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Success and Failure of Atlantic cod, *Gadus morhua* : a case study from coastal Newfoundland

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Abstract

Despite a century of study, ecologists still struggle to understand fluctuations in marine populations, including many commercial species whose fisheries have collapsed despite considerable management effort (Hjort 1914, Sissenwine 1984). We present data on Northwest Atlantic cod that encompasses the adult spawning to juvenile settlement stage and demonstrate that timing of spawning is critical, particularly as it relates to spawning location and coastal circulation in regulating recruitment success. In what is presently the largest commercially-exploited Atlantic cod (*Gadus morhua*) stock remaining in the Northwest Atlantic, we found that spawning occurred at consistent, discrete locations that were generally favorable for propagule retention within the bay. However, when cod spawned relatively early in the year (April - May), colder water led to slower development, and currents swept most eggs offshore before hatch. Spawning later in the year (June-August) resulted in faster hatching, thereby reducing duration of early and vulnerable life stages and the probability of being swept offshore. Elevated densities of pelagic larvae and settled juveniles were associated with late spawning. Successful recruitment to the coastal region therefore requires spawning at sites where propagules are likely to retained, and at times when egg development rates are maximized. This 'right time, right place hypothesis' suggests that in tandem with more traditional variables such as spawner biomass and condition, timing and location of spawning may be important to spawning success in marine populations that live in highly seasonal environments.

Résumé

Même après un siècle de travaux, les écologistes éprouvent toujours des difficultés à comprendre les fluctuations des populations marines, notamment de plusieurs espèces commerciales dont les pêches se sont effondrées en dépit d'efforts de gestion considérables (Hjort, 1914; Sissenwine 1984). Nous présentons des données sur la morue de l'Atlantique nord-ouest dont l'étendue va du stade du frai des adultes à celui de la fixation des juvéniles et qui démontrent que le moment du frai est critique, notamment en ce qui a trait au lieu de frai et à la circulation côtière qui régit la réussite du recrutement. Nous avons trouvé, pour ce qui est actuellement le plus important stock de morue de l'Atlantique (*Gadus morhua*) exploité de façon commerciale encore présent dans l'Atlantique nord-ouest, que le frai se produit de façon répétée en des lieux bien précis qui sont généralement favorables à la rétention des premiers stades au sein de la baie. Lorsque les morues fraient relativement tôt (avril-mai), les eaux froides ralentissent le développement et les courants entraînent la plupart des œufs au large, avant leur éclosion. Un frai survenant plus tard (juin-août) permet une éclosion plus rapide et, par conséquent, réduit la durée pendant laquelle les individus en sont à un stade plus jeune et plus vulnérable, de même que la probabilité d'un entraînement vers le large. Les densités élevées de larves pélagiques et de juvéniles fixés étaient associées à un frai tardif. La réussite du recrutement dans la région côtière suppose donc que le frai ait lieu dans des endroits où les premiers stades devraient être retenus et à un moment où le taux de développement des œufs est maximal. Cette hypothèse « du bon moment au bon endroit » porte à croire que, de pair avec les variables plus traditionnelles, comme la biomasse et la condition des géniteurs, le moment et le lieu du frai peuvent être des facteurs importants de la réussite du frai chez les populations marines qui vivent dans les environnements où la variation saisonnière est importante.

Introduction

A common theme in theories linking early life history survival with recruitment variation in marine species is a strong dependence on physical processes (Frank and Leggett 1982; Lasker, 1975; Ellertsen et al. 1989; Sinclair 1988). Temporal variation in recruitment in species with planktonic eggs and larvae is thought to be dependent on loss of individuals from the population's distributional area, most often due to physical oceanographic processes (Sinclair 1988). This concept was developed for Atlantic cod by deYoung and Rose (1993), who described the recruitment implications of spatial variation in offshore cod spawning and the concomitant advection of propagules away from suitable nursery areas, in their 'right site' hypothesis. On Georges Bank, Page *et al*. (1999) demonstrate that cod and haddock spawning occurs at times and locations predicted to maximize retention and suggest the importance of this retention to population regulation and stability.

Cod in coastal Newfoundland, much like offshore populations (Hutchings and Myers, 1994), display considerable variation in timing and location of reproduction (Bradbury *et al*., submitted A; Lawson and Rose, 1999). Bradbury *et al*. (1999) hypothesize that retention limited by an interaction between advection and temperature-dependent development may be important to recruitment variation in coastal Newfoundland cod populations.

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 the these stocks, it is important to understand potential consequences of highly variable inshore environments on egg and larval survival and growth.

Methods

Our spatial and temporal description of Atlantic cod in Placentia Bay examines four distinct life history stages: adults, eggs, larvae, and demersal juveniles. Acoustic surveys for adults employed either a standard sphere-calibrated BioSonics single beam DT4000 or Simrad EK500 split-beam system (38 kHz; specifications in Lawson and Rose (1999) and Rose and Lawson (1999)). Cod aggregations located by the echosounders were sampled using handlines with feather hooks, to verify acoustic measurements and provide biological samples. Only cod were ever captured, and previous acoustic and submersible surveys in this area indicate that acoustically-similar species to cod (e.g., haddock, pollock) are rare (Rose and Lawson 1999; Lawson and Rose 1999). Survey measurements of acoustic backscatter were scaled to areal density (cod m^{-2}) using a target strength derived from the distribution of captured cod lengths, and employing the relationship: $TS_{(dB)} = 20 \log_{10} Length_{(cm)} - 66$ (at 38kHz; Rose and Porter 1996). Female gonad condition was categorized visually as either immature, ripening, spawning, or spent according to Morrison (1990), and the proportion of fish that were female, mature, and spawning was used to scale total cod density to spawning female density. Acoustic surveys were conducted throughout the pre-spawning and spawning period which occurred from April to July. For further details see Lawson and Rose (1999).

Planktonic eggs and larvae were sampled over a set grid of 45 stations and consisting of six transects (Fig. 1). Sampling was conducted using a $4m^2$ Tucker trawl with double oblique tows to 40m depth. Eggs were staged according to Markle and Frost (1985) and because densities of haddock and witch flounder eggs and larvae were always very small (<1%) all CHW eggs were assumed to be cod. Predictions of egg development time in relation to temperature were made using the relationships from Pepin (unpublished data) and are found in Bradbury et al. (submitted B). In addition to ichthyoplankton sampling, CTD profiles were made at each of these stations; during 1998 water samples were collected for Chl *a* measurements. Ichthyoplankton sampling was conducted throughout the spawning and post-spawning periods from April to August (1997) and September (1998). Coastal circulation was measured in the spring of 1998 with a pair of s4 current meters (B. deYoung unpublished data), moored at depths of 10m on opposite sides of the bay (47° 14.1' N, 54° 37.1' W; 47° 07.3' N, 54° 10.5' W) from April to mid-June (see Fig. 1). In addition, a passive drift experiment and a two-day ADCP (Acoustic Doppler Current Profiler) cruise of the bay were used to supplement mooring data (see Bradbury et al. (1999) for details and discussion).

Demersal juveniles were collected with a 25m bottom seine at 18 sites through out the bay from September to December of both 1997 and 1998 (see Fig. 1). Sites were chosen based on distribution around the bay, accessibility by small craft, and the presence of eelgrass habitat. The sampling protocol and seine are described in Lear et al. (1980) and Schnieder et al. (1997). Sampled cod were aged through standard lapillus otolith techniques (see Stevenson and Campana 1992) See Robichaud and Rose (1999) for further details.

Results

The oceanography of the bay is characterized by currents that flow into the bay on the east side and exit on the western side (see Fig. 2). Seasonal temperatures cycle dramatically from near -1.5°C (spring) to 15°C (summer) (see Fig. 3) and phytoplankton blooms occur early in spring and fall. At other times during the summer, elevated phytoplankton productivity is observed primarily in upwelling areas in the northern and western portions of the bay.

Spawning females in 1997 and 1998 were concentrated at three locations with in the bay, at Cape St. Mary's, Oderin Bank, and Bar Haven shoals (see Fig. 4). Early stage egg distribution were highest in the head of the bay and associated with the Bar Haven ground. Late stage eggs and planktonic larvae were predominately found in the head and western side of the bay ‘downstream’ of the spawning grounds. The distribution of egg and larval developmental stages suggests advection by predominant currents. Post-settlement juveniles were concentrated in the head of the bay and on the western side (72% in 1997 and 78% in 1998).

Within-year temporal trends differed substantially between years despite the overall similarity in spatial pattern (Fig. 5). In 1997, adult spawner and early stage egg densities peaked in April. Low densities of larvae and demersal juveniles observed in 1997 suggest a poor recruitment year. Despite a reduction in spawning magnitude and early life stage densities in 1998, a delay in peak spawning until June resulted in shorter egg and larval development times because the propagules experienced warmer water temperatures. Propagules were therefore more likely to develop to the juvenile stage and settle to the bottom before being swept from the bay, and late stage egg and larval densities were two orders of magnitude greater in 1998 than in 1997. In keeping with the early life stages, demersal juvenile densities were 5 times those in 1997. Because propagules that experienced relatively cold water were less likely to hatch within the bay, we rarely observed larvae or demersal juveniles that were spawned before June despite an abundance of pre-June spawning.

Transport distances and mortality estimates were calculated for the entire planktonic egg stage. Transport distances between the centers of mass for stage one to stage four generally decreased with temperature for both years (Fig. 6). 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/s, and is consistent with along bay currents (Fig. 2). Pattern in mortality rates was similar to that observed in transport distances (Fig. 7). In April 1997, no stage four eggs were sampled so an estimate of mortality from stage one 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. The initial increase in mortality rates during early spring 1997 coincides with a strong offshore wind event which was the only monthly mean offshore wind observed (Bradbury et al. submitted A). Mortality estimates contain both physical (advection) and biological (starvation and predation) components. Though we cannot say definitively what component of our measured rates are due to advection, a comparison with predictions of both the size-dependent and the temperature-dependent mortality relationships suggests the changes in abundance are due primarily to advection. Alternate explanations would necessitate high survivorship at low temperatures and low survivorship at high temperatures which is inconsistent with the observed pattern in the loss rates (see Fig. 7).

Summary

We thus track recruitment from adult spawning through to juvenile settlement; abundance of the latter is often a reasonable predictor of population abundance at older ages when cod recruit to the fishery (Sissenwine 1984). In our study, cod spawned at sites characterized by local retention and elevated productivity, but spawning events were not always well timed to maximize recruitment to the bay. Strong recruitment was observed only when spawning occurred in warm waters favoring shorter development times resulting in shorter dispersal distances and lower morality rates.

Temporal variation in recruitment in species with planktonic eggs and larvae is thought to depend on loss of individuals from the population's distributional area, most often due to physical oceanographic transport (Sinclair 1988). Our work develops on the 'right site ' hypothesis where recruitment is influenced by spatial variation in offshore cod spawning (deYoung and Rose 1993) extending it to include spawning timing. It is noteworthy that larval appearance in the year of strong recruitment was decoupled from phytoplankton production peaks which occurred in early spring, suggesting a match to the seasonal productivity cycle was not essential to strong recruitment.

The lack of predictive power of recruitment indices such as spawner biomass (Marshall et al. 1998) or egg production documented in previous studies (Marteinsdottir and Thorarinsson 1998) may be partially explained by the impact of spawning time on propagule survival. In the present work, one of the largest spawning biomasses ever recorded in coastal Newfoundland waters (i.e., 1997) failed to yield successful recruitment of juveniles to Placentia Bay. Hence, spawner biomass by itself was unable to predict recruitment success. For such northern seasonal environments, late spawning may be particularly important to local recruitment success in marine species that live in seasonal environments. Whether transport out of the bay impacts recruitment in other areas remains a topic for further study.

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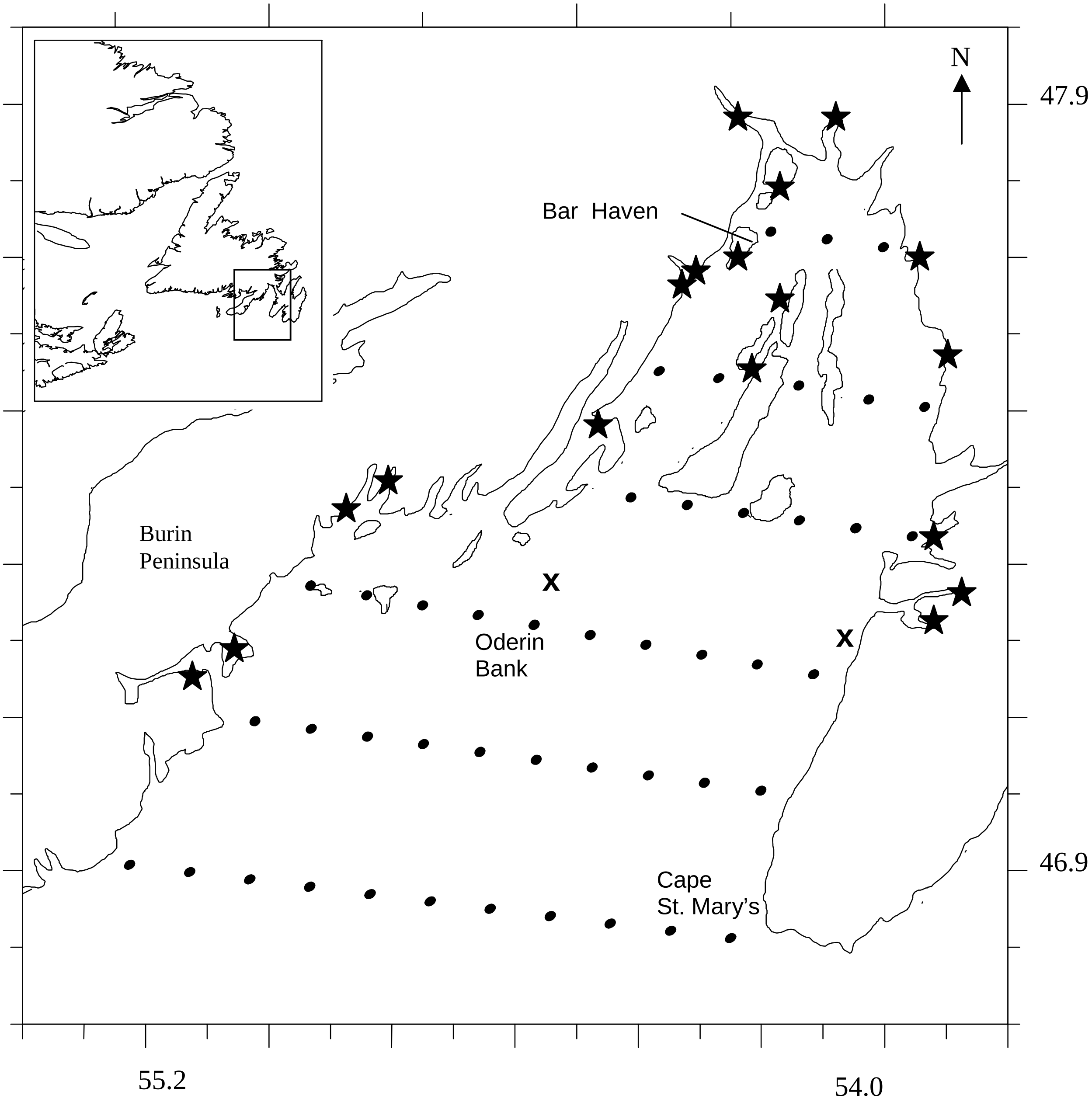

Figure 1. Chart of Placentia Bay; inset shows position of bay in relation to Newfoundland. Ichthyoplankton survey transects and stations indicated by dots; x's represent s4 mooring locations. Stars indicate juvenile survey sites. Adult survey transects correspond to these shown for ichthyoplankton except that additional transects were added halfway between those shown. Adaptive surveying for adults was done where spawning aggregations were identified.

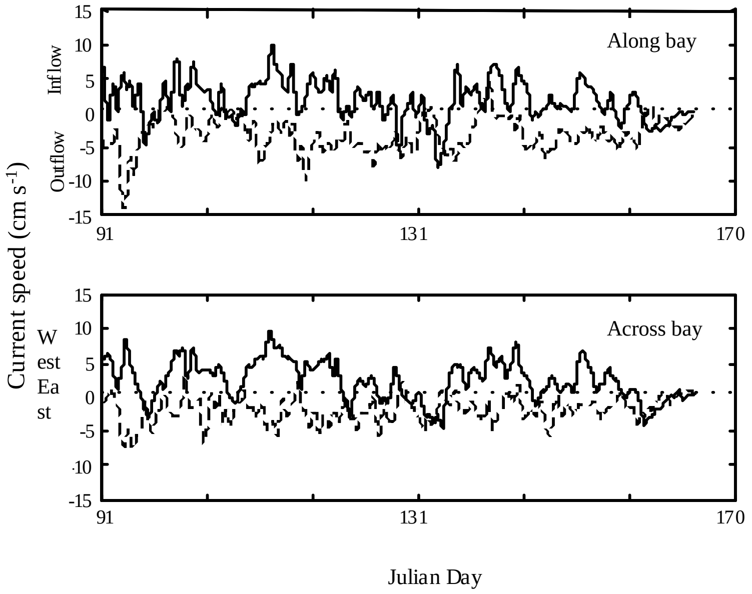

Figure 2. Along and across bay currents from the eastern (solid) and western (dashed) sides of the bay during the Spring 1998. All data lowpass filtered with a 8th order Butterworth filter and rotated to align with the bay.

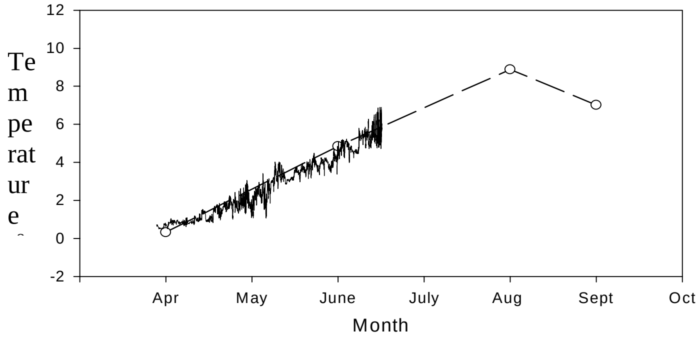

Figure 3. Average monthly temperatures measured for Placentia Bay from 0-40m and a temperature time series measured at 10m depth from the eastern of Placentia Bay during the Spring of 1998.

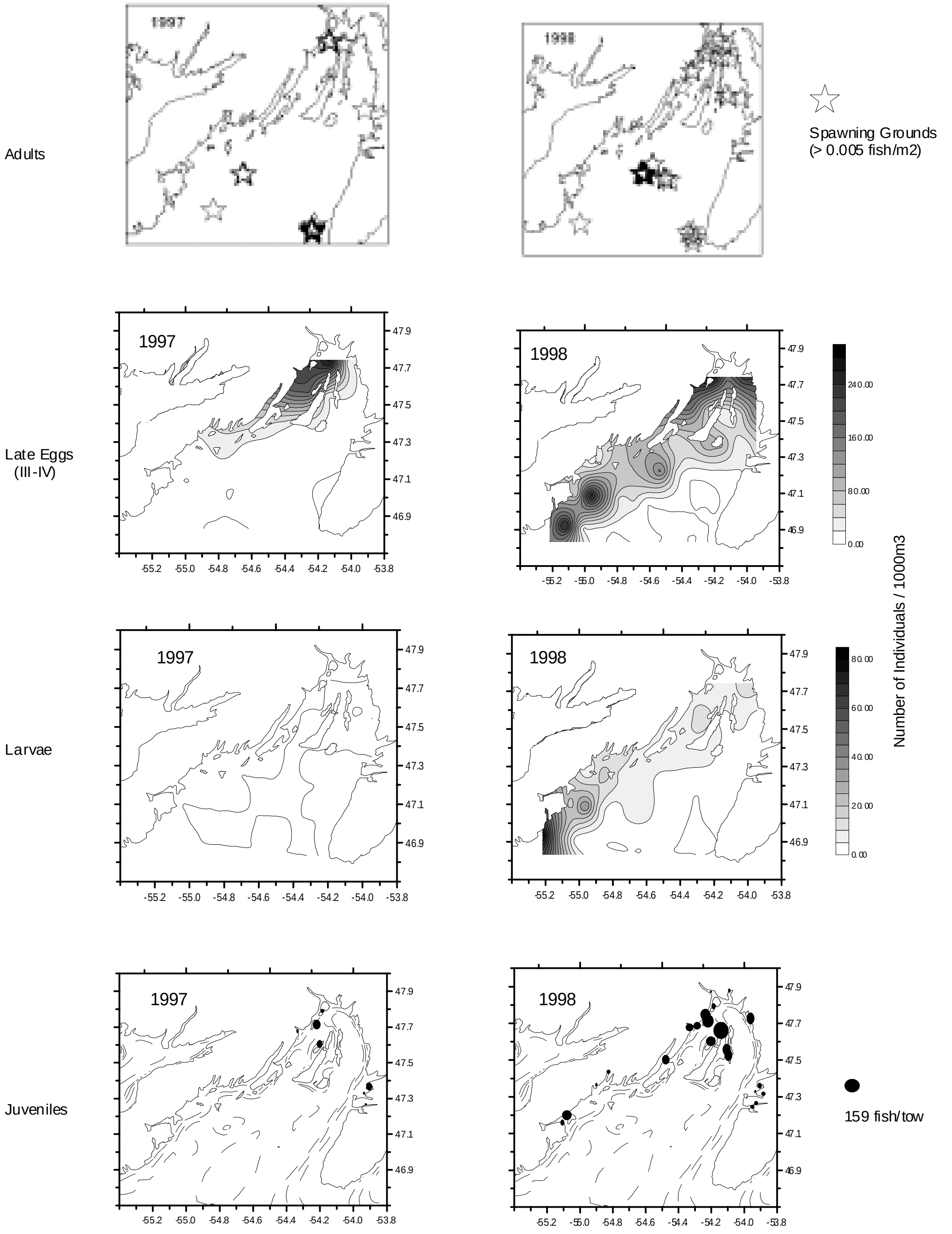

Figure 4. Spatial distribution of spawning females, late stage eggs (III-IV), larvae, and demersal juveniles for 1997 and 1998. Plots include all surveys with a given year.

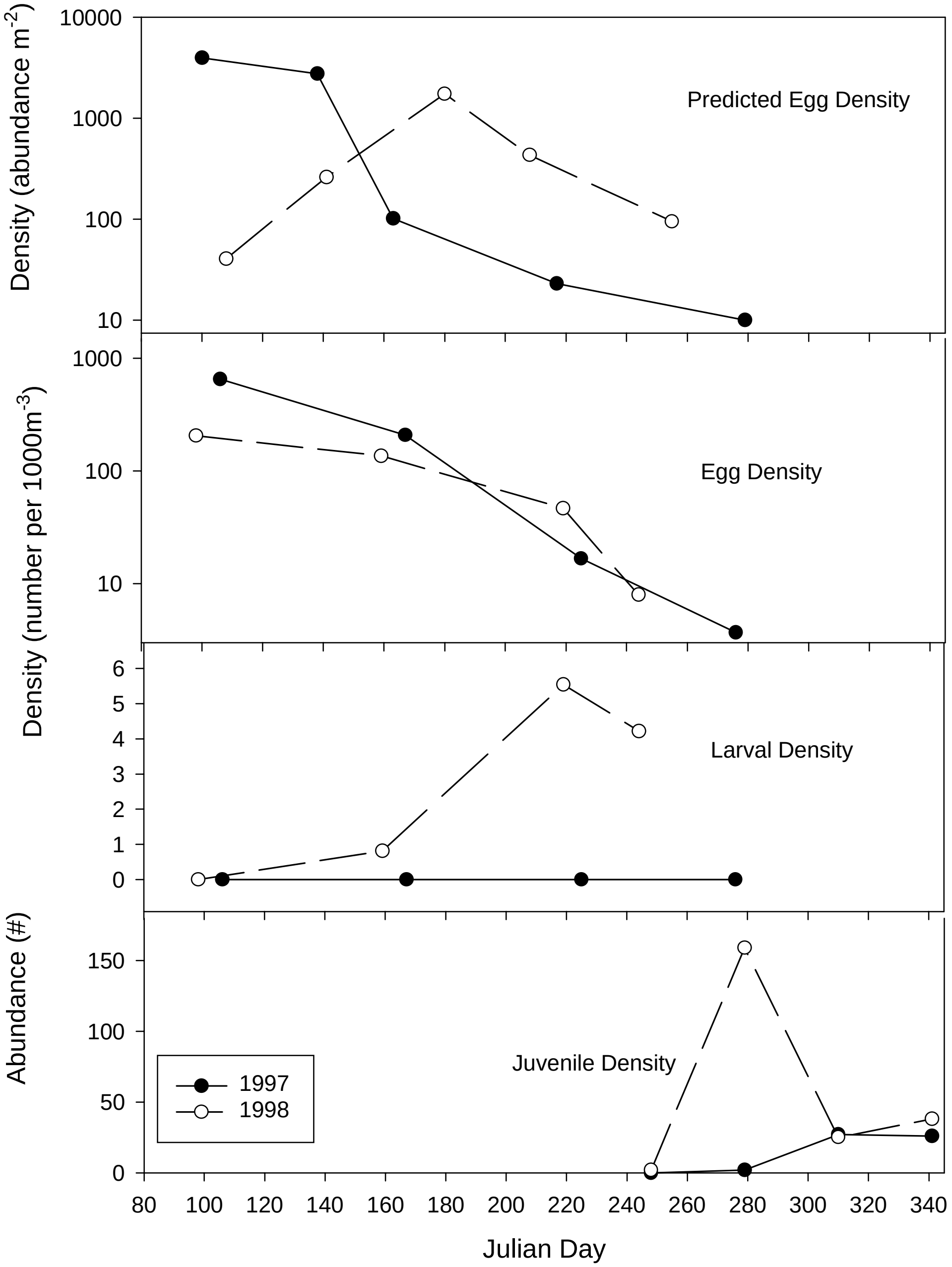

Figure 5. Temporal changes in density and abundance of Atlantic cod life history stages in Placentia Bay Newfoundland. Note log scales for adults and eggs.

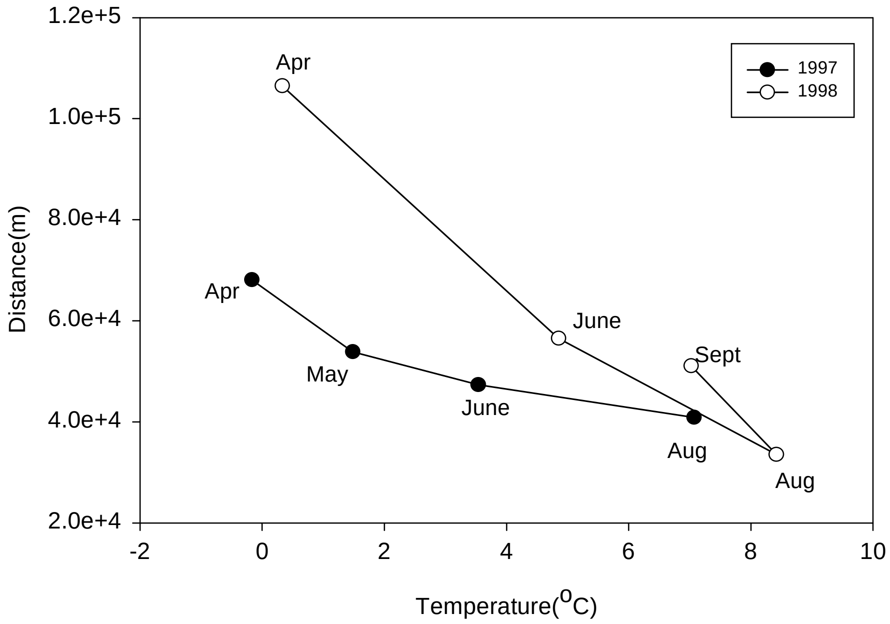

Figure 6. Distance between centers of mass for the egg stage with increases in temperature for 1997 and 1998.

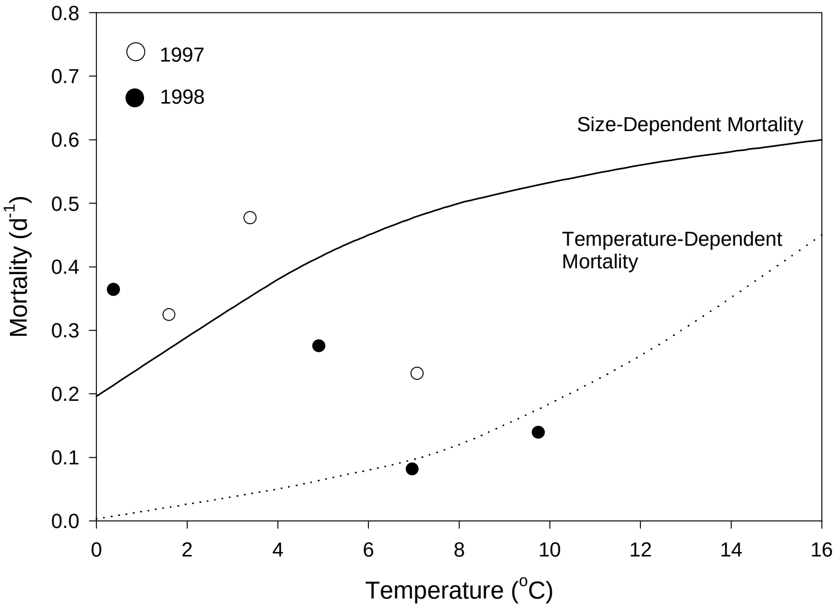

Figure 7. Estimated mortality from stage 1 to 4 and associated surface temperatures. Data is compared with relationships of mortality and temperature (Pepin 1991) and size-dependent mortality (Jaworski and Rjinsdorp 1989).