predicted flow velocities are such that invertebrate larvae have little capacity to regulate their transport. The increased horizontal swim speeds displayed by fish larvae however, suggests that fish may be able to "outswim" ambient flow speeds through a substantially larger portion of the boundary layer and active habitat selection may indeed be possible under a greater variety of flow conditions.

Comparison of Habitat Selection and Delayed Metamorphosis

Preferential settlement under realistic flow conditions has been demonstrated in several benthic invertebrate (Butman et al. 1988a; Grassle et al. 1992, Snelgrove et al. 1993) and fish larvae (Breitburg et al. 1995). Swimming of larvae of the naked goby, *Gobiosoma bosc*, is important in establishing fine-scale spatial patterns in settlement (Breitburg et al. 1995), but large-scale spatial patterns were determined primarily by physical processes. Thus, fish larvae may also depend on passive and active contributions to spatial pattern as has been suggested for invertebrates (Butman 1987). Swimming in invertebrate larvae is probably most important in the boundary layer when swimming distances of millimeters into the water column transports larvae to new habitat by physical processes (Butman et al. 1988b, Grassle et al. 1992; Pawlik & Butman 1993). Many invertebrate larvae are essentially passive except within a few mm of the bottom, and weak-swimming larvae may utilize passive transport to sample multiple habitats without having to expend much swimming effort (Grassle et al. 1992). But the range of flow speeds suitable for such behavior may be limited (e.g., Jonsson et al. 1991; Grassle et al. 1992), and selectivity in still water may be weaker than in flow for this reason (Snelgrove et al. 1998). In extremely high flows, larvae may be resuspended off the bottom and therefore unable to settle (Pawlik and Butman 1993). Interestingly, recent evidence has shown that some invertebrate larvae preferentially settle at slack tide (Whitlatch and Olson 1998) raising questions of how these species locate suitable habitat. Though most studies of invertebrate larvae habitat selection are lab-based flume experiments, Snelgrove et al. (1999) demonstrate in the field that though transport and larval supply may be variable, settlement patterns in some soft-sediment invertebrates is determined by active habitat selection by settling larvae.

Active habitat selection akin to that observed in the invertebrate species summarized above has been described for only a few fish species. Marliave (1977) conducted a series of still-water experiments in which six temperate species of larval fish were presented with different substrata and their settlement preferences inferred. There was a tendency for five of the six larvae to choose one habitat repeatedly over the others, suggesting a clear habitat preference. Several studies have suggested that coral reef fish may display preferential settlement site selection, selecting habitats based on conspecific (Sweatman 1983; Booth and Beretta 1994) or chemical (Sweatman 1988; Elliott et al. 1995) cues. Settlement dynamics for reef fish are reviewed in more detail by Cowen and Sponaugle (1997).

Habitat selection in settling fish larvae is more difficult to identify than in invertebrates because settled juveniles often have the capacity to actively select habitat (Gotceitas and Brown 1993, Sponaugle and Cowen 1996) that exceeds larval capacity. Thus, an examination of the distribution of settled juveniles provides more useful information about habitat selection during settlement in invertebrates than in fish larvae. For example, Tupper and Boutilier (1995) concluded from their study of Atlantic cod that there was no difference in settlement between habitat sites, but, post-settlement juvenile densities were higher in more complex habitats. Thus, the study of settlement processes in fish larvae requires both comprehensive pre- and post-settlement data (e.g., Sponaugle and Cowen 1996) in order to evaluate the importance of behavorial processes.

Delayed Metamorphosis

Clearly the PLD can have significant effects on transport and subsequent recruitment success. The ability to prolong the competency period should result in an increase in the geographical range of habitats available for settlement. Evidence for delayed metamorphosis in benthic invertebrate larvae has been documented in both field and laboratory studies (see Pechenik 1990).

Field studies, while able to suggest that in many cases delayed metamorphosis does occur (Hadfield 1978; Emlet 1986; Pechenik 1986), have found evidence for delayed metamorphosis in only some instances. Laboratory studies have found extensive evidence for delayed metamorphosis in almost all groups of benthic invertebrates (Pechenik 1990). But how representative these studies are of settlement in the field is unclear given that several environmental factors (e.g., temperature, Bayne 1965; Pechenik 1984) influence the capacity to delay metamorphosis.

There are relatively fewer published examples of delayed metamorphosis in fish (e.g., Victor 1986; Cowen 1991; Chambers and Leggett 1992; Jenkins and May 1994; Sponaugle and Cowen 1994). Cowen and Sponaugle (1997) suggest that in three of these cases (Cowen 1991; Jenkins and May 1994; Sponaugle and Cowen 1994), the individuals exhibiting delays were either a long distance from normal spawning grounds or in the presence of highly variable currents. Larval duration has also been shown to be dependent on environmental factors such as temperature and food availability (Fig. 1.4) and these variables may have a large effect on the duration of the pre-competent period.

1.5 Conclusions and Discusion

Similarities and Differences Between Groups

This review of transport and retention of fish and invertebrate eggs and larvae reveals examples in both groups where passive mechanisms are thought to be predominant in pattern formation. Thus, pattern formation in fish and invertebrates may be determined by a surprisingly similar suite of mechanisms . For some processes, there is evidence that the life cycles of fish and invertebrates may be influenced in similar ways. For other processes, such as internal waves and vent plumes, the evidence that invertebrates utilize such features has not yet been matched by studies of fish. Thus for both groups, on large spatial scales such as ocean basins and continental shelves, pattern appears largely to be determined by passive mechanisms, however, as the spatial scale decreases, the influence of active modifications to passive dispersal becomes more predominant.

A similarity between invertebrate and fish dispersal is also suggested by the lack of a significant difference in larval durations. If planktonic dispersal is indeed a function of planktonic larval duration, then dispersal potential in the two groups may be comparable.

When evaluated with respect to geographic range and dispersal potential, similarities between invertebrates and fish again emerge.

The fact that few studies have documented delayed metamorphosis in fish larvae suggests it may not be a common occurrence. Moreover, in these accounts (e.g., Victor 1986), only a small proportion of the sampled fish displayed a delay in time to settlement, suggesting that even within species that are able to delay metamorphosis, only a small fraction may actually do so. This contrast with invertebrates may be related to the limited adult mobility and rigid habitat requirements of many benthic invertebrates compared with fish.

Because benthic invertebrate adult forms are generally non-mobile, invertebrates may be subject to more rigid habitat restrictions. In contrast, adult fish are generally not constrained to a specific area and are free to occupy new habitats. Invertebrates may therefore be necessarily more selective during settlement and more able to delay settlement when conditions are unsuitable. The relatively few examples of active habitat selection in fish larvae preclude any rigid test of this hypothesis.

Advantages and Disadvantages of Fish and Invertebrates as Study Organisms

Invertebrates and fish both possess advantages and disadvantages as study organisms. Because the adult stage of invertebrates is often sessile, processes affecting recruitment such as transport and active settlement habitat selection can be studied using newly-settled individuals with little concern for post-settlement habitat selection. The increased mobility of fish and the possibility of post-settlement movement complicates studies. But recent advances in aging larvae and juveniles allows examination of temporal variability in recruitment processes. Aging fish has become possible through the analysis of daily growth rings, most often on otoliths. In contrast, most invertebrates lack structures that allow precise aging, and aging is presently possible only through relatively crude estimates based on size.

Problems and Recommendations

The dynamic pelagic environment encountered by marine larvae necessitates that researchers be well versed in the physical and biological oceanography of their study system. An understanding of both the physics and biology, while improving (Bakun 1986; Wolanski and Hammer 1988; Sammarco and Heron 1994), is still a major deficit in studies of marine dispersal. As stated by Leis (1991) and Cowen and Sponaugle (1997), interdisciplinary studies of early life history pattern are essential if our understanding of recruitment processes is to improve.

Ultimately, the study of transport of eggs and larvae of benthic invertebrates and fish is united by the common purpose of understanding pattern in adult populations in the world's oceans. Although there may be differences between fish and invertebrates related to the contribution of active behavior to dispersal, the mechanisms affecting one group are nonetheless extremely relevant to the other. The ability to step back and focus on the mechanisms of passive and active dispersal and the scales on which these processes are important in planktonic marine animals may be crucial to the understanding of these processes and the management of populations. It is clear that there is much to be gained by cross-fertilization between invertebrate and fish ecologists.

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Table 1.1. Summary of invertebrate and fish species planktonic period duration and geographic range.

Species	Duration	Dispersal mode	Reference	Habitat	Range
Porifera					
Halichondria magniconulosa	<'1 week	Anchiplanic	Maldonado & Young (1996)	Rocky(0-100m)	cosmopolitan
Halichondria panicea	< 1 week	Anchiplanic	Amano(1986)	Rocky Shores (0-50m)	cosmopolitan
Haliclona tubifera	< 1 week	Anchiplanic	Maldonado & Young (1996)		
Sigmadocia caerulea	< 1 week	Anchiplanic	Maldonado & Young (1996)		
Tedania ignis	< 1 week	Anchiplanic	Maldonado & Young (1996)		
Cnidaria					
Acropora hyacinthus	13 weeks	Teleplanic	Harrison et al. (1984)		
Favia fragum	< 10 min	Anchiplanic	Carlon & Olson (1993)	Shallow reefs	Florida; Bahamas; Caribbean
Catyophyllia smithi	8 - 10 weeks	Teleplanic	Tranter et al 1982		
Cribrinopsis fernaldi	< 8weeks	Acataeplanic	Seibert & Spaulding(1976)		
Cyphastrea serailia	12 - 26	Actaeplanic	Wilson & Harrison (1998)		
Agaricia agaricites	< 1 week	Anchiplanic	Carlon & Olson (1993)	Reefs; walls	Florida; Bahamas; Caribbean
Heteroxenia fuscenscens	6-7 weeks	Actaeplanic	Zaslow and Benayahu (1996)		
Metridium senile	< 1 week	Anchiplanic	Chia (1976); Hoffmann (1987)	Rocky (0-100')	Polar seas to Catalina Island
Urtricina crassicornis	<8weeks	Actaeplanic	Chia & Spaulding (1972)		
Stylatula elongata	<8weeks	Acataeplanic	Morris et al (1980)	Sand to Mud (0-200')	British Columbia to San Diego
Annelida					
Crucigera zygophora	<8 weeks	Actaeplanic	Strathmann (1987)		
Protula pacifica	<2 weeks	Anchiplanic	Parker & Tunnicliffe(1994)		
Phylloddoce maculata	<8 weeks	Actaeplanic	Parker & Tunnicliffe(1994)	Broad (0-360)	Greenland; Iceland; Norway; France; Rhode Island; Alaska to British Columbia; Japan Sea
Nereis procera	< 1 week	Anchiplanic	Strathmann (1987)		
Serpula vermicularis	< 1 week	Anchiplanic	Morris et al (1980)		
Lumbrineris inflata	< 1 week	Anchiplanic	Chia (1976); Strathmann (1987)	0-700 fa	English Channel to Mediterranean; Mass. To Florida; Bermuda ;West Indes; Gulf of Mexico; Alaska to California; West and South Africa
cirratulid sp.	< 1 week	Anchiplanic	Morris et al (1980); Strathmann (1987)		
Plexauara kuna	<1 week	Anchiplanic	Lasker & Kim (1996)		
Arthropoda					
Carcinus maenas	64.36	teleplanic	Dawirs (1985)		
harpacticoid copepod	< 1 week	Anchiplanic	Hicks & Coull (1983)		
Chorilia longipes	<8 weeks	Actaeplanic	Hines (1986)		
Oregonia gracilis	<8 weeks	Actaeplanic	Hines (1986)		
Cancridae	65 (SD- 11)	Teleplanic	Hines (1986)	Nearshore to Deep	Labrador to Tortugas
Grapsidae	39 (SD-8)	Actaeplanic	Hines (1986)		North Carolina to Montevideo; Bermuda; Mediterranean; California to Peru

Species	Duration	Dispersal mode	Reference	Habitat	Range
Majidae	30 (SD- 4)	Actaeplanic	Hines (1986)	Soft mud to Coarse (27-682)	Cape Lookout to Brazil
Ocypodidae	29 (SD-16)	Actaeplanic	Hines (1986)	Beaches	Rhode Island to Brazil
Pinnotheridae	40 (SD-6)	Actaeplanic	Hines (1986)	Sand (0-50m)	Massachusetts to Florida
Portunidae	45 (SD-7)	Actaeplanic	Hines (1986)	Sand (0-100m)	Iceland and the British Iles
Xanthidae	31 (SD-3)	Actaeplanic	Hines (1986)	Coarse (0-70m)	Cape Lookout to West Indies
Rhithropanopeus harrisii	18	Actaeplanic	McKenny and Costlow (1982)		
Chionoecetes opilio	> 8 weeks	Teleplanic	Squires (1996)	Mud bottom (20-310m)	Greenland - St Lawrence Estuary; Alaska and N.E. Siberia through the Berring Strait to Alaskan Peninsula; Okhotsk Sea and South to Japan.
Hyas araneus	103	Teleplanic	Anger (1983)	Mud / Pebble(0-730m)	W. Greenland; Labrador to Rhode Island;Between Greenland and Iceland; British Isles, N.W. France to Spitsbergen and Kara Sea.
Hyas coarctatus	> 8 weeks	Teleplanic	Squires (1996)	Mud / Pebble(55-550m)	North Carolina, eastward to N.W. Europe, Arctic and Murman Sea; Northwest Atlantic; Davis and Hudson Straits to Bering Sea and south to Puget Sound and Sea of Japan
Cancer irroratus	> 8 weeks	Teleplanic	Squires (1996)	Sand (0-575m)	Labrador to off Miami
Homarus americanus	> 8 weeks	Teleplanic	Squires (1996)	Rock(10-200m)	Strait of Bell Isle; Newfoundland to Cape Hatteras, N.C.
Pandalus borealis	> 8 weeks	Teleplanic	Squires (1996)	Mud(50-700m)	Greenland to Martha's Vineyard; Iceland; Spitsbergen to northern Europe including Britian; Berring sea southward to San Diego and south Korea
Pandalus montagui	> 8 weeks	Teleplanic	Squires (1996)	Sand(80-252m)	Greenland to Rhode Island; Northern Europe including Britian
Lebbeus polaris	> 8 weeks	Teleplanic	Squires (1996)	(0-400m)	Circumarctic; south to Chesapeake Bay; Bering Sea, British Columbia; Sea of Okhotsk
Lebbeus groenlandicus	> 8 weeks	Teleplanic	Squires (1996)	(45-160m)	Greenland to Rhode Island; Arctic Canada and Alaska; Chuckchi Sea; Bering Sea to Puget Sound and Sea of Okhotsk south to Vladivostok
Sclerocrangon boreas	> 8 weeks	Teleplanic	Squires (1996)	Rock / Mud(75-105m)	Greenland south to Cape cod; and S.E. to Nantucket; Arctic Canada and North east Alaska; Chukchi Sea south to British Columbia; Faroes; Norway and to Spitsbergen
Eualus pusiolus	> 8 weeks	Teleplanic	Squires (1996)	Sand (0-500m)	Gulf of St. Lawrence to off Cape Henry; Bering Island; Alaska Pen.

Species	Duration	Dispersal mode	Reference	Habitat	Range
					and Aleutian Islands; Iceland; Murman coast to Channel Islands; south to Bay of Biscay to Spain.
Eualus gaimardi	> 8 weeks	Teleplanic	Squires (1996)	Hard(60-230m)	Circumarctic southward to Cape Cod; North Sea; Alaska; Siberia
Eualus fabricii	> 8 weeks	Teleplanic	Squires (1996)	Broad (64-260m)	N. E. Greenland to Cape Cod; arctic Alaska to Cook Inlet; Siberian Sea coast; Sea of Japan
Mollusca					
Anachis avara	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	Cape Cod - Antilles
Anachis translirata	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	Newfoundland - Gulf of Mexico
Aporrhais occidentalis	< 8 weeks	Actaeplanic	Scheltema (1989)		Arctic Canada - North Carolina
Archidoris montereyensis		Anchiplanic	Morris et al (1980)		
Architectonica nobilis	> 8 weeks	Teleplanic	Scheltema (1989)	Intertidal	North Carolina - Brazil
A. peracuta	> 8 weeks	Teleplanic	Scheltema (1989)	Intertidal	North Carolina - Venezuela
Bittium varium	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	Cape Cod- Venezuela
Bittium virginicum	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	Newfoundland - Gulf of Mexico
Bursa thomae	> 8 weeks	Teleplanic	Scheltema (1989)	Intertidal	North Carolina - Brazil
Caecum cooperi	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	Cape Cod - Gulf of Mexico
Caecum pulchellum	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	Newfoundland - Brazil
Calliostoma annulatum		Anchiplanic	Hadfield & Strathmann (1990); Strathmann (1987)	1-20m	Alaska to South California
Callistoma ligatum		Anchiplanic	Holyoak (1988)		
Cerithiopsis greeni	> 8 weeks	Teleplanic	Scheltema (1989)	Intertidal	Cape Cod – Brazil
Cerithiopsis subulata	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	Cape Cod – Brazil
C. floridanum	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	Cape Cod – Brazil
Cheilea equestris	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	North Carolina – Brazil
Cirsoterma dalli	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	North Carolina – Brazil
Conus sozoni	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	North Carolina - Gulf of Mexico
Coralliophila deburghiae	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	North Carolina – Brazil
Crassodoma gigantea		teleplanic	Morris et al (1980)		
Crepidula fornicata	26.5 (5.0)	Actaeplanic	Pechenick and Lima (1984)	Intertidal	Newfoundland - Greater Antilles; N.W. Europe
C. plana	19.32(4.9)	Actaeplanic	Pechenick and Lima (1984)	Intertidal	Newfoundland – Brazil
Cymatium cynocephalum	> 8 weeks	Teleplanic	Scheltema (1989)	Intertidal	North Carolina – Brazil
C. gracile	> 8 weeks	Teleplanic	Scheltema (1989)	Intertidal	North Carolina – Brazil
C. labiosum	> 8 weeks	Teleplanic	Scheltema (1989)	Intertidal	North Carolina – Brazil; Indo-Pacific
C. martinianum	> 8 weeks	Teleplanic	Scheltema (1989)	Intertidal	North Carolina – Brazil
C. parthenopeum	> 8 weeks	Teleplanic	Scheltema (1989)	Intertidal	North Carolina – Brazil; California to Galapagos
Cypraea cervus	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	North Carolina - Greater Antilles
C. spurca acicularis	> 8 weeks	Teleplanic	Scheltema (1989)	Intertidal	North Carolina – Brazil; Mediterranean to S. Africa
C. zebra	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	North Carolina – Brazil
Cypraecassis testiculus	> 8 weeks	Teleplanic	Scheltema (1989)	Intertidal	North Carolina – Brazil

Species	Duration	Dispersal mode	Reference	Habitat	Range
Distorsio clathrata	> 8 weeks	Teleplanic	Scheltema (1989)	Intertidal	North Carolina – Brazil
D. constricta mcgintyi	> 8 weeks	Teleplanic	Scheltema (1989)	Intertidal	North Carolina – Brazil
Epitonium krebsii	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	North Carolina - Brazil
E. rupicolumn	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	Newfoundland - Gulf of Mexico
Erato maugeriae	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	North Carolina - Brazil
Eudolium crosseanum	> 8 weeks	Teleplanic	Scheltema (1989)	Intertidal	North Carolina - Greater Antilles
Kurtziella limonitella	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	North Carolina - Gulf of Mexico
Littorina irrorata	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	North Carolina - Gulf of Mexico
Lunatia heros	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	Arctic Canada - North Carolina
Macoma balthica	< 8 weeks	Actaeplanic	Gilbert (1978)	Shallow	Arctic Seas; W. Europe; N.E. States
Mercenaria mercenaria	< 1week	Anchiplanic	Bachelet et al. (1992)	fine sediments	Gulf of Mexico to Cape Cod; (0-60)
Mitrella lunata	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	Cape Cod- Venezuela
Mitra nodulosa	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	North Carolina - Brazil
Modulus modulus	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	North Carolina - Brazil
Moliolus modiolus	< 8 weeks	Actaeplanic	DeSchweinitz & Lutz (1976)	Shallow	Arctic to New Jersey; Europe; Arctic to California
Mulinia lateralis	<2 weeks	Anchiplanic	Grassle et al (1992)	Muddy bottoms	E. Canada to W. Indies
Mya arenaria				Muddy bottoms	Sub Arctic to Cape Hatteras
Nassarius ambiguus	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	North Carolina - Brazil
N. obsoletus	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	Newfoundland - North Carolina
N. trivittatus	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	Newfoundland - North Carolina
N. vibex	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	Cape Cod - Brazil
Natica canrena	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	North Carolina - Brazil
Neosimna acicularis	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	North Carolina - Greater Antilles
N. uniplicata	> 8 weeks	Teleplanic	Scheltema (1989)	Intertidal	Cape Cod - Brazil
Phalium granulatum	> 8 weeks	Teleplanic	Scheltema (1989)	Intertidal	North Carolina - Brazil
Philippia krebsi	> 8 weeks	Teleplanic	Scheltema (1989)	Intertidal	North Carolina - Brazil
Placopectien magellamicus		Actaeplanic	Tremblay and Sinclair (1990)	0-180m	Labrador to Cape Cod
Polinices lacteus	> 8 weeks	Teleplanic	Scheltema (1989)	Intertidal	North Carolina - Brazil
Polinices duplicatus	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	Cape Cod - Gulf of Mexico
Rissoina decussata	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	North Carolina - Brazil
Seila adamsi	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	Cape Cod - Brazil
Spisula solidissima	<8 weeks	Actaeplanic	Snelgrove et al. (1998)	Intertidal ; medium to coarse sand and gravel	Labrador to South Carolina
Strombus alatus	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	North Carolina - Gulf of Mexico
Thais haemastoma	> 8 weeks	Teleplanic	Scheltema (1989)	Intertidal	North Carolina - Brazil
Tonna galea	> 8 weeks	Teleplanic	Scheltema (1989)	Intertidal	North Carolina - Brazil; Mediterranean and Indo-Pacific
Torina bisculata	> 8 weeks	Teleplanic	Scheltema (1989)	Intertidal	North Carolina - Brazil
Triphora nigocincta	> 8 weeks	Teleplanic	Scheltema (1989)	Intertidal	Cape Cod - Brazil
Trivia candidula	< 8 weeks	Actaeplanic	Scheltema (1989)	Intertidal	North Carolina - Brazil
Pecten maximus	31	Actaeplanic	Beamont and Barnes (1992)		
Petricola pholadiformis	<8 weeks	Actaeplanic	Mackie (1984)	Intertidal	E. Canada; Uruguay; Norway to Black Sea
hiatellid sp.	>8 weeks	Teleplanic	Morris et al (1983)	Cold; Deep; Mud	

Species	Duration	Dispersal mode	Reference	Habitat	Range
Sinonovacula constricta	< 1 month	Actaeplanic	Wang & Xu (1997)	Estuaries; Mud	South E. Asia
solemyid sp.	< 1 week	Anchiplanic	Gustafson (1985)		
Brachiopoda					
Laqueus californianus	< 1 weeks	Anchiplanic	Valentine and Jablonski (1983)		
Terebratulina sp.	< 1 weeks	Anchiplanic	Valentine and Jablonski (1983)	(9-1262m)	Eastern Atlantic and Mediterranean
Platidia hornii	< 1 weeks	Anchiplanic	Rudwick (1970)		Eastern Atlantic; Mediterranean; Florida and Cuba
Bryozoa					
Bugula stolonifera	approx 5hr	Anchiplanic	Woollaott et al (1989)	Submerged structures on algae etc (0-100m)	Both Sides of Atlantic; Mediterranean
Bicrisia edwardsiana	< 1 weeks	Anchiplanic	Nielsen (1970); Woollacott & Zimmer (1978)		British Iles; Mediterranean; Indo-Pacific
Crisia occidentalis	< 1 weeks	Anchiplanic	Nielsen (1970); Woollacott & Zimmer (1978)		
Filacrisia franciscana	< 1 weeks	Anchiplanic	Nielsen (1970); Woollacott & Zimmer (1978)		
Rhamphostomella spinigera	< 1 weeks	Anchiplanic	Woollacott & Zimmer (1978)		
Borgiola pustulosa	< 1 weeks	Anchiplanic	Woollacott & Zimmer (1978)		
Lyrula sp.	< 1 weeks	Anchiplanic	Woolacott & Zimmer (1978)		
Sipuncula					
Phascolosoma agassizi	< 1 weeks	Anchiplanic	Rice (1967); Strathmann (1987)		North Atlantic; Mediterranean
Echinodermata					
Pycnopdia helianthoides	>8 weeks	Teleplanic	Greer (1962); Lambert(1981); Morris et al (1980); Strathmann (1978)	Varried (0-450)	Eastern Pacific
Crossaster papposus	< 8 weeks	Actaeplanic	Lambert (1981); Strathmann (1987)	Rock and Sand (0-1200m)	Northern Hemisphere
Hippasterias spinosa	< 1 weeks	Anchiplanic	Lambert (1981)		
Florometra serratissima	4.5 - 9 days	Anchiplanic	McEdward et al (1980); Mladenov & Chia (1983); Strathmann(1978)		
Loxechinus albus	20.5	Actaeplanic	Gonalez et al. (1987)		Peru to Chile
Strongylocentrotus franciscanus	>8 weeks	Teleplanic	Morris et al (1980); Strathmann(1978); Strathmann (1987)		
Chordata					
Ascidiacea					
Ascidia ceratodes	< 1 weeks	Anchiplanic	Millar (1971)		
Botrylloides sp.	< 1hr	Anchiplanic	Worcester (1994)	Rocky Reefs (5-20m)	North West Atlantic; Mediterranean; Caribbean
Didemnum molle	2 days		Olson (1985)	Reefs (0-60m)	Indo-Pacific
Ecteinascidia turbinata	3 days		Olson (1985)		
Osteicthyes					
Ammotretis rostratus	69	teleplanic	Chambers and Leggett (1987)		
Clupea harengus	160* (46-550)	teleplanlic	Houde (1989)	Broad (0-200m)	North Atlantic
Chanos chanos	43.5 * (36.6-51.8)	actaeplanic	Houde(1989)		
Anchoa lamprotaenia	34.0*	actaeplanic	Houde(1989)		

Species	Duration	Dispersal mode	Reference	Habitat	Range
Anchoa mitchilli	34.8*(21.2-49.5)	actaeplanic	Houde(1989)	Shallow Bays	Gulf of Maine to Florida; Gulf of Mexico to Yucatan
Engraulis mordax	34.8*(23.8-50.9)	actaeplanic	Houde(1989)		
Gadus morhua	100.9*(41.2-247.1)	teleplanlic	Houde(1989)	Broad(0-457m)	North Atlantic
Melanogrammus aeglefinus	127.7*(34.4-460.5)	teleplanlic	Houde(1989)	inshore-continental shelf	North Atlantic
Meluccius productus	88.0*	teleplanlic	Houde(1989)		Bering Sea to Gulf of California
Thelagra chalcogramma	108.3*(42.5-276.1)	teleplanlic	Houde(1989)		Sea of Japan; Aleutians; N. California
Menidia menidia	35.4	actaeplanic	Houde(1989)	Sand - Gravel	Gulf of St Lawrence – Florida
Menidia peninsulae	41.0* (23.2-72.6)	actaeplanic	Houde(1989)	Creeks and marshes	N.E. Fla. And Gulf of Mexico to S. Florida and Veracruz
Morone americana	84.5*(34.5-207.2)	teleplanlic	Houde(1989)	Estuaries and Freshwater	Gulf of St Lawrence - South Carolina
Morone saxatalis	33.0*(22.7-48.0)	actaeplanic	Houde(1989)	Estuaries and Freshwater	Gulf of St Lawrence – Florida
Dicentrarchus labrax	45.6*(28.4-73.1)	actaeplanic	Houde(1989)		
Haemulon flavolineatum	18.7*(14.3-24.4)	actaeplanic	Houde(1989)	Reefs; mud; grass	Bermuda; S. California; Gulf of Mexcio to Brazil;
Archosargus rhomboidalis	21*(15.0-29.3)	actaeplanic	Houde(1989)		New Jersey to Gulf of Mexico to Brazil and West Indes
Pargus major	46.6*(19.9-109.2)	actaeplanic	Houde(1989)		
Sparus aurata	49.5*(41.8-58.6)	actaeplanic	Houde(1989)		
Cynoscion nebulosus	19.4*(10.3-36.6)	actaeplanic	Houde(1989)	Bays and Banks	New York to S. Fla.; Gulf of Mexico
Ammodytes americanus	159.1*(46.0-550)	teleplanlic	Houde(1989)	Sandy (6-20m)	Hudson Bay – Virginia
Paralichthys dentatus	98.8	teleplanlic	Houde(1989)		Maine – Florida
Scophthalmus maximus	39.3*(24.9-62.1)	actaeplanic	Houde(1989)		
Platichthys stellatus	65	teleplanic	Chambers and Leggett (1987)		
Palalichthys olivaceus	70	teleplanic	Chambers and Leggett (1987)		
Pleuronectes americanus	87.0*(32.9-230.3)	teleplanlic	Houde(1989)	Mud (1.8-37m)	Labrador – Georgia
Achrius lineatus	23.0*(16.0-33.1)	actaeplanic	Houde(1989)	Coastal	
Solea solea	35.1*(24.2-50.8)	actaeplanic	Houde(1989)		
Sebastes helvomaculatus	> 8 weeks	teleplanic	Boehlert & Yoklavich (1984)	100- 350m	Alaska to Baja California
Sebastes paucispinus	> 8 weeks	teleplanic	Boehlert & Yoklavich (1984)	0-320m	Alaska to Baja California
Sebastes entomelas	> 8 weeks	teleplanic	Boehlert & Yoklavich (1984)	25-375m	Alaska to Baja California
Sebastes ruberrimus	> 8 weeks	teleplanic	Boehlert & Yoklavich (1984)	37-375m	Alaska to Baja California
Rhombosolea tapirina	65	teleplanic	Chambers and Leggett (1987)		
Apongon doederleni	22.6(16-27)	actaeplanic	Brothers et al (1983)	Coral reef	Northern Indian Ocean to Japan
Cheilodipterus quinqeulineata	23.1(17-29)	actaeplanic	Brothers et al (1983)	Coral reef	Northern Indian Ocean to Japan
Petroscirtes fallax	21	actaeplanic	Brothers et al (1983)	Coral reef	
Petroscrites mitratus	24.5(24-25)	actaeplanic	Brothers et al (1983)	Shallow pools	Red Sea and Entire Indo-Pacific
Naso sp.	84	teleplanic	Brothers et al (1983)	Coral reef	Indo-Pacific
Chaetodon rainfordi	35	actaeplanic	Brothers et al (1983)	Coral reef	Red Sea to India; China; Taiwan; Philippines; Australia
Chelmon rostratus	25.5(25-26)	actaeplanic	Brothers et al (1983)	Coral reef	
Amblygobius rainfordi	40.3(40-41)	actaeplanic	Brothers et al (1983)	Coral reef	

Species	Duration	Dispersal mode	Reference	Habitat	Range
Gobiodon sp.	22	actaeplanic	Brothers et al (1983)	Coral reef	
Paragobiodon enchinocephalus	36	actaeplanic	Brothers et al (1983)	Coral reef ; Coral pools	Red Sea; E. Africa; Madagascar; E. Indies; China; Philippines; Australia
Cirrhilabrus temminki	28(26-30)	actaeplanic	Brothers et al (1983)	Coral reef	Japan and Philippines
Coris variegata	28	actaeplanic	Brothers et al (1983)	Coral reef	
Halichoeres hoeveni	27.5(27-28)	actaeplanic	Brothers et al (1983)	Coral reef	E. Indies; Fiji; Philippines
Labroides dimidatus	26	actaeplanic	Brothers et al (1983)	Coral reef	Entire Indo-Pacific
Thalassoma lunare	54.7(53-56)	actaeplanic	Brothers et al (1983)	Coral reef	Indian Ocean; Philippines; Hong Kong; New Guinea; Australia
Lethrinus nebulosus	37	actaeplanic	Brothers et al (1983)	Coral reef	Entire indo-Pacific (not Hawaii); Red Sea; Queensland
Monacanthus chinensis	20	actaeplanic	Brothers et al (1983)	Coral reef	Australia; Indonesia; Philippines; China
Paraluteres prionurus	28	actaeplanic	Brothers et al (1983)	Coral reef	East Africa to E. Indies;
Scolopsis dubiosus	19.0(15-24)	actaeplanic	Brothers et al (1983)	Coral reef	E. Indies; Queensland; Fiji
Abudefduf abdominalis	17.5(17-18)	actaeplanic	Wellington & Victor (1989)	Coral reef	Hawaii
A. sexfasciatus	17.3(16-18)	actaeplanic	Wellington & Victor (1989)	Coral reef	Indo-Pacific (not Hawaii)
A. sordidus	26.1(23-31)	actaeplanic	Wellington & Victor (1989)	Coral reef	Through out Indopacific; Red Sea; Hawaii
Amblyglyphidodon aureus	16	actaeplanic	Wellington & Victor (1989)	Coral reef	Tropical Indo-Pacific; Western Pacific
A. curacao	13.1(12-15)	actaeplanic	Wellington & Victor (1989)	Coral reef	Tropical Indo-Pacific; Western Pacific
Amphiprion chrysopterus	17.0	actaeplanic	Wellington & Victor (1989)	Coral reef	
A. clarkii	15.5(15-16)	actaeplanic	Wellington & Victor (1989)	Coral reef	Persian Gulf; Indonesia; Philippines; China; Japan; Australia
A. melanopus	18.6(15-22)	actaeplanic	Wellington & Victor (1989)	Coral reef	Indonesia; Queensland
A. perideraion	18.0	actaeplanic	Wellington & Victor (1989)	Coral reef	Tropical Indian Ocean; West Pacific
Cheloprion labiatus	16.5(15-19)	actaeplanic	Wellington & Victor (1989)	Coral reef	
Chromis agilis	32.7(30-35)	actaeplanic	Wellington & Victor (1989)	Coral reef	East Africa; Indian Ocean
C. cyanea	29.9(27-34)	actaeplanic	Wellington & Victor (1989)	Coral reef	Caribbean; Florida; Bahamas
C. delta	24.0(23-25)	actaeplanic	Wellington & Victor (1989)	Coral reef	
C. hanui	27.0	actaeplanic	Wellington & Victor (1989)	Coral reef	
C. insolata	19.8(18-21)	actaeplanic	Wellington & Victor (1989)	Coral reef	N. Carolina to Florida and Gulf of Mexico
C. multilineata	25.8(24-30)	actaeplanic	Wellington & Victor (1989)	Coral reef	Florida to Brazil
C. ternatensis	28.3(25-31)	actaeplanic	Wellington & Victor (1989)	Coral reef	E. Indies; Philippines
C. vanderbilti	31.0(30-32)	actaeplanic	Wellington & Victor (1989)	Coral reef	Hawaii
Chrysiptera biocellata	18.2(17-20)	actaeplanic	Wellington & Victor (1989)	Coral reef	
Dascyllus albisella	26.8(25-29)	actaeplanic	Wellington & Victor (1989)	Coral reef	Hawaii
D. aranus	20.0(16-24)	actaeplanic	Wellington & Victor (1989)	Coral reef	Entire Indo-Pacific (not Hawaii)
D. melanurus	21.2(20-22)	actaeplanic	Wellington & Victor (1989)	Coral reef	E. Indies; Philippines
D. reticulatus	20.6(23-30)	actaeplanic	Wellington & Victor (1989)	Coral reef	Entire Indo-Pacific (not Red Sea or Hawaii)
D. trimaculatus	26.0(23-30)	actaeplanic	Wellington & Victor (1989)	Coral reef	Entire Indo-Pacific (not Hawaii)
Dischistodus chrysopoecilus	19.5(16-23)	actaeplanic	Wellington & Victor (1989)	Coral reef	
D. pseudochrysopoecilus	13.8(12-15)	actaeplanic	Wellington & Victor (1989)	Coral reef	

Species	Duration	Dispersal mode	Reference	Habitat	Range
Hemiglyphidodon plagiometopon	18.0(16-20)	actaeplanic	Wellington & Victor (1989)	Coral reef	E. Indies; Melanesia
Hypsypops rubicundus	20.0(18-22)	actaeplanic	Wellington & Victor (1989)	Coral reef	
Microspathodon chrysurus	23.0(21-27)	actaeplanic	Wellington & Victor (1989)	Coral reef	Florida; Bahamas; Gulf of Mexico
M. dorsalis	34.0	actaeplanic	Wellington & Victor (1989)	Coral reef	
Neopomacentrus nemurus	19.2(16-24)	actaeplanic	Wellington & Victor (1989)	Coral reef	
Paraglyphidodon melas	16.1(14-18)	actaeplanic	Wellington & Victor (1989)	Coral reef	
P. nigoris	21.7(19-24)	actaeplanic	Wellington & Victor (1989)	Coral reef	
Plectroglyphidodon dickii	26.6(25-28)	actaeplanic	Wellington & Victor (1989)	Coral reef	
Chromis sp.	23.7(20-26)	actaeplanic	Brothers et al (1983)	Coral reef	
Dischistodus pseudochrysopoecilus	23	actaeplanic	Brothers et al (1983)	Coral reef	
Dascyllus aruanus	24.4(20-28)	actaeplanic	Brothers et al (1983)	Coral reef	Entire Indo-Pacific (not Hawaii)
Glyphidodontops rollandi	23.3(23-24)	actaeplanic	Brothers et al (1983)	Coral reef	
G. talboti	22	actaeplanic	Brothers et al (1983)	Coral reef	
Neopomacentrus azysron	24	actaeplanic	Brothers et al (1983)	Coral reef	
Pomacentrus amboinensis	21.0(17-26)	actaeplanic	Brothers et al (1983)	Coral reef	E. Indies; Queensland; Fiji
P. moluccensis	19.6(18-23)	actaeplanic	Wellington & Victor (1989)	Coral reef	E. Indies; Philippines; Okinawa
P. pavo	22.4(20-27)	actaeplanic	Wellington & Victor (1989)	Coral reef	South and East Africa; E. Indies; Queensland and Tahiti
Stegastes acapulcoensis	14.0	actaeplanic	Wellington & Victor (1989)	Coral reef	
Labridae		actaeplanic			
Anampses chrysocephalus	29.5(28-31)	actaeplanic	Victor(1986)	Coral reef	Hawaii
A. cuvier	44.5(37-52)	actaeplanic	Victor(1986)	Coral reef	Hawaii
A. twistii	28.8(23-38)	actaeplanic	Victor(1986)	Coral reef	E. Africa; E. Indies; Fiji
Bodianus axillaris	23.5(18-28)	actaeplanic	Victor(1986)	Coral reef	Tropical Indian Ocean; Western Pacific
B. rufus	41.6(32-51)	actaeplanic	Victor(1986)	Coral reef	Florida to Brazil
Cheilinus bimaculatus	54.3(51-60)	actaeplanic	Victor(1986)	Coral reef	
C. chlorourus	27.1(25-30)	actaeplanic	Victor(1986)	Coral reef	Indo-Pacific (not Hawaii)
C. digrammus	26.1(21-36)	actaeplanic	Victor(1986)	Coral reef	
C fasciatus	25.7(24-27)	actaeplanic	Victor(1986)	Coral reef	Indo-Pacific (not Hawaii)
C. trilobatus	29.6(26-36)	actaeplanic	Victor(1986)	Coral reef	Indo-Pacific (not Hawaii)
C. undulatus	34.3(29-40)	actaeplanic	Victor(1986)	Coral reef	Indo-Pacific (not Hawaii)
C. unifasciatus	36.2(31-42)	actaeplanic	Victor(1986)	Coral reef	
Cheilio inermis	56.1(43-73)	actaeplanic	Victor(1986)	Coral reef	Indo-Pacific; Hawaii; Red Sea; Australia
Choerodon anchorago	19.3(17-23)	actaeplanic	Victor(1986)	Coral reef	India to Indonesia; Philippines; Australia; Palau
Cirrhilabrus cyanopleura	21.1(19-24)	actaeplanic	Victor(1986)	Coral reef	E. Indies; Philippines; New Guinea
Clepticus parrae	38.5(35-49)	actaeplanic	Victor(1986)	Coral reef	N. Carolina to Gulf of Mexico
Coris flavovittata	53.0(52-54)	actaeplanic	Victor(1986)	Coral reef	Caribbean; Western Pacific; and Hawaii
C. gaimard	44.9(42-53)	actaeplanic	Victor(1986)	Coral reef	Indo-Pacific
C. variegata	22.0(19-25)	actaeplanic	Victor(1986)	Coral reef	

Species	Duration	Dispersal mode	Reference	Habitat	Range
C. venusta	46.1(40-50)	actaeplanic	Victor(1986)	Coral reef	
Cymolutes lecluse	75.9(60-91)	teleplanic	Victor(1986)	Coral reef	E. Africa to E. Indies; Philippines; Fiji; Hawaii
C. praetextatus	71.0	teleplanic	Victor(1986)	Coral reef	
Diproctacanthus xanthurus	17.3(15-20)	actaeplanic	Victor(1986)	Coral reef	Florida; Bermuda
Doratonotus megalepis	21.9(20-24)	actaeplanic	Victor(1986)	Coral reef	E. Africa; Mauritius; E. Indies; Philippines; Australia
Epibulus insidiator	30.4(25-38)	actaeplanic	Victor(1986)	Coral reef	Indo-Pacific
Gomphosus varius	65.3(62-72)	teleplanic	Victor(1986)	Coral reef	
G. varius	51.8(42-60)	actaeplanic	Victor(1986)	Coral reef	E. Indies; Philippines; China; Fiji
Halichoeres argus	25.0(22-27)	actaeplanic	Victor(1986)	Coral reef	
H. biocellatus	24.8(20-28)	actaeplanic	Victor(1986)	Coral reef	N. Carolina to Brazil
H bivittatus	24.1(22-26)	actaeplanic	Victor(1986)	Coral reef	
H chierchaie	31.3(25-38)	actaeplanic	Victor(1986)	Coral reef	E. Indies to Philippines
H. margaritaceus	21.7(18-26)	actaeplanic	Victor(1986)	Coral reef	Indian Ocean; Indo-Pacific
H. marginatus	22.2(20-25)	actaeplanic	Victor(1986)	Coral reef	Red Sea; E. Africa; E. Indies; Philippines;
H. melanurus	22.1(20-24)	actaeplanic	Victor(1986)	Coral reef	E. Indies
H. nebulosus	23.9(20-26)	actaeplanic	Victor(1986)	Coral reef	E. Indies; Philippines; Queensland; Fiji
H. nicholsi	32.4(26-38)	actaeplanic	Victor(1986)	Coral reef	
H. ornatissimus	39.5(33-56)	actaeplanic	Victor(1986)	Coral reef	Hawaii
H. scalularis	24.4(21-28)	actaeplanic	Victor(1986)	Coral reef	Indo-Pacific (not Hawaii)
H. semicinctus	29.9(24-36)	actaeplanic	Victor(1986)	Coral reef	
H. trimaculatus	26.8(21-32)	actaeplanic	Victor(1986)	Coral reef	
Hemigymnus fasciatus	25.8(19-34)	actaeplanic	Victor(1986)	Coral reef	
H. melapterus	23.9(20-29)	actaeplanic	Victor(1986)	Coral reef	
Labrichthys unilineatus	19.2(17-24)	actaeplanic	Victor(1986)	Coral reef	
Labroides bicolor	24.5(23-26)	actaeplanic	Victor(1986)	Coral reef	E. Africa; E. Indies to Philippines; Okinawa
L. dimidiatus	20.3(18-24)	actaeplanic	Victor(1986)	Coral reef	Indo-Pacific (not Hawaii)
L. pectoralis	26.8(22-31)	actaeplanic	Victor(1986)	Coral reef	
L. phthirophagus	32.1(27-38)	actaeplanic	Victor(1986)	Coral reef	Hawaii
Labropsis micronesica	22.0	actaeplanic	Victor(1986)	Coral reef	
Lachnolaimus maximus	25.8(21-30)	actaeplanic	Victor(1986)	Coral reef	Florida; N. Carolina to Gulf of Mexico
Macropharyngodon geoffroy	32.3(25-43)	actaeplanic	Victor(1986)	Coral reef	Hawaii; Indonesia; Philippines
M. meleagris	25.0(20-36)	actaeplanic	Victor(1986)	Coral reef	Indonesia; Philippines; New Guinea
M. negrosensis	25.0	actaeplanic	Victor(1986)	Coral reef	
Novaculichthys taeniourus	73.5(73-74)	teleplanic	Victor(1986)	Coral reef	
N. macrolepidotus	70.5(64-77)	teleplanic	Victor(1986)	Coral reef	
Oxyjulis californica	39.4(36-43)	actaeplanic	Victor(1986)	Coral reef	
Pseudocheilinus evanidus	49.4(38-72)	actaeplanic	Victor(1986)	Coral reef	Hawaii
P. hexataenia	35.0(36-46)	actaeplanic	Victor(1986)	Coral reef	Red Sea; E. Africa; Madagascar; E. Indies; Philippines;
P. octotaenia	47.7(38-55)	actaeplanic	Victor(1986)	Coral reef	Hawaii

Species	Duration	Dispersal mode	Reference	Habitat	Range
P. tetrataenia	49.3(42-55)	actaeplanic	Victor(1986)	Coral reef	Hawaii
Pseudojulis melanotis	35.7(31-40)	actaeplanic	Victor(1986)	Coral reef	
P. notospilus	37.6(35-42)	actaeplanic	Victor(1986)	Coral reef	
Pseudojuloides cerasinus	42.4(34-52)	actaeplanic	Victor(1986)	Coral reef	Hawaii
Pteragogus cryptus	20.6(19-22)	actaeplanic	Victor(1986)	Coral reef	
Semicossyphus pulcher	37.4(34-52)	actaeplanic	Victor(1986)	Coral reef	
Stethojulis balteata	42.1(35-48)	actaeplanic	Victor(1986)	Coral reef	
Tautoga onitis	25.4(22-30)	actaeplanic	Victor(1986)	Coral reef	Nova Scotia to S. Carolina
Tautogolabris adspersis	28.4(25-32)	actaeplanic	Victor(1986)	Coral reef	Newfoundland to Chesapeake Bay
Thalassoma amblycephalum	72.4(53-90)	teleplanic	Victor(1986)	Coral reef	Indo-Pacific
T. ballieui	84.0(65-121)	teleplanic	Victor(1986)	Coral reef	Hawaii
T. bifasciatum	49.3(38.78)	actaeplanic	Victor(1986)	Coral reef	Florida to Gulf of Mexico
T. duperrey	89.2(75-114)	teleplanic	Victor(1986)	Coral reef	Hawaii
T. hardwicke	47.0(39-63)	actaeplanic	Victor(1986)	Coral reef	Indo-Pacific (not Hawaii)
T. janseni	63.3(50-85)	teleplanic	Victor(1986)	Coral reef	E. Indies; Philippines; New Guinea; Fiji; Queensland; Australia
T. lucasanun	74.3(62-94)	teleplanic	Victor(1986)	Coral reef	
T. lunare	46.8(39-55)	actaeplanic	Victor(1986)	Coral reef	
T. lutescens	78.0	teleplanic	Victor(1986)	Coral reef	Hawaii; Queensland
T. quinquevittatun	56.4(46-68)	actaeplanic	Victor(1986)	Coral reef	Okinawa; E. Indies; Melanesia;
T. trilobatum	78.3(60-99)	teleplanic	Victor(1986)	Coral reef	
Xyichatys martinicensis	78.3(59-98)	teleplanic	Victor(1986)	Coral reef	
X. novacula	50.5(38-62)	actaeplanic	Victor(1986)	Coral reef	
X. pavoninus	57.0	actaeplanic	Victor(1986)	Coral reef	
X. splendens	103.9(85-114)	teleplanic	Victor(1986)	Coral reef	

(Species Ranges from : Abbott 1974; Abbott & Dance 1982; Böhlke & Chaplin 1968; Coad et al 1995; Coleman 1991; Cutler 1994; Eales 1967; Gotshall & Laurent 1979; Hayward & Ryland 1979; Human 1994; Howard et al. 1979; Howard et al. 1977; Morris 1973; Pettibone 1963; Robins & Ray 1986; Squires 1996; Stokes 1980; Voss 1976; Williams 1984)

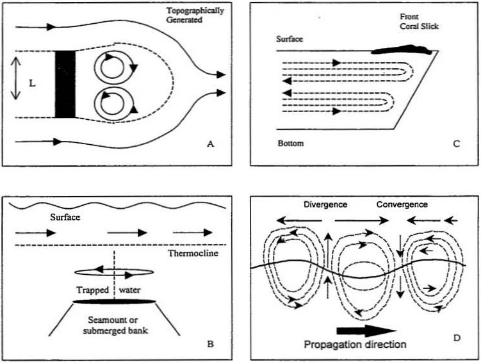


Figure 1.1. Schematic diagram illustrating the retention and concentration of spawning products in eddies (A); fronts (B); Taylor columns (C); and convergences (D). (A and B adapted from Wolanski and Hammer 1988; C adapted from Bakun 1986; D adapted from Bakun 1994).

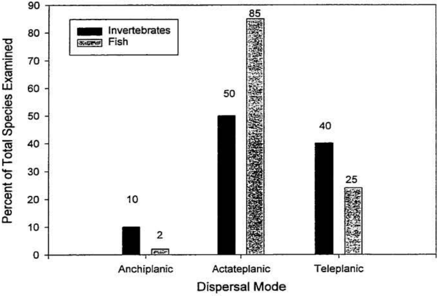


Figure 1.2. Classification of dispersal potential in benthic fish and invertebrate species. Data from Table 1.1. Anchiplanic, actaeplanic, and teleplanic refer to species which are planktonic for several hours to a week, a week to two months, and greater than two months, respectively.

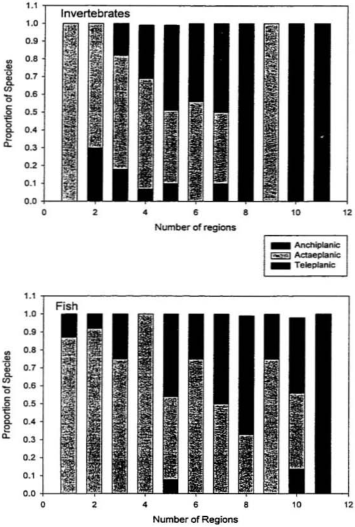
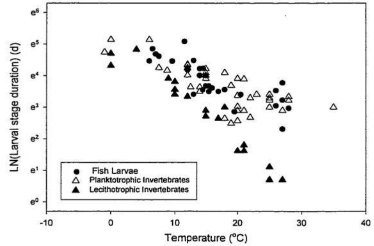


Figure 1.3. Dispersal potential of benthic invertebrates and fish in relation to their geographic range. All data from Table 1.1, see caption from Fig. 1.2 for description of development terms.



Larvae stage duration plotted in relation to temperature for both invertebrate and fish larvae.

Figure 1.4. Planktonic stage duration in relation to water temperature for benthic invertebrates. (References : Thorson 1961; Chia and Spaulding 1972; McKenney and Costlow 1982; Policansky 1982; Anger 1983; Crawford 1984; Pechenik and Lima 1984; Dawirs 1985; Chambers and Leggett 1987; Gonzalez et al. 1987; Fukuhara 1991; Zimmerman and Pechenik 1991; Beaumont and Barnes 1992; Chambers and Leggett 1992; Keefe and Able 1993; Amara and Lagardère 1995; Hoegh-Guldberg and Pearse 1995; McCormick and Molony 1995)

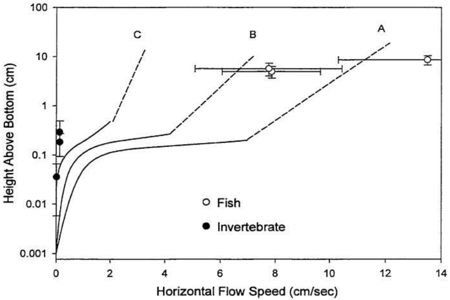


Figure 1.5. Maximum fish and invertebrate larval swim speeds in relation to smooth turbulent boundary layer velocity profiles (A,B,C) from Butman (1986). Data references (Chia and Buckland-Nicks 1984; Butman 1986; Williams et al. 1996)

Chapter 2. Transport and development of eggs and larvae of Atlantic cod, *Gadus morhua,* in relation to spawning time and location in coastal Newfoundland.

2.1 Introduction

Despite many theories linking recruitment variation to survival and transport in the early life history of marine fish (Hjort 1914; Cushing 1969; Sinclair 1988) our understanding of factors influencing spatial and temporal distribution of ichthyoplankton is still limited. Spatial and temporal pattern and survival of planktonic eggs and larvae should be dictated by adult distribution and spawning characteristics (Walford 1938; Pepin and Helbig 1997; Leising and Franks 1999), environmental conditions (McGurk 1986; Laprise and Pepin 1995), transport processes (Pepin et al. 1995), and interactions between these three factors. Although there have been detailed studies on each of these factors in relation to cod, few have attempted to link them within a single study.

Large annual spatial and temporal variation in the abundance of Atlantic cod eggs and larvae has been observed since the beginning of the twentieth century in the northwest Atlantic off the coast of Newfoundland (Hjort 1919; Thompson 1943; Postolaky 1974; Laprise and Pepin 1995). In Conception Bay, Newfoundland, Pepin et al. (1995) concluded that wind stress contributed significantly to transport and changes in larval fish abundance, and could have a significant impact on the interpretation of potentially important biological processes (predation and starvation). Although these density-dependent factors vary seasonally (Cushing 1990), environmental factors that influence egg and larval distributions and vital rates, such as water temperature and wind stress, also display distinct seasonal cycles off the coast of Newfoundland (Petrie et al. 1991).

Atlantic cod spawn off Newfoundland over a protracted period, often occurring from March to September (Myers et al. 1993; Hutchings and Myers 1994), greatly increasing the potential range of conditions during which egg and larval development occur. Thus, the effect of environmental conditions in a given year, and a comprehensive evaluation of environmental regulation of egg and larval abundance requires sampling throughout the spawning peak and detailed knowledge of spatial and temporal variation in spawning biology.

The idea that cod egg and larval survival and subsequent recruitment are spatially regulated has been refered to as the 'right site hypothesis' (deYoung and Rose 1993). This hypothesis states that during cold years, Atlantic cod on the Newfoundland shelf shift their spawning distribution to the south where retention is poor, resulting in years of poor recruitment. This hypothesis has been supported by the co-occurrence of cold conditions, southerly spawning distributions, and poor recruitment during the early 1990's (Rose et al. *in press*.). Laprise and Pepin (1995) suggest that if larval growth and survival are considerably higher in coastal areas (Frank and Leggett 1982; Taggart and Leggett 1987), then even a small proportion of coastal spawners could contribute significantly to the number of recruits to the population. Undoubtedly, the availability of inshore resources and habitat to developing eggs and larvae will depend on the advective properties of the system and subsequent coastal residency times for eggs and larvae.

The importance of inshore spawners for Atlantic cod off Newfoundland has been compounded in recent years as a larger portion of the spawner biomass is now found in the bays along the coast (Rose 1996; Anonymous 1998). With this relative increase in inshore spawner abundance, and a recent study that observed no recruitment signal from an unusually large inshore spawning aggregation (Smedbol et al. 1998), our need to understand processes affecting transport and survival in the inshore is greater than ever.

Placentia Bay, Newfoundland is one of the few areas in Atlantic Canada where spawner biomass, and thus egg and larval supply, are considered to be reasonably healthy at this time. Moreover, the absence of sea ice allows sampling throughout the spawning period. The objective of this study is to determine how spatial and temporal distribution and development of cod eggs and larvae in Placentia Bay are related to adult spawning location and timing, and environmental conditions (circulation, temperature, salinity, and chlorophyll a). These comparisons provide a framework in which to consider how year to year variation in these factors may ultimately affect the success of larval settlement in coastal habitats.

2.2 Materials and Methods

Study Area

Placentia Bay is a large embayment on the southeast coast of Newfoundland (Fig. 2.1), measuring ~130 km along a longitudinal axis that runs ~ 025° (east of north), and ~100km wide at the open southern mouth of the bay. Although scattered banks contribute to considerable variability in bottom depth, many areas of the bay are hundreds of meters deep, and the sides of the bay are quite steep. Elongate islands subdivide the northern portion of the bay into three channels, and anecdotal evidence suggests that currents flow into the bay along the eastern side and out along the western side.

Current and Wind Data

In order to describe circulation patterns in Placentia Bay I used several approaches. First, 500 grapefruit were released as passive drifters from each of two sites near Bar Haven and Perch Rock (see Fig. 2.1), in June of 1997; these sites were previously identified from acoustic surveys as major spawning locations in the bay for that year (Lawson and Rose 1999). Grapefruit were individually numbered by burning to allow linkage between release and recovery points. A brief survey of the outer bay the day following release failed to locate any of the drifters, and the numerous local fishermen working in the area were asked to collect and report any drifters. All of the recovered drifters were reported by fishermen within two weeks of release. Further investigations of the coastal circulation were made in the spring of 1998 using a pair of s4 current meters (B. deYoung unpublished data), moored at depths of 10 m on opposite sides of the bay (N 47° 14.1' W 54° 37.1'; N 47° 07.3' W 54° 10.5') from April to mid June.

Wind data recorded at a station in Argentia (Fig. 2.1) on the eastern side of the bay (recorded on a tower 10 m high) for 1997 and 1998 were obtained from the Canadian Atmospheric and Environment Service. The data were rotated 25° to align with the axis of the bay, converted to wind stress (Large and Pond 1981), and filtered using an 8th order Butterworth lowpass filter (Pepin et al. 1995). The current meter data were similarly rotated and filtered.

Ichthyoplankton and Oceanographic Sampling

During the spring and summer of 1997 and 1998, Placentia Bay was surveyed for ichthyoplankton along a set survey grid of six parallel transects (see Fig. 2.1) that were perpendicular to the long axis of the bay. Transects were eight nautical miles apart and stations were four nautical miles apart along each transect. Survey gear consisted of a 2 m x 2 m Tucker trawl with decreasing mesh sizes of 1000, 570, and 333 μm. Two General Oceanic flowmeters were placed at the mouth to allow estimates of filtered volumes. Double oblique tows to a maximum depth of 40 m and of 15 min. duration were collected at a towing speed of ~2 knots. This depth range was chosen because several studies have shown that > 95% of the ichthyoplankton in coastal Newfoundland are found in the upper 40 m (Frank and Leggett 1982; deYoung et al. 1993; Laprise and Pepin 1995).

Ichthyoplankton samples were preserved in 4% buffered formalin in seawater. For sample processing, cod egg and larval abundances exceeding 300 individuals per sample were subsampled using a Motoda splitter (except April and June 1998, which were processed by the Atlantic Reference Center and subsampled using the beaker technique of van Guelpen et al, 1982). All eggs and larvae were identified to the lowest taxonomic level possible and measured to the nearest 0.1 and 0.5 mm respectively. All eggs were grouped into the 4 development stages (Table 1) presented by Markle and Frost (1985). The difficulty in separating early stage cod eggs from those of witch flounder and haddock necessitated the CHW grouping (e.g., Brander and Hurley 1992). Nonetheless, careful identification of many late stage eggs and larvae indicated only incidental numbers of these other species, and it is therefore reasonable to assume the majority (>99%) of sampled CHW eggs were Atlantic cod.

Vertical CTD casts for salinity and temperature were collected concurrently with ichthyoplankton samples at each station using either a Seabird 19 (May and June 1997) or Seabird 25 (all other cruises). During the April 1997 cruise, a CTD-mounted fluorometer was used. Mixed layer temperatures and salinities were determined by averaging the upper 40 m from each profile. Although the mixed layer depth was shallower in late summer, altering sampling depth for ichthyoplankton, temperature, and salinity between months would have complicated comparisons.

For all 1998 cruises except April, concentrations of chlorophyll a and phaeopigments were measured from triplicate 100 ml samples collected with a 5 L Niskin bottle at 5-m depth and filtered through a Whatman GF/F filter at sea. In the lab, samples were extracted in darkness for 24 h in 90% acetone at -20^{0}C and pre- and post-acidification fluorescence (Parsons et al. 1985) were measured with a Turner Designs fluorometer (Model AU-10).

Data Analysis

Ichthyoplankton abundances were corrected for the volume filtered and expressed as number of individuals • 1000 m^{-3}. Spatial distribution of eggs and larvae was examined using contoured density plots generated with Surfer 6.0 for Windows 95. This contouring allowed interpolation, smoothed the variability inherent in ichthyoplankton sampling, and helped clarify spatial patterns.

Spatial analysis of the association between the egg and larval stages and the various environmental variables was explored using Pearson correlations with Bonferroni-adjusted p-values. Linear seasonal trends were removed from all variables by calculating the residuals of a linear regression between each variable against day of year, and correlations were then based on residuals from this analysis. Six environmental variables were examined : temperature and salinity at 5 m, average temperature and salinity from 5-40 m, bottom depth, and chlorophyll a concentration.

2.3 Results

Coastal Circulation and Wind Stress

Of the 1000 drifters released, a total of 124 were recovered, and all were recovered northward of the islands (see Fig. 2.1). Drifters were recovered in the Eastern Channel (40% of total recoveries, all released from Perch Rock), the head of the bay (6.5% of total recoveries, all released from Bar Haven), and the Western Channel (53% of total recoveries, 5% released from Perch Rock and 95% released from Bar Haven).

Current measurements show predominant currents on the eastern side were into the bay compared with currents measured on the western side, which were predominantly out of the bay (Fig. 2.2). The across-bay flow was also reversed between sides of the bay, with flow predominantly to the east on the eastern side and to the west on the western side.

The average monthly along-bay and across-bay currents from the eastern side of the bay decreased gradually from April to June, whereas the currents from the western side did not indicate similar seasonal changes (Fig. 2.2). Cross-correlations of along-bay currents from the eastern and western sides of the bay gave significant correlations at both negative (+ correlation coefficients at lags of 13 & 14 days) and positive (- correlation coefficients at lags of 6 & 7 days) lags.

In both years the predominant winds were from the southwest and decreased in magnitude from spring through to early fall. Along-bay and across-bay components of the wind stress were very similar between years, with the exception of a period of high offshore winds early in 1997 (Fig. 2.3). The means and standard deviations in the monthly along-bay and across-bay bay winds were consistent between years. Analysis of variance of the frequencies from Fourier transformations of the u and v components shows that although the 1997 and 1998 along-bay stress were not significantly different (F=0.000, p=0.993, df=3570), the across-bay stress frequencies were significantly different (F=8.581, p=0.003, df=3466). Cross-correlations between the along-bay wind stress and along-bay currents were not significant for the western or eastern sides of the bay at positive lags from 0 to 18 days.

Environmental Conditions

Surface and mixed layer temperature averages (upper 40 m) for the entire bay indicated a 1-2 °C annual increase for corresponding time periods from 1997 to 1998. Salinity measurements at the surface indicated no consistent between-year differences and varied between 31.5 and 31.9 psu. Vertical profiles of density (Fig. 2.4) show a slight stratification in June and a well-defined pycnocline by August of both years. By early fall (October 1997, September 1998) of both years, the pycnocline began to break down .

The April data show a very homogenous bay with less than 1°C increase from the northern to southern boundaries (Fig. 2.5). By June of 1997 there was evidence of localized upwelling through the presence of cold water associated with the islands. In 1998, however, this cold water was not evident, and the northeast part of the bay was characterised by cold water. Patterns in August of both years were very similar, with low temperatures on the south western side of the bay and near Cape St. Mary's. There was also the suggestion of a decreasing gradient in surface and mixed-layer temperatures from north to south.

The range in salinity at the surface within a cruise was typically 1 psu, and was seasonally invariant except for a Bar Haven station with 26.5 psu during April of 1998. Despite the modest range in salinity, a consistent salinity gradient was associated with the western side of the bay in both years, with lower salinity to the north and higher salinity at the southern boundary. This gradient was evident in June and August of 1997 and June of 1998, and is consistent with a freshwater inflow at the head of the bay and the entrainment of this water in the predominant southern flow along the western channel. Stability ($\Delta\sigma_\tau$ 5–40 m) values were higher in 1998, but an examination of the spatial pattern in stability during June of both years consistently showed an area of well-mixed water near the center of the bay, suggestive of increased vertical mixing. This well-mixed area near the center was also observed in August 1997, however, the dominant feature at this time was a band of vertically well-mixed water along the southwest coast of the bay.

The measurements of chlorophyll a concentrations that were taken using different instruments were compared separately. The April 1997 fluorometer readings at 5 m ranged from 3.0 ug l^{-1} in the head of the bay to 0.60 ug l^{-1} near the mouth, with a general trend of decreasing chlorophyll *a* concentrations with increased distance out of the bay. Chlorophyll a extraction data varied considerably from June to September (Fig. 6). Relatively high concentrations were associated with the head of the bay (June and August 1998) and the western side (August 1998) and ranged from 0.75 ug l^{-1} to 1.2 ug l^{-1}. The pattern evident in September was quite different from the spring and summer, with the peak in concentration of 2.8 ug l^{-1} occurring in the center of the bay. These spatial and temporal patterns in chlorophyll a were similar to the distribution of chlorophyll a observed in SeaWifs images for the corresponding time period (images supplied by L. Pazzant B.I.O.).

Ichthyoplankton

Densities of stage I eggs were highest in April of both years (particularly April, 1997) suggesting associated spawning peaks (see Fig. 2.7). Highest densities of stage I eggs were observed at stations near Bar Haven, Cape St. Mary's, and Oderin Bank, coincident with adult cod spawning aggregations (Lawson and Rose 1999). Late stage eggs usually occurred on the western side of the outer bay where predominant circulation patterns would have allowed the longest development time for eggs spawned within the bay. The temporal peak in late stage eggs was observed in May of 1997 (stage 3 and 4), but occurred in June (stage 3) and August (stage 4) of 1998. The average densities of late stage eggs (stages 3 & 4) and larvae were higher in 1998 than in 1997.

Larval densities were highest on the southwestern side of the outer bay (Fig. 2.7) corresponding to the pattern observed in late stage eggs. Although egg densities in April 1997 were higher than at any other time in the two years of the study, larval densities were very low in all of 1997 and highest in August of 1998 (Fig. 2.9). Back calculations of the spawning period expected to result in these peaks in larval density (Fig. 2.9) were based on mixed layer water temperatures and temperature-dependent development relationships (see Pepin et al. 1997). The range of larval ages was based on the 95% confidence intervals for the larval lengths of individuals collected during each cruise and a 0.33mm d^{-1} growth rate from Pepin et al. (1995). This calculation predicts that the spawning activity that produced the observed hatching likely occurred in mid-March and early July for 1997, and in mid-July for 1998.

A temporal examination of the density of stage I eggs at each of the identified spawning grounds (Fig. 2.10) shows similar patterns between years, with Bar Haven (A1) peaking in April and decreasing in subsequent months. In contrast, Oderin Bank (D4) eggs peaked in June of 1997 and in August of 1998.

In most of the samples taken, the numbers of cod larvae sampled were too few to make any inferences about size structure. However, in August of 1998, over 900 cod larvae were sampled, in contrast to a total of 41 larvae in all of 1997. Comparison of mean larval length, measured for each transect, indicates increases in larval size from the inner to the outer bay, a pattern consistent with predicted coastal flow patterns as larvae develop and are transported south along the western side of the bay. There was also a significant decrease in larval length between August and September 1998 (GLM, $p<0.000$, $F = 28.077$, $df = 1070$)

The correlations between environmental variables and ichthyoplankton densities (Table 2) show no consistent pattern, although surface salinity more than any other variable was significantly correlated with egg and ichthyoplankton densities.

2.4 Discussion

One of the challenges for marine fish is to place reproductive propagules into an environment where they are likely to hatch and settle into an appropriate habitat (Harden Jones 1968). In cod, there is increasing evidence that spawning occurs in multiple coastal areas of Newfoundland (Smedbol et al. 1998; Lawson and Rose 1999) and that coastal areas may be characterized by higher survival (Frank and Leggett 1982) and growth rates (Pepin et al. 1995) than offshore habitats. But whether coastal spawning is likely to confer any eventual habitat advantage for juveniles depends on successful hatching near the coastal habitat, which in turn depends on timing and locating of spawning in relation to water temperature and surface currents.

Spawning Location

During the two years of our study, stage I eggs were concentrated in three areas; Perch Rock, Bar Haven, and Oderin Bank (Fig. 2.1). The distribution pattern in these early stage eggs suggests that most of the spawning activity in Placentia Bay was confined to these sites and the majority of cod eggs and larvae collected in the bay were produced by these spawning aggregations. Although the duration of stage I eggs is on the order of 1-2 weeks in water temperatures typical of April (see Pepin et al. 1997), by June and August the stage I duration would be on the order of days, thus suggesting limited drift and a greater likelihood that spawning occurred near where eggs were collected in highest abundance.

These same inshore locations in Placentia Bay have been identified by Lawson and Rose (1999) as major spawning sites based on acoustic surveys and samples of adults collected to evaluate gonad condition. The reasons for the repeated use of these discrete spawning areas by cod is unclear, but chlorophyll data (Fig. 2.6) and SeaWiFs imagery for spring and summer indicate that algal biomass is usually highest at the head and western side of the bay. This increased agal biomass may translate into a more favorable feeding habitat for adults, but in addition it may provide greater food resources for hatching larvae. This point will be discussed later in reference to larval transport.

Although spawning may occur broadly on offshore shelf regions south of our study area (Myers et al. 1993), it is unlikely that offshore spawning contributed significantly to egg and larval distributions within Placentia Bay. Late stage eggs and larvae were largely absent from the eastern side of the bay, and were consistently associated with the head or western side. From these data, it is impossible to predict how important inshore spawning is for south coast Newfoundland cod recruitment, but it is clear that significant inshore spawning occurs at spatially consistent sites in Placentia Bay, and that these spawning events are responsible for most of the cod reproductive propagules within the bay.

Timing of Spawning

The delay in egg production at Oderin Bank is consistent with direct observations of adult spawning in the area (Lawson and Rose 1999). Reasons for the delay in spawning in 1998 remain unclear. However, the increase in egg production later in the spawning season in 1998 resulted in higher numbers of eggs spawned in warmer water (a difference of 8.65 °C between April and August 1998). The delay in spawning therefore likely led to faster development times (from 18.9 days to less than 7 days, relationships from Pepin et al. 1997) and much shorter dispersal distances prior to hatching.

Egg and Larval Transport

The circulation data suggest an embayment with mean currents moving counter clockwise northeast along the eastern side and to the southwest along the western side, exiting the bay near the southwest boundary. There is some suggestion (ADCP survey, Hodder et al. 1972; Lawrence et al. 1973) that there may be less directionality to the flow patterns in the head of the bay and near the center of the outer bay, but flow at the periphery is generally strong and consistent in direction.

Coastal circulation has been studied in greater detail in other Newfoundland bays (e.g., Trinity Bay (Yao 1986), Conception Bay (deYoung and Sanderson 1995). In Trinity Bay, a major part of the near-surface current variance could be accounted for by along-bay wind stress. However, in early summer when counterclockwise flow patterns were observed, the currents were not coherent with the wind and the author suggests non-local forcing as a possible explanation (Yao 1986). The importance of non-local forcing has also been demonstrated for Conception Bay (deYoung et al. 1993). The observation that the current variance could not be explained using along-bay wind stress when predominant flow patterns in Placentia and Trinity Bay were similar may suggest the influence of nonlocal forcing in Placentia Bay.

The location of the major freshwater source in Placentia Bay is just north of Bar Haven, and allows utilization of salinity as a passive tracer of predominant drift patterns. The consistent significant correlation coefficients with surface salinity and egg and larval densities suggest similarities in pattern formation (Table 2.2). These correlations, as well as the spatial pattern in salinity, which shows a tight gradient along the western coast, provide further support for the predominant drift out of the bay on the western side.

The transport of cod eggs from these discrete spawning locations was tracked through the development stages (see Methods). Although early stage eggs were concentrated near the spawning grounds, peaks in late stage eggs (3 & 4) were observed on the western side where predominant flow exits the bay. The highest larval densities were also sampled in this area near the mouth of the bay on the western side, generally to the south of the late stage eggs. The location of the highest larval densities coincided with the areas of highest phytoplankton abundance and may have significant consequences for larval survival through increasing food availability (Cushing 1990). Consistent with this hypothesis is the fact that the largest mean larval lengths in August 1998 were observed in areas of elevated algal biomass. However because patterns in larval length (Fig. 2.10) do not closely reflect patterns of chlorophyll (Fig. 2.10) when the entire bay is considered, it is more likely that larger size reflects older individuals and longer transport rather than superior feeding conditions.

Seasonal and Annual trends

The seasonal variation observed in the environment, coupled with the extremely protracted spawning period, suggests the potential for large, environmentally-driven seasonal variation in egg and larval spatial and temporal distributions, development, and retention. This seasonal influence was most evident in the occurrence of larvae in the bay. Although peaks in mean egg density were observed in April of both years, relatively high larval densities were only observed in late summer (August 1997 & 1998, September 1998). Based on temperature-dependent development rates (Pepin et al. 1997), eggs spawned during April should have hatched around mid-May and been observed in May (1997) and June (1997 and 1998). The absence of larvae at these times suggests high loss rates either through flushing from the bay or reduced survival. The lack of larvae from the peak in egg abundance is in contrast with the presence of large numbers of larvae in August samples when egg production was low.

There are several possible reasons for the seasonal variation in hatch rates that generally either assume differences in resultant transport or differential survival. Seasonal differences in transport rates could account for differences in hatch rates, however, there is no evidence from either the wind stress or the current data to suggest this was the cause. Seasonal variation in location of spawning relative to reduced flow speeds could result in variation in hatch rates within the bay. Spawning, however, as indicated from the stage I egg distribution, was spatially consistent within years, suggesting this was not the case. Differential survival could be either caused by increases in starvation or predation. The most common phenomenon related to larval starvation and foraging success is a match or mismatch to the annual spring phytoplankton bloom (Cushing 1969). In 1998, SeaWiFs data allowed us to examine the timing and duration of the spring phytoplankton bloom that occurred in early April and was short lived (lasting~2-3 weeks). The highest larval densities were observed in August and were clearly decoupled from the spring bloom, suggesting minimal potential for influence. Similar observations made by Gagné and O'Boyle (1984) for the Laurentian Channel area suggest extensive cod spawning in summer despite spring and fall algal blooms.

The most plausible explanation for the seasonal differences in hatch rates is that environmental effects on the egg vital rates resulted in faster development (less than the residency time) during the summer months that resulted in increased hatching within the bay. Therefore, the predominant offshore flow for Placentia Bay could limit the occurrence of larvae to warm months when time to hatch does not exceed residency time.

This theory is consistent with the spatial pattern observed in both the eggs and larvae. The dramatic increase in larval abundance in 1998 relative to 1997 could then be attributed to increased egg production late in the spawning season. This explanation suggests an extension of both the member-vagrant (Sinclair 1989) and the right site hypothesis (deYoung and Rose 1993). In contrast to deYoung and Rose (1993) who describe the recruitment implications of spatial variation in offshore spawning, these results suggest that in coastal areas where spawning appears spatially consistent, temporal variation in spawning influences development times and therefore has similar consequences for retention.

Differential seasonal retention could be influenced by seasonal patterns in egg predation. Temperature-dependent development results in prolonged development and could increase the likelihood of predatory losses. Slow development rates have previously been suggested as a cause of low recruitment through increased predation on eggs and larvae (Ricker-Forester hypothesis, Cushing 1995) . Thus slow development rates as a consequence of spawning at cold water temperatures results in increased vagrancy from the local population, which may be amplified by predation losses.

Although both physical and biological factors influence recruitment, the relative importance of these factors is still debated (Sinclair 1988, Leggett and Deblois 1994). Bjorke and Sundby (1986) present a significant correlation between cod larval numbers and year class strength, suggesting that larval sampling could be an effective tool to estimate recruitment (see also Rijnsdorp et al. 1985 (*Pleuronectes platessa*), and

Sammons and Bettoli 1998 (*Pomoxis* sp.)). If larval abundances can be interpreted as indications of future recruitment (as similarities between the patterns in larval fish observed here and juvenile patterns suggest, see Robichaud and Rose 1999), then late spawning may be critical to successful recruitment within Placentia Bay. The eventual fate of eggs and larvae advected from the bay remains unresolved. Recent studies of the genetic (Beecham et al. 1999; Ruzzante et al. 1996) and behavioral (Wroblewski et al. 1996) aspects of coastal cod populations suggest distinct subpopulations. If these subpopulations do indeed exist, then the potential for gene flow between the populations of inshore and offshore cod may be relatively small and survivorship of eggs advected offshore may be poor. A comprehensive survey examining both the inshore and offshore areas throughout the spawning season is needed to address this question.

Summary

Peaks in stage I egg density in April of both years resulted in low densities of larvae, suggesting that eggs spawned early in the season are flushed out of the bay and/or are subject to high mortality as a result of increased exposure to predation and decreased hatch rates at low temperatures. High egg densities were observed late in the spawning season in 1998, suggesting increased spawning later in 1998 relative to 1997. Acoustic surveys of the bay for adults showed that peak spawning period was delayed by 6-10 weeks in 1998 (Lawson and Rose 1999), and juvenile abundances also show an increase in 1998 (Robichaud and Rose 1999). Our data suggest that this delay in spawning peak, in combination with an increase in mixed layer temperature, are responsible for the increase in larval densities in 1998. Thus, the densities of early stage eggs may be a poor indicator of subsequent larval abundance in coastal Newfoundland. In addition, peaks in inshore spawning may be less important to larval production when they occur in early spring. It may be the late spawners that contribute most to successful hatching of larvae and a subsequent inshore settlement and recruitment.

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Table 2.1. Egg staging scheme using in the classification of CHW eggs based on Markle and Frost (1985).

Stage	Description
I	From fertilization until the formation of an embryonic axis
II	From the formation of an embryonic axis until the embryo is halfway around the yolk
III	From stage II until the tip of the tail almost touches the head
IV	From stage III to hatch

Table 2.2. Egg Density (per stage) and environmental variable *correlations. Only significant correlations (p - values adjusted) were reported.

	Cruise Date							
Stage	Apr -97	May-97	June-97	Aug-97	Apr-98	June-98	Aug-98	Sept-98
One				-d, -ss, -ms	st, -ss, -ms	ch, st, mt, -ss, -ms	-d, ch	-d
Two		-d				ch, mt		
Three		-d, st, mt		-ss				
Four	mt			-ss, -ms	st,' mt		ch,	-ss
Larvae				-st		ch, -ss, -ms		

* d, ch, st, mt, ss, ms, represent depth, chlorophyll a, surface and mixed layer temperature and surface and mixed layer salinity respectively. Sign tests identified depth with stage 1 and 3, as well as mixed layer salinity with stage 3 as significantly ($\alpha=0.05$) negative.

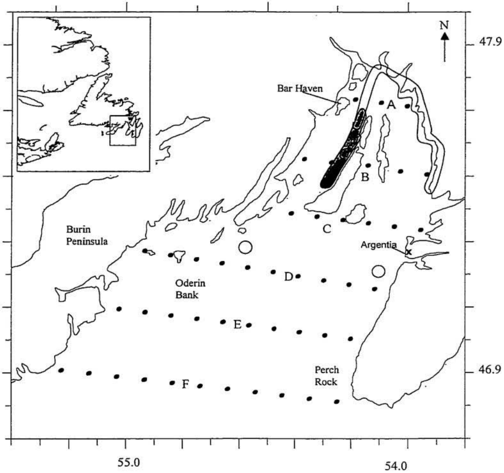
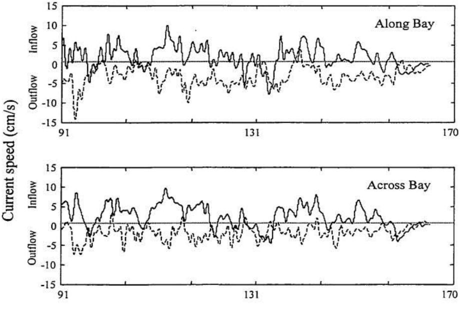


Figure 2.1. Chart of Placentia Bay survey transects (A -F) and stations; inset shows position of bay in relation to Newfoundland; open circles represent s4 mooring locations; Shading represents Perch Rock (light shading) and Bar Haven (dark shading) sites released drifter were recovered.



Julian Day

Figure 2.2. Along- and across-bay currents from the eastern (solid) and western (dashed) sides of the bay. All data lowpass filtered with an 8th order Butterworth filter and rotated to align with the bay.

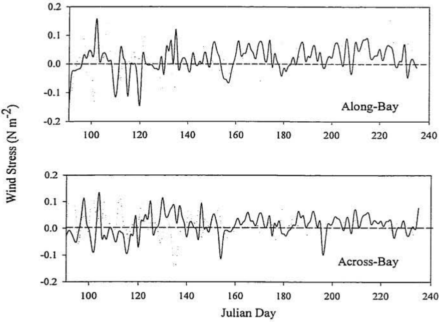


Figure 2.3. Along- and across-bay wind stress from the 1997 (solid) and 1998 (dotted). All data lowpass filtered with an 8th order Butterworth filter and rotated to align with the bay.

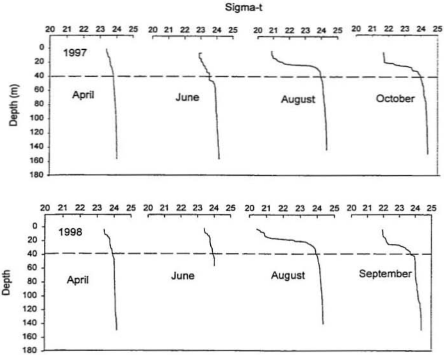


Figure 2.4. Vertical profiles of density (sigma - t) from station A2 (middle point in transect A in Fig. 1.) measured from April to October(1997) and April to September (1998).

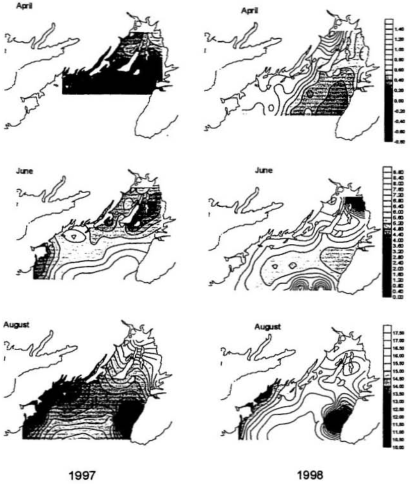


Figure 2.5. Distribution of sea surface temperatures in Placentia Bay (5m) for 1997 and 1998 surveys based on CTD profiles (note scales are different for different months).

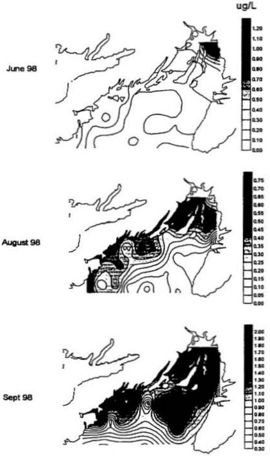


Figure 2.6. Distribution of chlorophyll a (5m) in Placentia Bay Newfoundland based on extractions from water samples taken during June, August, September 1998 survey cruises.

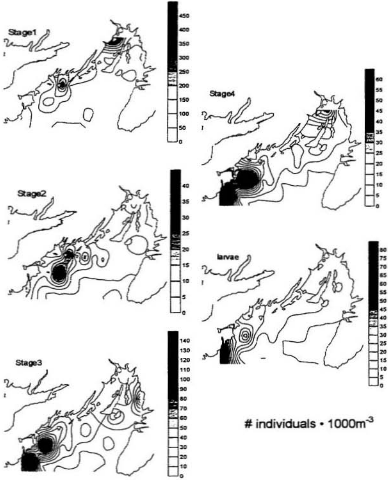


Figure 2.7. Distribution of cod eggs and larvae sampled during the August 1998 (# of individuals•1000m^{-3}). Note different scales.

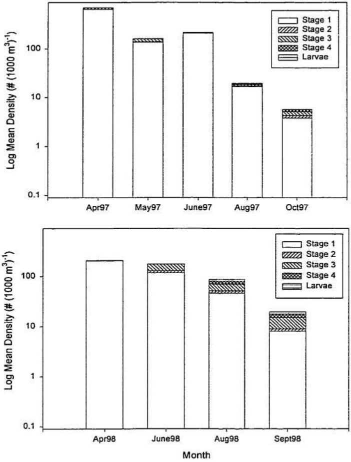


Figure 2.8. Temporal changes in mean egg stage and larval density in Placentia Bay during the Spring and Summer of 1997 and 1998, based on Tucker trawl survey data.

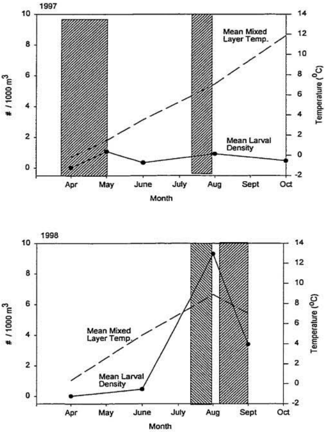


Figure 2.9. Seasonal changes in mean larval density for Placentia Bay. Solid points indicate survey dates and each bar represents the predicted period during which spawning would have to occur to produce the larvae sampled at each indicated peak in larval density. Back calculation of spawning period based on relationships in Pepin et al. (1997) and a maximum larval life based on 95% CI of larval lengths and a 0.33 mm day^{-1} growth rate (Pepin et al. 1995).

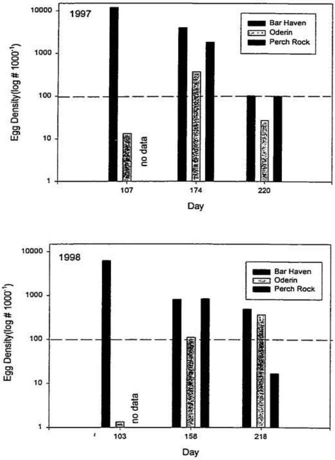


Figure 2.10. Density (# of individuals•$1000m^{-3}$) of stage one eggs at each of the spawning sites for 1997 and 1998.

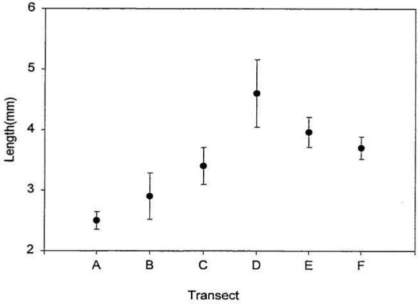


Figure 2.11. Changes in larval size with transect based on data collected during Tucker trawl surveys. Lengths are averaged across each transect.

Chapter 3 - The influence of temperature on loss of Atlantic cod (*Gadus morhua*) eggs and larvae from the inshore environment : a combined modeling and observational approach.

3.1 Introduction

A common theme in theories linking early life history survival with recruitment variation is a strong dependence on physical processes (Lasker 1975; Frank and Leggett 1982; Sinclair 1988; Ellertsen et al. 1989). Several studies suggest a regulatory link between temperature and strong year classes (e.g., Ellertsen et al. 1986; deYoung and Rose 1993). Variations in temperature affect the survival of developing eggs and larvae through high mortalities at extreme temperatures (Iversen and Danielssen 1984), a temporal mismatch with primary production (Cushing 1969), and reduced development rates resulting in prolonged exposure to predation (e.g., Bannister et al. 1974; Graham et al. 1972; Dahlberg 1979).

The interpretation of mortality estimates is often problematic because various processes may co-occur and interact to produce a loss rate. Though much attention has been given to the contribution of starvation and predation on mortality rates, in many systems transport may account for a large proportion of the loss rate observed (Taggart and Frank 1990; Pepin et al. 1995; Helbig and Pepin 1999). As the availability of suitable habitat for settlement becomes limited, as on isolated reefs (Cowan 1985) and in intertidal habitats (Gaines and Roughgarden 1987), the importance of limiting dispersal increases dramatically. Reduced development rates resulting from cold water temperatures therefore could increase the proportion of vagrants lost from the population through advection. Moreover, this link between vagrancy and water temperature could be particularly important for species with variable or protracted spawning periods if large variations in temperatures occur during egg and larval development. Page et al. (1999) demonstrate that cod and haddock spawn on Georges Bank at times and locations characterized by high predicted retention and suggest the importance of this retention to population regulation and stability. We hypothesize (see chapter 2) that retention is limited by an interaction between advection and temperature-dependent development may be important to recruitment variation in coastal Newfoundland cod populations.

Cod in coastal Newfoundland, much like offshore cod (Hutchings and Myers 1994), display considerable variation in timing and location of reproduction (chapter 2; Lawson and Rose 1999). With the collapse and slow recovery of offshore cod populations over the last decade, coastal populations have comprised an increasingly important component of the current Northwest Atlantic cod stock complex spawner biomass (Rose 1996; Taggart 1997). Because inshore populations are now a large component of these stocks, our need to understand consequences of highly variable inshore water temperatures on egg and larval survival and growth has become critical.

Studies on the effect of temperature on fish eggs, and cod in particular, date back to the turn of the century. Early work focused on determining the range of temperatures at which hatch was possible (Dannevig 1894; Johansen and Krogh 1914) and later turned to temperature effects on mortality (Bonnet 1939). Hatching in Atlantic cod eggs occurs at temperatures from -1 to 14 °C, but low hatch rates have been reported for extreme temperatures (-1 °C, Pepin et al. 1997; above 14°C, Iversen and Danielsen 1984). These and more recent experiments (Laurence and Rogers 1976; Page and Frank 1989; Pepin 1991; Pepin et al. 1997), have shown that development rate, often measured as a stage duration or time to hatch, decreases with increased temperature. In addition, mortality has been shown to be both temperature (Pepin 1991) and size-dependent (Jaworski and Rijnsdorp 1989), with higher losses at low temperatures and smaller sizes.

In this paper I use a simple model of egg development and mortality to develop several hypotheses on the consequences of inshore spawning. Specifically, the hypothesis is that loss rates are dependent on the interaction between temperature-dependent development and transport patterns, such that increases in development times are associated with increases in loss rates. These hypotheses are then examined using data on cod egg and larval distributions from Placentia Bay Newfoundland for 1997 and 1998.

3.2 Methods

The Simulation

The egg staging scheme used here (see Table 2.1, chapter 2) is presented in Markle and Frost (1985) and Pepin et al. (1997). Although many variables may influence development rates (i.e., temperature, salinity, and size), temperature has been reported as the dominant factor in egg development (Pauly and Pullin 1988, Page and Frank 1989, Pepin 1991). The relationships for stage transition times (days) and temperature used for this model are from P. Pepin (unpublished data) and vary for each development stage.

$$\text{Stage I} = e^{(2.36 + T(-0.12))} \tag{1}$$
$$\text{Stage II} = e^{(3.12 + T(-0.15))} \tag{2}$$
$$\text{Stage III} = e^{(3.45 + T(-0.17))} \tag{3}$$

$$\text{(4)} \qquad \text{Stage IV} = e^{(3.65\ +T(-0.12))}$$

In this simulation, these temperature-dependent development functions are coupled with mortality functions; three treatments were used. The first mortality treatment sets the mortality rate at a constant percent loss per day where the fixed value for mortality (M) is set at 10, 20, and 50%. These mortality rates are thought to be representative based on studies of egg mortality such as Dahlberg (1979) or Jaworski and Rijnsdorp (1989). The second mortality treatment uses Pepin's (1991) exponential equation relating mortality to temperature for multispecies data and assumes the relationship is suitable for within-species comparisons.

$$\text{(5)} \qquad M_e = 0.03e^{0.18T}$$

The third mortality treatment, uses a relationship for size-selective mortality on Atlantic cod eggs (Jaworski and Rijnsdorp 1989) and is combined with a temperature dependency based on a relationship relating egg size and temperature (author's unpublished data). Although the direct size dependency has been removed, the result is nonetheless consistent with a size dependency.

$$\text{(6)} \qquad M = 0.6896 - 0.3251(10^{(0.181-0.049T)})$$

For each treatment, the model was run for daily time steps on which development is accumulated as a percent of the total stage duration at the present temperature, and mortality functions as a percent loss of the daily abundance. Simulations continued until cumulative losses were greater than 99%.

Field Observations

Physical Observations

To link the simulation model to field observations, a fixed temperature time series taken from Placentia Bay Newfoundland was used. In addition, a simple 'bay-like' frozen circulation field was set up with horizontal temperature gradients dictated from SST images, and development and mortality were tracked in this field (velocity field and particle tracking scripts courtesy Dr B. deYoung Dept. of Physics and Physical Oceanography, Memorial University of Newfoundland). The required temperature measurements were made from a pair of s4 current meters (B. deYoung, unpublished data), moored at a depth of 10 m below the surface on opposite sides of the bay (N 47° 14.1' W 54° 37.1'; N 47° 07.3' W 54° 10.5') from April to mid-June of 1998 (see Fig. 3.1). Because temperature measurements recorded at both moorings were very similar, the eastern mooring was selected and this time series was extended using an extrapolation based on the average monthly temperatures for the bay (see Bradbury et al. 1999; chapter 2). Continuous temperature data were not available for 1997. Horizontal temperature fields were estimated from AVHRR (Advanced Very High Resolution Radar) SST (Sea Surface Temperature) images for Placentia Bay for the spring and summer of 1997 and 1998 (Dr P. Cornillion, U.R.I.; L. Pazzant, BIO).

The spatial model was run with absorptive boundaries and propagules moving out of the domain ended the simulation. The spatial model bears only a general similarity to Placentia Bay and the circulation data necessary to generate an accurate circulation field is unavailable. The goal of this simulation is to examine the impact of spatial variability in temperature rather than advection.

The second analysis of egg movement used the mean along-bay current speeds (Bradbury et al. 1999, chapter 2) and expected flow patterns (Hodder et al. 1971; Sheng and Thompson 1996; Bradbury et al. 1999; chapter 2) to generate an expected temperature exposure time series. This exposure time series was used in conjunction with the development model (Fig. 3.2c) to explore the transport potential in relation to temperature within Placentia Bay. Because these flow patterns are only approximations and speeds are estimated using straight-line distances, these estimates probably represent the minimum residency times since complex flow patterns are present in some areas the bay (see Chapter 2).

Biological Observations

Ichthyoplankton samples were taken throughout the spawning and post-spawning seasons along a set station grid. Surveys produced data on abundance of each cod egg stage at 45 stations in Placentia for April, May, June, and August of 1997 and April, June, August, and September 1998. Details on sampling and annual patterns and trends may be found in Bradbury et al. (1999) and chapter 2. Seasonal variations in transport were examined through the calculation of the centers of mass for each stage and the distance between consecutive stages. The center of mass for each stage and cruise was calculated based on the formula;

(7) $$Z = \sum_{i=1}^{n}(X*D)*N^{-1} / \sum_{i=1}^{n}(D)*N^{-1}$$

where Z is equal to the center of mass based on either the latitude or longitude , X is the latitude or longitude in degrees, with minutes converted to decimal, D is the density of ichthyoplankton, and N is the number of stations. The center was calculated separately for the latitude and longitude. Based on the centers of mass of successive stages within a given survey grid, the transport distances between stages was calculated. This analysis assumes that individuals collected within a given survey were all spawned at the same general location and that mortality was uniform. The assumption of constant spawning locations is not unreasonable. Data on adult spatial pattern (Lawson and Rose 1999) suggest that spawning in 1997 and 1998 was consistently aggregated near the southwest mouth of the bay, near the head of the bay, and on a bank on the western side of the bay (although in different proportions between years). Transport rate between each stage was then calculated using the predicted stage durations from Pepin et al. (1997, unpublished data).

The loss rate (instantaneous mortality) was calculated based on the equation,

(8) $$L = \ln(N_1/N_0) * (t_1 - t_0)^{-1}$$

where N_1 and N_0 are the mean abundances of the various stages per month, t_1 and t_0 are the predicted stage duration. This loss rate was calculated independently for each survey.

3.3 Results

The Simulation

For the different temperatures, the model projections gave ranges of hatch times (8 to 41 days) consistent with other studies (Lauwrence and Rogers 1978; Page and Frank 1989), suggesting that the model assumptions were realistic. The initial runs were based on single spawning events limited to a single day (Fig. 3.2a). All simulations in this section use a constant mortality rate set at 10%. Alternate treatments of mortality are explored further in the results. Increasing temperature resulted in increases in percent survival to hatch from ~ 5% at -1 °C to 45 % at 10 °C. Spawning was modified to a multiday event (Fig. 3.2b) and more realistically to a normally distributed spawning curve (Fig. 3.2c).

The effect of variation in spawning date was explored using a temperature time series from Placentia Bay (Fig. 3.3). The daily spawning version of the model discussed above with a normal spawning curve was run starting from April 1, June 1, and August 1, corresponding to observed annual variation in spawning peaks (Lawson and Rose 1999; the temperature time series was extended using averages for the bay for the month of August, Fig. 3.3). As peak spawning is delayed, the survival and numbers of eggs that hatch increases because increases in development rate reduce cumulative mortality (Fig. 3.4).

Size- and Temperature-Dependent Mortality Treatments

Simulations similar to those described above were performed using both the size-dependent and the temperature-dependent mortality treatments. These mortality relationships resulted in high survivorship at low temperatures and low survivorship at high temperatures (Fig. 3.5). Thus, these simulations suggest increases in dispersal distance and increases in survivorship with lower temperatures (Fig. 3.5). The suitability of these different treatments in relation to field observations will be dealt with in the Discussion. The remainder of the Results explores the influence of temperature on dispersal at a set mortality rate (m=10%).

Lagrangian Applications

The SST images from spring (May/June) show that Placentia Bay lacks horizontal temperature structure and is homogeneous at ~ 2°C. Under these conditions the simulation predicted a time to hatch of 25 days with a survival rate of <10%. Assuming spawning took place near the mouth of the bay on the eastern side, the frozen velocity field predicts the point of hatch occurs near the south western boundary of the domain. By summer (July), the temperature in the head of the Bay had risen to 10°C, and the outer Bay was 8 °C. Because of the warmer water temperature, the July hatching occurred in only 12 days, resulting in 40% survival and placing hatch at the head of the bay.

The application of the egg development model to the predicted temperature exposure time series generated using the current meter data yielded similar results. For spring conditions, the model predicts hatch at 18 days with a 15% survival to hatch. In contrast, utilising summer temperature patterns the model predicts hatch in 11 days and a 40% survival to hatch.

These analyses of egg movement suggest that eggs spawned in summer travelled half the distance and suffered much lower mortalities than eggs spawned in spring. This transport resulted in late stage eggs concentrated at the outer southwest portion of the velocity field from spring spawning and at the northern portion of the field during summer spawning, suggesting transport distances may have halved as a result of an 8°C temperature increase. Moreover, these simulations suggest that because drift out of an area may be temperature dependent and spawning events that occur closer to exit boundary for an area or bay may be more prone to higher losses, later spawning may be much more important for successful hatching.

Field Observations - Physical and Biological

Temperatures recorded at 10 m below the surface from the eastern side of the bay show an increase of about 8 °C from April to mid June 1998 (Fig. 3.2). The egg and larval distributions for 1998 (Fig. 3.7) show peaks in stage I eggs in April at the head of the bay, whereas the peak in late stage eggs (3 and 4) occurred in August and near the outer western side of the bay. Throughout both June and August a southwest progression in egg development was observed.

Transport distances from stage I to stage IV generally decreased with increasing temperature for both years (Fig. 3.8). Indeed, in September 1998 as the temperature decreased, transport distances began to increase again. Mean transport rates ranged between 0.5 and 4.0 $cm \cdot s^{-1}$, and an increase in transport rate was observed from April to August of both years. Pattern in mortality rates was similar to that observed in transport distances. Because there are only four egg stages, relationships between duration of all stages and transport differences were rarely significant. In addition, in April 1997 there were no stage IV eggs sampled so an estimate of mortality from stage I to four was not possible. There was an obvious decreasing trend in mortality rates with temperature in 1998 and the later part (June to August) of 1997 (Fig. 3.5).

3.4 Discussion

Evidence for the presence of persistent spawning locations and discrete egg and larval distributions for Atlantic cod has been described throughout this century for many stocks (see Sinclair 1988). Several authors (e.g., Ellertsen et al. 1986) have suggested that well-defined spawning locations affect the physical transport and retention of cod reproductive propagules, and underlie the structure and stability of cod populations. Although much of the work focussing on egg and larval transport in cod has focussed on drift and dispersal to nursery areas (Harden Jones 1968), the location of spawning sites in association with well-defined hydrographic structures such as Browns Bank (O'Boyle et al. 1984), the Flemish Cap (Andersen 1982), and Georges Bank (Walford 1938), suggests that spawning and nursery areas may coincide or be geographically tightly linked in some stocks. Therefore, if there is decreased survival outside of embayments such as Placentia Bay (see Frank and Leggett 1982), within which nursery habitats may be more abundant and suitable, then it may be advantageous to complete egg and larval development within its boundaries. Even if there is no decrease in survival rates in the offshore, individuals transported offshore may be effectively lost from the population (Sinclair 1988). The vagrancy of eggs and larvae from these populations should be dependent on dispersal potential and loss rates, both of which are influenced by hydrography and development time.

The simulation

The simulation allowed the exploration of the temperature-dependent dynamics of development at fixed levels of mortality, and suggests that temperature plays a predominant regulatory role in development and dispersal through its influence on stage duration. Simulated spawning events that were earlier in the temperature time series (i.e. spring) produced eggs that suffered higher mortality (Fig. 3.4), and dispersed greater distances as a result of increased egg stage duration (Fig. 3.6). By contrast, later spawning events (i.e., summer) produced eggs that hatched sooner and geographically closer to the spawning site. Therefore, assuming all other factors (i.e., predation or starvation) are constant or of reduced importance with respect to predicted patterns, spawning during summer temperatures should result in highest hatch rates and shortest dispersal distances. This hypothesis is similar to those put forth by other authors (see Sinclair 1988), suggesting that physical retention and transport mechanisms have a great influence on life histories. Food availability and predation may become more important during larval stages but prehatch conditions clearly have a large impact on hatch rates within a given area.

In contrast to the set mortality rate used above, several studies have suggested both biological and physical dependencies of mortality. The temperature-dependent and size-dependent mortality treatments (Jaworski and Rijsdorp 1989; Pepin 1991) gave a poor fit to the observed loss rates from the survey data (Fig. 3.5). The increases in mortality and dispersal with increases in temperature predicted by these mortality treatments suggests that within Placentia Bay, egg loss is linked primarily to physical transport and not to predation.

The importance of spawning in warm water to limiting dispersal and mortality is also supported by the Lagrangian application of the development model (Fig. 3.6). The velocity field is representative of a simple embayment and a simplification of the patterns observed in Placentia Bay, in that a counter-clockwise flow pattern predominates. Despite the simplification of the velocity field, the effect of the seasonal warming of water temperatures is quite dramatic. Moreover, this decrease in dispersal distance and mortality rates associated with increases in temperature is supported by the application of flow speeds and distances for Placentia Bay in the generation of a temperature exposure time series. In summary, the simulations provide consistent predictions of expected spatial pattern in eggs and larvae that can be compared to observational data.

Survey Data

Recent work on the circulation in Placentia Bay (summarized in Bradbury et al. 1999; chapter 2) provides evidence for strong directional flow and a potential for high offshore transport. The impact of this flow regime can be seen in the spatial distribution of the various egg stages (Fig. 3.7). Specifically, late stage eggs and larvae (see Bradbury et al. 1999; chapter 2) are concentrated near the exit boundary for the bay and occur only in summer, suggesting a strong seasonal constraint to retention within the bay that is linked to development and predominant flow. Center of mass calculations support model predictions relating both loss rates and dispersal to temperature, with decreases in transport distances (Fig. 3.8) and loss rates (Fig. 3.5; except for early 1997) associated with increases in water temperature during 1997 and 1998. The link between egg transport distance and temperature is further supported by the similarity in transport distances in June and September 1998. Transport rates calculated from the distances and predicted stage durations give very similar values to along-bay current measurements from Placentia Bay for a corresponding time period.

The loss rate, as defined in this study, is based on the assumption that late stage eggs and larvae that were sampled must have developed from the same population of eggs that were sampled, and that import into the system was therefore limited. Because the probability of egg import into the system is assumed to be very low (see Bradbury et al. 1999; chapter 2), only transport out of the bay has potential to influence the loss rate. Given the consistency and directionality of the flow patterns in Placentia Bay, this assumption is not unreasonable. The loss rate was defined as the total loss for all egg stages (see Campana et al. 1989) because it was the best approximation of removal from the system and not subject to high variation present in estimates of each stage loss

Comparison of Simulation and Survey Data

Model predictions are consistent with observations based on the plankton surveys in Placentia Bay for 1997 and 1998 where peaks in late egg stages and larvae occurred in late summer despite mean spawning peaks in April. At the highest water temperatures observed, the measured loss rates reach a minimum at the same time that the predicted loss rates from both the size-dependent treatment and temperature- dependent relationship predict a maximum (Fig. 3.5). Thus, low summer mortality rates may be a direct result of decreased incubation times with high summer water temperatures. Moreover the simulation predicts that the total egg stage duration would decrease from April to August by almost 30 days, suggesting that the influence of timing of spawning on transport may be significant (Fig. 3.6). In light of the observation that net transport may be out of the bay (Fig. 3.7; see Bradbury et al. 1999, chapter 2), the most parsimonious explanation for the observed pattern is that the occurrence of late stage eggs and larvae is limited by temperature-dependent development rates.

Although the model predictions of increased loss with colder temperatures are generally supported by the data, increases in loss rates occurred early in 1997 despite decreases in dispersal distance with increased temperature (Fig. 3.5). The presence of the only sustained offshore wind observed during our study period occurred early in 1997 (Bradbury et al. 1999), coincident with this increase in loss rates, and may offer an explanation. Several other authors have suggested that wind stress is a dominant influence on the spatial pattern of eggs and larvae in coastal Newfoundland (Taggart and Leggett 1987; Pepin et al. 1995), particularly where surface currents respond primarily to local wind forcing.

The importance of temperature to dispersal and survival of planktonic eggs and larvae has been suggested by other authors. Beverton and Lee (1965, cited from Harden Jones

1974) suggested that cold temperatures prolonged the planktonic period in cod eggs and resulted in transport closer to the nursery grounds. Their study showed that the cumulative distance between the centers of distribution of the various egg stages was much greater in a cold year relative to a warm year suggesting a direct link between temperature and transport. In the Northwest Atlantic deYoung and Rose (1993) use a variation of Iles and Sinclair's (1982) spatial recruitment model and hypothesize that spawning location has a direct influence on residency times on the Newfoundland shelf. Residency times on the southern shelf are likely much lower than to the north (Helbig et al. 1992; Davidson and deYoung 1995), suggesting that in cold years, when spawning is more southern, there is higher egg and larval loss from the shelf and therefore reduced recruitment.

The advective (density-independent) component of the loss term may be examined through a comparison of several geographical areas because of its dependence on local topography and hydrography. Pepin et al. (1995) suggest that the relative significance of transport to variations in egg and larval abundance may be influenced by the size of the system, and demonstrate the importance of advection into and out of a study area when estimating mortality (see also Helbig and Pepin 1998). Just as the advective component of the loss rate may be scale-dependent, a temperature dependency may occur through temperature-regulated development rates. Therefore, although the slope of the relationship between the advective loss rates and the area of the system is constant, the line may decrease in elevation with increases in development rates.

This documentation of a temperature dependency on the advective component of mortality estimates may help in the assessment of the potential biases associated with mortality estimates. In addition, documenting the importance of temperature to survival and recruitment in coastal Newfoundland may have direct implications for summer harvests, where later spawning may result in higher retention and therefore higher survivorship. Moreover, commercial harvests target the older individuals, which in turn could truncate the spawning period (Trippel and Morgan 1994) and restrict incubation to cooler spring temperatures. In light of this study, the consequences of extensive harvests or pre-summer versus summer harvests may be dramatic for local recruitment.

Summary

Recent increases in fishing pressure off coastal Newfoundland dictate that continued stability of coastal cod populations will depend in part on the annual recruitment success of inshore spawning aggregations. Because eggs are effectively passive particles, the interaction of coastal hydrography and temperature-dependent development and mortality rates will have dramatic consequences on hatch rates and larval pattern. Therefore, the occurrence of late stage cod eggs and larvae in Placentia Bay, where circulation is complex but characterised by strong advection, is likely dependent on temperature-dependent development rates. Temperature may therefore be a predominant factor in determining settlement and subsequent recruitment to Placentia Bay.

3.5 References

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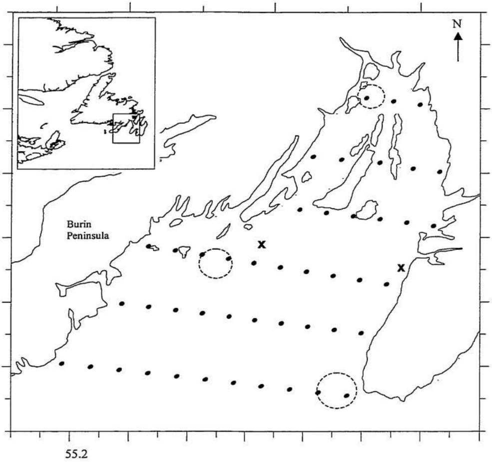

Figure 3.1. Chart of Placentia Bay survey transects (A -F) and stations. Inset shows position of bay in relation to Newfoundland. Open circles represent major spawning sites (Lawson and Rose 1999; Bradbury et al. 1999; chapter 2) and X's represent s4 mooring locations.

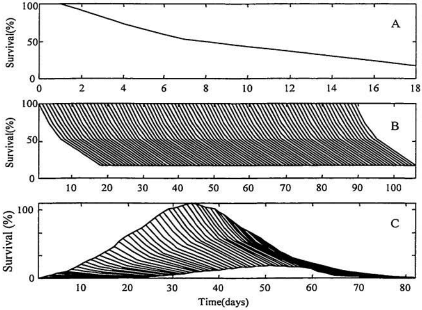

Figure 3.2. Simulated egg development and mortality from a single (A), multiday (B), and normally distributed (C) spawning event (mortality set at 10%).

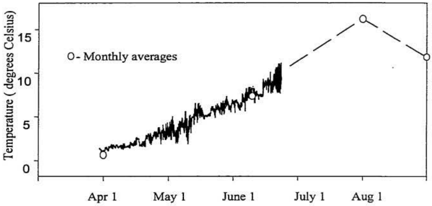

Figure 3.3. Temperature time series from 10 m depth from the eastern side of Placentia Bay during 1998. The time series is extrapolated using mean temperatures at 10 m for August and September (data from CTD surveys, see chapter 2)

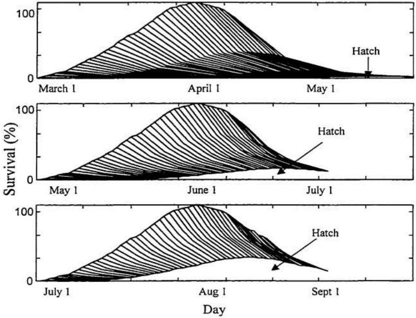

Figure 3.4. Simulated egg development and mortality based on a temperature time series from Placentia Bay Newfoundland 1998. Normal curve centered on April 1st, June 1st, and August 1st.

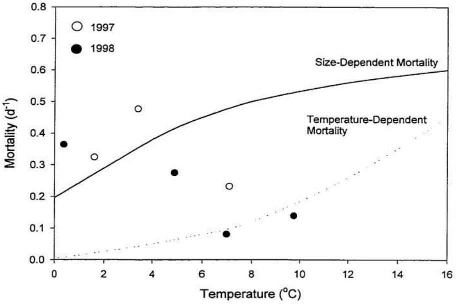

Figure 3.5. Estimated mortality from stage 1 to stage 4 and associated surface temperatures. Data is compared with relationships of mortality and temperature (Pepin 1991), and size-dependent mortality (Jaworski and Rijnsdorp 1989).

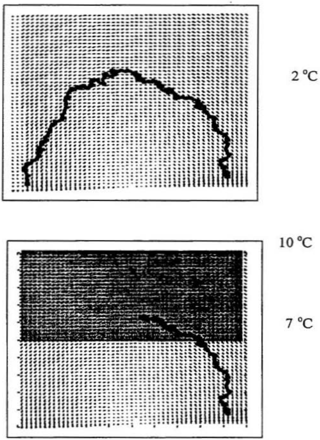

Figure 3.6. Simulated drift and development of cod eggs through a uniform (2°C) and non uniform temperature field (7 & 10°C) with a bay-like frozen circulation field.

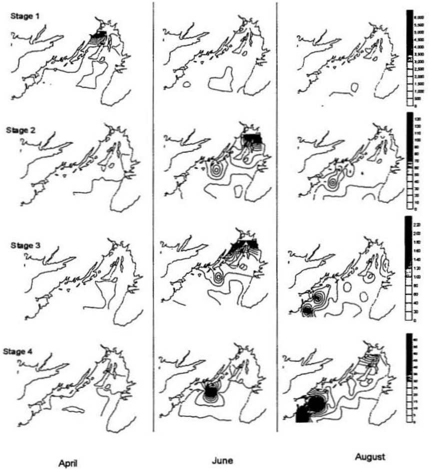

Figure 3.7. Distribution of stages 1-4 of cod eggs sampled during April, June, and August 1998 (# of individuals • $1000m^{-3}$).

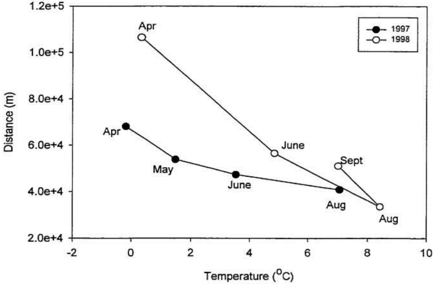

Figure 3.8. Distance between centers of mass for stages one to four with increases in temperature for 1997 and 1998

Summary and Conclusions

My review of the literature emphasises the importance of variables such as temperature and transport to egg and larval pattern. Moreover, it suggests that planktonic duration may be a critical factor in determining dispersal potential and the geographic range of a species. Despite a discontinuity between the studies of fish and invertebrate early life history, these fields appear to have much in common and may benefit greatly from a "cross-fertilisation" of ideas.

The influence of planktonic duration and environmental conditions on egg and larval pattern is evident in the distribution of Atlantic cod eggs and larvae from Placentia Bay. Variation in location and timing of spawning of Atlantic cod has a major impact on occurrence, distribution and development of eggs and larvae. Patterns in egg development stages and larval size suggest that development reflects circulation patterns, in that later egg stages and larger larvae were observed on the outer western side of the bay. Although spatial pattern in egg production was consistent during the two years of sampling, large temporal variability was observed. Higher egg densities in mid-summer of 1998 compared to 1997, suggest more eggs were released in warmer waters in 1998. Late releases in warmer waters likely resulted in faster development times and shorter dispersal distances and dramatic increases in larval densities in 1998 relative to 1997.

A simple simulation of egg development and mortality predicts increases in hatch rates and shorter dispersal distances with increases in water temperature. These predictions are supported by field data that indicate a decrease in loss rate (1998) and total distance travelled (1997, 1998) for egg development in warmer water. These simulations suggest that the density-dependent components of the loss term are small relative to the advective contribution within this system, and that the interaction between advection and temperature-dependent vital rates of eggs and larvae may have dramatic consequences for coastal retention of propagules from inshore spawning events. In terms of larval production, late spawners may be particularly important to successful egg hatching, in coastal Newfoundland.

Although the fate of eggs and larvae lost from the bay is not known, it is reasonable to hypothesize that they are effectively lost from the population. If so, the spawning success of these coastal populations of Atlantic cod may be directly influenced by the interaction of spawning time and environmental conditions. Although some evidence for distinct coastal populations of cod off Newfoundland exists, the extent and dynamics of propagule exchange between the offshore and inshore is unknown. This work suggests that during years when peak spawning is early, most of the eggs are transported out of the bay and offshore. Thus, depending on the survival of these eggs and larvae, early spawning events may result in elevated egg and larval densities and recruitment on offshore banks downstream of Placentia Bay. However, a large-scale examination of egg and larval distributions encompassing both inshore and possible offshore habitat is necessary to address this question. From a management perspective, the relative success of post-spring spawning in producing eggs that hatch within the bay suggests that targeting spring spawning may be particularly detrimental, and that early summer spawning should be allowed to occur without disturbance and adult mortality from fishing activity.