Life history dynamics and biogeography of a nudibranch with contrasting developmental modes: A hypothesis for the evolution of larval types

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Abstract
The biogeographical distribution of invertebrates with different life history traits has frequently been linked with surrounding ecological factors selecting for these characteristics. This study documents the distribution of congeneric nudibranchs with lecithotrophic and planktotrophic larvae in the Gulf of Maine. Representative coastal study sites in the north-east and south-west regions of the Gulf of Maine were monitored for seasonal abundance of two Dendronotus species and their thecate hydroid prey, and mean water temperatures. The different dispersal potentials of the larvae from the two incipient species of nudibranch may correlate with differences in seasonal resource availability of the north-east and south-west coastal regions of the Gulf of Maine, while seasonal water temperature variability may be an indirect indicator of the trophic stability of the region. Seasonal resource stability (i.e. hydroid abundance) is the most likely selective agent for the distribution of these two species and their different life history strategies.

Keywords: Dendronotus, dispersal, larval type

Introduction
Ecological patterns such as the distribution of organisms can help identify potential selective agents involved in the evolution of life history traits. For example, Thorson (1950) observed an increased proportion of certain benthic invertebrates that lack a planktonic larval stage (i.e. ecologically direct development) in polar seas. Conversely, he documented an increase in the percentage of these invertebrate groups with a long-term planktonic larval stage at lower latitudes. He hypothesized that this trend in the proportion of invertebrate species with direct development increased on a latitudinal gradient in both hemispheres, and correlated this distribution with differences in water temperature. According to Thorson (1950), invertebrate larval stages are more sensitive than adults to water temperature and therefore limit the distribution of adults along geographical temperature gradients.
Miliekevsky (1971) later expanded this hypothesis and referred to it as “Thorson’s rule”, suggesting that food availability may also be a selective agent influencing these larvae. Later researchers modified Thorson’s hypothesis by questioning the role of water temperature in directly selecting for benthic invertebrates with different life history traits (Clarke 1993) and by describing it as a group-specific trend rather than a “rule” (Pearse et al. 1991; Clarke 1992; Gallardo and Penchasadeh 2001).

Clark and Goetzfried (1978) modified Thorson’s rule by narrowing the focus to opisthobranch gastropods including Nudibranchia and Saccoglossa. They based their hypothesis on the relationship of trophic stability with developmental modes within the group. In this case, water temperature differences associated with latitudinal gradients are not a direct mechanism for selection of different developmental types, only a factor that co-varies with patterns of trophic stability. They found evidence for an increase in relative abundance of slugs that have either short-term planktonic larvae or no planktonic dispersal stage in areas with high trophic stability (i.e. a seasonally stable supply of prey). These geographical areas also had low seasonal ranges in water temperature, but were located at high and low latitudes. In between, at temperate areas with a high range of water temperatures and high variability of planktonic food resources, they found a higher percentage of slugs with long-term planktotrophic larvae. This hypothesis is a viable one because the majority of opisthobranchs are stenophagous, and because many have a high degree of variability in reproductive characteristics (Todd et al. 2001).

The Clark and Goetzfried (1978) hypothesis is based on a wide range of opisthobranch species and the developmental modes of many species across the Atlantic Ocean. More specific evolutionary processes involved with the divergence of life history characteristics can be identified by applying this hypothesis to a pair of closely related species with different larval types. Ideally, these species should be closely related, have recapitulative embryonic or larval development, and have overlapping distributions in similar habitats, including types of prey (Clark and Goetzfried 1978).

In the Gulf of Maine, two nudibranchs in the genus *Dendronotus* are potential subjects for testing this hypothesis. *Dendronotus frondosus* (Ascanius, 1774) has a wide distribution in north coastal waters, including the Gulf of Maine. Traditionally, *D. frondosus* has planktotrophic larvae (Williams 1971; Clark 1975; Sisson 2002a) and a reported seasonally variable abundance associated with hydroid colonies in the north-west Atlantic (Clark 1975; Lambert 1991). An ongoing re-evaluation of the taxonomy within this genus focuses on the description of an apparent sibling species to *D. frondosus*. This incipient species of *Dendronotus* has lecithotrophic larvae, and seasonally persistent adult populations in the northern Gulf of Maine (Sisson 2002a, 2002b; Aiken 2003). Despite morphological similarities of adults, the larvae from these two species of *Dendronotus* have significantly different planktonic dispersal potentials (Sisson 2002b, 2004). The aim of this study was to formulate a testable hypothesis to explain the evolution of different larval types within this genus.

Questions answered in this study aimed at establishing this hypothesis include:

1. What are the distributional limits of the two species of *Dendronotus* in shallow-water habitats in the western Gulf of Maine?
2. Is the abundance of hydroid prey variable in areas of this range, while relatively constant in other areas?
3. What are the seasonal abundance and spawning cycles of adults in this species complex relative to the abundance of their prey?
4. Do ranges of water temperature correlate either with the distribution of the two species or with the seasonal differences in prey abundance?

I monitored representative populations of these nudibranchs and their hydroid prey at the latitudinal extremes of the western Gulf of Maine and mapped the distribution of the two species across this gradient. Temperature ranges were also documented and interpreted in the context of more continuous geographical data.

**Materials and methods**

_Voucher specimens and species recognition_

This paper compares two species of *Dendronotus* from the Gulf of Maine. I will refer to *Dendronotus frondosus* from the traditional taxonomic description with planktotrophic larvae (see Robilliard 1970 for review). I will refer to the incipient sibling species (Sisson 2002b) as *Dendronotus* sp. throughout the paper. *Dendronotus* sp. produces lecithotrophic larvae (Sisson 2002a) and has distinctive morphological features of the radula and muscle layers. Voucher specimens of *Dendronotus* sp. from West Quoddy Head, Lubec, Maine, USA (Table I; Figure 1) were placed at the American Museum of Natural History, New York (AMNH 305753) and the Harvard University Museum of Comparative Zoology, Cambridge, Massachusetts (MCZ 330903–05). Voucher specimens of *Dendronotus frondosus* from York, Maine were also placed in these collections (AMNH 305757, MCZ 330906).

| Site          | Site name          | Latitude (N) | Longitude (W) | Species       | Larvae |
|---------------|--------------------|--------------|---------------|---------------|--------|
| 1             | Isles of Shoals (S)| 42.97        | 70.63         | *D. frondosus*| P      |
| 1             | Isles of Shoals (I)|              |               | *D. frondosus*| P      |
| 2             | York (S)           | 43.17        | 70.60         | *D. frondosus*| P      |
| 3             | Biddeford Pool (S)| 43.44        | 70.34         | *D. frondosus*| P      |
| 4             | Cliff Is. (S)      | 43.68        | 70.12         | *D. frondosus*| P      |
| 5             | Long Is. (S)       | 43.68        | 70.16         | *D. frondosus*| P      |
| 6             | Christmas Cove (S) | 43.84        | 69.55         | *D. frondosus*| P      |
| 7             | Horsehead Is. (S)  | 44.24        | 68.86         | *D. frondosus*| P      |
| 7             | Horsehead Is. (S)  |              |               | *Dendronotus* sp.| L     |
| 8             | Little Spruce Head Is. (S) | 44.23 | 68.86 | *D. frondosus* | P      |
| 8             | Little Spruce Head Is. (S) |              |               | *Dendronotus sp.| L     |
| 9             | Winter Harbor (S)  | 44.35        | 68.08         | *D. frondosus*| P      |
| 9             | Winter Harbor (S)  |              |               | *Dendronotus sp.| L     |
| 10            | Corea (S)          | 44.40        | 67.97         | *Dendronotus sp.| P      |
| 11            | Pembroke (S)       | 44.90        | 66.98         | *D. frondosus*| P      |
| 12            | West Quoddy Head (I)| 44.82 | 66.95 | *Dendronotus sp.| L     |
| 13            | Eastport (S)       | 44.90        | 66.98         | *D. frondosus*| P      |

Cartesian coordinates presented as decimals. Larvae were typed as either planktotrophic (P) or lecithotrophic (L) veligers based on their competence to metamorphose upon hatching. When larvae were not available, adults were identified by radula morphology and general external morphological features (Sisson 2002b).
Geographical distribution

I visited sites on the Maine coastline between July 1999 and July 2001 to search for the two species of *Dendronotus* in shallow subtidal waters. The majority of dives were made during the summer months (June, July) to maximize the likelihood of individuals being present. At each site I used scuba to search for the nudibranchs and their spawn masses at 5–20 m depth among thecate hydroid colonies in cobble and bedrock benthic communities. A minimum search time of 30 min was conducted at each site once a cluster of hydroid colonies was found.

Adult nudibranchs and spawn masses that could be directly associated with an individual or group of *Dendronotus* were collected at each site. The live adults and spawn masses were then observed for general morphological characteristics. If adults were found with no spawn masses associated with them, individuals were collected as live samples. These adults were maintained in the laboratory at 10°C in seawater on a diet of *Obelia geniculata* (L.) for 1–20 weeks until they spawned. Spawn masses were isolated and gently aerated until veligers began to hatch from the egg capsule and spawn matrix. At that time the veligers were measured and identified as either planktotrophic or lecithotrophic according to morphological features indicating metamorphic competence (Sisson 2002a).

Seasonal abundance of predator and prey

Sites in northern and southern Gulf of Maine were chosen for monitoring the seasonal abundance of the two *Dendronotus* species and their hydroid prey. In the northern Gulf of
Maine, a subtidal site in Eastport, Maine, and a nearby intertidal site at West Quoddy Head in Lubec, Maine were chosen for monitoring once every two calendar months. In the southern Gulf of Maine a site at Cape Neddick in York, Maine was selected for monthly observation (see Figure 1 and Table I for coordinates).

At each site, an approximately vertical wall was identified by topographic features of the bedrock as a permanent quadrat for sampling. The area of each wall was measured to the nearest 0.1 m² for calculation of abundance data. Sampling at each site included measurements of hydroid percentage cover and the total number of nudibranchs and their spawn masses. Due to the nature of the two habitats, different sampling techniques were used for intertidal and subtidal sites.

I sampled subtidal sites using scuba, and collected data from each time period either in a single dive or in a subsequent dive on the same day. Both subtidal sites had seasonally abundant thecate and athecate hydroid colonies on bedrock and algal surfaces. The wall at York had a total surface area of 18.4 m² and a lower depth of 7 m below mean low water (MLW). The wall had little algal growth, and a seasonally high colonial tunicate abundance. It is located on the inside of a north-east-facing cove, and is part of a rocky ledge with a cobble slope at the base leading down to a large subtidal sand flat. There is considerable wave action, especially with weather from the north-east.

The wall at Eastport had a surface area of 23.8 m² and a lower depth of 10 m below MLW. The kelp *Agarum cribrosum* frequently grew with the hydroid *O. geniculata* as an epiphyte. The site is exposed to high water currents in a channel connected to the mouth of the Bay of Fundy, but has very little wave action. Below the wall, a gradual sandy slope descends to a deep channel (30+ m) (also see Harris and Chester 1996 for site description).

During each dive, I measured hydroid abundance by counting the number of colonies of thecate hydroids on the wall and recording a representative diameter of each colony. These hydroids tend to grow in patches on the wall, so the representative diameter was measured on a horizontal line across the widest part of each colony to the nearest 0.01 m. The fronds of kelp were also sampled for hydroid cover, and the maximum length and width of each frond with hydroids on it was also recorded. The surface area of kelp was estimated (length × width) and added to the total surface area of wall sampled for that date. Total hydroid surface area was estimated by assuming each colony was a circle, using the measured diameter. The total surface area of hydroid colonies covering the subtidal wall was calculated for each period sampled and presented as a percentage of the total area of wall at each site.

The total number of *Dendronotus* individuals within the search area at each wall was tallied for each sample period to calculate a sample abundance of slugs per m². When present, the number of spawn masses was also recorded. *Dendronotus* species have a characteristic Type B (Hurst 1967) spawn mass that made this identification possible. A subsample of 5–10 spawn masses was collected and later identified as either producing planktotrophic or lecithotrophic veligers by morphological features indicating metamorphic competence (Sisson 2002a).

Two intertidal walls were sampled at West Quoddy Head approximately midway through the littoral zone, in dense beds of the brown alga *Ascophyllum nodosum* (L.). Both walls are approximately vertical, facing perpendicular to a north-north-west heading with overhanging fronds of *A. nodosum*. The walls were 3.9 and 2.9 m² at approximately 4 m above MLW, and faced away from the prevailing direction of oncoming waves. Both walls were sampled for the number of *Dendronotus* individuals and their spawn masses in order to get
an estimate of seasonal variability of the population at this site, although I only sampled one wall for hydroid abundance.

Hydroid abundance was quantified by separate methods. First, 10 quadrats (0.25 m$^2$) with 25 equally spaced points were randomly placed along the length of the wall to estimate the percentage cover of hydroid (Obelia sp. or Sertularia pumila (L.)) and of A. nodosum. Algal fronds hanging over the wall from outside of the sample area were moved aside, and the quadrant was placed over the remaining A. nodosum and hydroids. The number of points with A. nodosum was counted, followed by the number of points with either Obelia sp. or S. pumila. The hydroids were both epiphytic and epilithic, so some points were counted as containing both the alga and hydroid. Within each quadrant, the overall lengths of 10 individual fronds of A. nodosum were measured, together with the length of the frond that had S. pumila growing on it ($\pm$ 1 cm). S. pumila grows from the base of the alga, so this was then expressed as a percentage of the total length of algae covered by hydroid.

**Water temperature**

Data loggers (HOBO Temp, Onset Computer Corporation) were placed at the base of the walls at Eastport and York to monitor water temperature ($\pm$ 0.7°C) for approximately 12 months beginning in August 2000. Monthly exchanges of the devices in York and bimonthly exchanges in Eastport allowed for continuous recording of temperature data at 12- and 16-min intervals, respectively. These data were used to calculate weekly mean temperatures at each site.

**Results**

**Geographical distribution**

Dendronotus frondosus were collected from contiguous subtidal sites between the Isles of Shoals, New Hampshire through Eastport, Maine. Dendronotus sp. (lecithotrophic larval spawners) were collected sporadically from Eastport south through the Penobscot Bay area (Figure 1; Table I). No Dendronotus sp. individuals were seen or collected south of the Penobscot Bay area, nor were any slugs or spawn masses collected that matched their physical appearance or lecithotrophic larval type. In two instances larval type could not be established and differences were determined in adults according to established characters of body musculature, radula morphology and ceras morphology (Figure 1; Table I).

During one dive at Horsehead Island in eastern Penobscot Bay, I found specimens of both species of Dendronotus in shallow water (8 m) within 50 m of each other and associated with substantial colonies of Obelia geniculata. Dendronotus frondosus observed at this site (29 individuals) were associated with at least seven spawn masses attached to the hydroid colonies. These spawn masses contained developing veligers that later hatched as planktotrophic larvae. At least three individuals of this species collected on this dive later deposited spawn masses in the laboratory that also yielded planktotrophic veligers. Dendronotus sp. collected on this dive were robust, purple slugs that were not actively depositing spawn masses in the field. Three individuals collected at this site were maintained for 4 months until they began depositing spawn masses. Embryos in these spawn masses developed for several weeks before hatching as metamorphically competent lecithotrophic veligers.
The dominant hydroids at the subtidal site monitored at York were *O. geniculata* and *Tubularia larynx* (Ellis and Solander, 1786). *Obelia geniculata* was seasonally abundant in January through June, with a peak in abundance in April of 2000 and 2001 (Figure 2a). Later in the summer and early fall, *Eudendrium* spp. were common along the same wall, but *D. frondosus* was not associated with this hydroid. Only *D. frondosus* was found at this site and in adjacent deeper waters (to 20 m). *Dendronotus frondosus* peaked in abundance during April and May in 2000 (Figure 2a), with a smaller peak in 2001 from February through May. *Dendronotus frondosus* spawn masses were present from April through June with the highest peaks in May 2000 and April 2001 (Figure 3a). The presence of spawn masses usually coincided with the presence of adults; however, adults were found in January through March 2001 without any sign of spawn masses.

At the Eastport site, *O. geniculata* was commonest on fronds of *Agarum cribrosum* and the stalked tunicate *Boltenia ovifera* (L.). Other thecate hydroids (e.g. *Abietinaria* spp., *Campanularia* spp.) were present in lower abundance, except for *Tubularia indivisa* (L.) and *T. larynx* which were common year round in small colonies. Thcate hydroids were present in all of the months sampled between May 2000 through July 2001, with a peak abundance in July 2000 (Figure 2b). Although I had collected *Dendronotus* sp. with lecithotrophic larvae at this site previously, I only found *D. frondosus* during this study. *Dendronotus frondosus* at this site were generally larger (up to approximately 7 cm) than those at York, especially in the spring and early summer. The highest abundance of this nudibranch was in July (Figure 2b), and spawn masses were present in May through September (Figure 3b). The highest abundance of spawn masses was in July (Figure 3b).

At the intertidal site at West Quoddy Head only a couple of very small *Obelia* sp. colonies were found during the period of study. The habitat was essentially a monoculture of *S. pumila* on algae and bedrock that remained relatively constant in abundance throughout the year (Figure 2c). This was documented by three different sampling methods, including the percentage cover data presented in Figure 2c. The mean proportion (in length) of *S. pumila* colonies at the base of *A. nodosum* fronds varied from 11% (±6% SD) in July 2001 to 27% (±9%) in November 2000. The mean number of *A. nodosum* fronds (out of a sample of 10) with hydroids epiphytes ranged from 3 (±1) in July 2001 to 6 (±1) in September 2000. All three measurements demonstrate a seasonally constant supply of the hydroid *S. pumila* as a prey resource. *Dendronotus* sp. with lecithotrophic larvae was the only species found and was present throughout the year, but in highest numbers in September through November (Figure 2c). I commonly observed the bryozoan-feeding dorid nudibranch *Acanthodoris pilosa* (Abildgaard, 1789) in the same habitat, and rarely the anemone-feeding aeolid *Aeolidia papillosa* (L.). *Dendronotus* sp. spawned at both areas in May through July, although it peaked in July (Figure 3c). In the following sampling period in September, no spawn masses were found, although very small juveniles (0.25–2 cm) were abundant. The largest animals were found in May (2–2.5 cm), just prior to spawning.

During the collection of *Dendronotus* in the Gulf of Maine, aside from these three permanent sites, several observations were made relating to nudibranch abundance and their hydroid prey. For example, in June 2000 I sampled a shallow-water site at Cliff Island in Casco Bay (Figure 1) and found two *D. frondosus* adults across a 3 m line transect at 5 m depth with 10–20% cover of *O. geniculata* on the surface of the kelps *Laminaria saccharina* (L.) and *Agarum cribrosum*. Several more individuals were found later in the dive with similar hydroid cover. I marked the site, and returned 6 weeks later to observe hydroid and *D. frondosus* abundance. Upon return, no *D. frondosus* were found during 40 min search.
Figure 2. Seasonal abundance of *Dendronotus* spp. (in number of slugs per m$^2$) and their thecate hydroid prey (in percentage cover). (a) The shallow subtidal site at York, Maine collected every calendar month. (b) The subtidal site at Eastport, Maine and (c) the intertidal site at West Quoddy Head in Lubec, Maine collected every two calendar months. Hydroid abundance data were sampled using point coordinates and averaged for 10 samples per sampling area ($\pm$ SD).
time, and only sparse small colonies of *O. geniculata* remained. Instead, the introduced bryozoan *Membranipora membranacea* (L.) had a 100% occurrence on blades of *L. saccharina* and *A. cribosum*, with an estimated 50–80% cover.

Figure 3. Abundance of spawn masses deposited by *Dendronotus* spp. at: (a) York, Maine, (b) Eastport, Maine and (c) the intertidal site at West Quoddy Head, Lubec, Maine.
Water temperature was highly variable in May through September at York, Maine (Figure 4). Destratification events regularly occurred at this site, resulting in minimum temperatures as low as 7.0°C in the middle of July. Water temperatures at Eastport, Maine were less variable during the summer and early fall, but there were similar stable temperatures during the winter months (Figure 4). Maximum temperatures never rose

Figure 4. Weekly mean (± SD), minimum and maximum water temperature (in ºC) at the subtidal sampling sites in York and Eastport, Maine.

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above 15°C in Eastport, while at York they regularly rose above this mark in the summer and early fall (Figure 4). Minimum temperatures for the year occurred during the same week of March at both sites (York 1.2°C; Eastport 0.73°C).

Discussion

*Dendronotus frondosus* with planktotrophic larvae has a continuous distribution in shallow coastal waters in the western Gulf of Maine (Figure 1) with a southern limit in southern New England (Clark 1975) and New Jersey (Loveland et al. 1969). *Dendronotus* sp. with lecithotrophic larvae was only found in areas north of the Penobscot Bay region (Figure 1), with sympatric populations of the two species at Penobscot Bay and Winter Harbor (Table I). The two species at Winter Harbor were identified by external morphology only (not by larval type or radula). However, this suggests a southern limit for *Dendronotus* sp. in coastal waters in the region of Penobscot Bay. Because of earlier taxonomic confusion, it is unclear what the northern geographical limits are in the western Atlantic for these two species. However, *D. frondosus sensu lato* has been reported north to Greenland in the Western Atlantic (Just and Edmunds 1985). There are also reports of *D. frondosus* associated with the hydroid *Sertularia pumila* on intertidal rockweed beds through Nova Scotia and Cape Breton Island (Meyer 1971) and southern New Brunswick (Gionet and Aiken 1992; Aiken 2003). This habitat may indicate that at least some of the nudibranchs Meyer (1971) collected were actually the *Dendronotus* sp. described in this study, which would extend its reported range northward. Aiken (2003) also describes a seasonal abundance and spawning cycle similar to that of *Dendronotus* sp. with lecithotrophic larvae in this study.

Accompanying the geographical distribution of adults, there are also differences in the larval dispersal potential for these two species. Although drifting may occur occasionally for adults that are dislodged from their benthic habitats, immigration of adults into thecate hydroid colonies such as those in this study generally does not affect nudibranch population size (Lambert 1991). Planktonic larvae remain the major dispersal phase for most nudibranchs, including *Dendronotus* species. Laboratory studies have shown that planktotrophic *D. frondosus* larvae have the potential for at least 11 weeks in the water column (Sisson 2005), while lecithotrophic larvae from some populations of *Dendronotus* sp. can only remain in the plankton for 1 week before metamorphosing (Sisson 2002b). Although different populations may have different realized larval periods, these two species have potentially distinct planktonic larval dispersal (Figure 5).

These differences in ecological larval characteristics considered in the context of the geographical distribution of the two *Dendronotus* species in the Gulf of Maine suggest correlative environmental factors. Surrounding environmental conditions across this distribution represent potential selective agents in the evolution of these two life history strategies. I will discuss four groups of environmental factors that are most likely involved with the selection of the two life history strategies (although more possibilities exist): prevailing oceanographic currents, water temperature and hydroid prey resource abundance.

Simple circulation patterns in the Gulf of Maine could also result in these range limitations by affecting larval dispersal patterns (Gaylord and Gaines 2000). Near the Penobscot Bay region there is a slight offshore water current that sets up an eddy southwest of the bay (Brooks and Townsend 1989). However, using the model proposed by Gaylord and Gaines (2000), this eddy would be a predicted restriction to the northward expansion of a species in this area and would not restrict settlement in a southward
direction. Even larvae with a potentially short planktonic phase such as *Dendronotus* sp. lecithotrophs (Figure 5) can overcome currents of this magnitude and settle in new areas (Scheltema 1989). Therefore, the transport of *Dendronotus* sp. from northern populations either as adults or lecithotrophic larvae to coastal locations south of Penobscot Bay is possible, if not likely, given these conditions.

The easiest trend to identify is the difference in water temperatures north and south of the Penobscot Bay region. To the north, water temperatures are less seasonally variable, and generally colder than those found further south, due to less seasonal stratification of the water column (Apollonio and Mann 1995; Yoder et al. 2002). This trend is supported by the water temperature data collected at Eastport and York, Maine (Figure 4). This pattern appears to support Thorson’s (1950) hypothesis of colder waters selecting for benthic invertebrates with shorter planktonic larval dispersal. However, it is unlikely that temperature has a direct effect on the survivorship of *Dendronotus* adults or larvae. *Dendronotus frondosus* is found throughout both temperature regimes and is reproductively active. Both species of *Dendronotus* are found associated with intertidal rockweed communities where they are exposed to both high and low air temperatures that are considerably more extreme than water temperatures in the subtidal benthic environment. *Dendronotus* sp. is particularly successful in this habitat, occurring both in mid-summer and mid-winter (Figure 2c; Aiken 2003), and has exhibited freeze-tolerant characteristics (Gionet and Aiken 1992). This suggests a high tolerance of adult *Dendronotus* species to thermal stress, and that temperature does not directly limit their distribution.

The preferred prey species for both species of *Dendronotus, Obelia geniculata*, (Sisson 2002a) may also be affected by seasonal temperature fluctuations. Laboratory experiments indicate that temperature does not have a direct effect on the survivorship of this thecate hydroid, although it does have significantly different growth forms at 5, 10 and 15°C (C. G. Sisson, in preparation). For most suspension-feeding hydroids, temperature has a minor role in determining seasonal fluctuations in abundance, with food availability having a more significant influence (Coma et al. 2000). Populations of *O. geniculata* and other thecate hydroids may be seasonal (Figure 2) because of local adaptations to temperature regimes, differences in predation pressures (i.e. by nudibranchs) or differences in planktonic productivity in the two geographical extremes of the Gulf of Maine. The low range of

![Figure 5. Summary of the larval dispersal potential of *Dendronotus frondosus* and *Dendronotus* sp. in laboratory cultures at 10°C (Sisson 2002b, 2004). The “egg-to-juvenile” period lasts from spawn deposition through larval settlement and metamorphosis.](image)
temperatures north-east of Penobscot Bay directly correlates with higher nutrient levels and primary productivity (Apollonio and Mann 1995; Yoder et al. 2002) which may directly impact planktonic food availability for these suspension-feeders (Coma et al. 2000). The seasonal persistence of benthic hydroids in the north-eastern Gulf of Maine (Figure 2) may therefore be a result of consistently high abundance of planktonic food.

The data in this study on the abundance of nudibranch predators and their hydroid prey establish the potential for stable prey resources in the north and unstable resources in southern Gulf of Maine. At the York site, high abundance of thecate hydroids coincides with high *D. frondosus* abundance (Figure 2a) and is followed by the production of spawn masses (Figure 3a). Hydroid abundance at this site is seasonally ephemeral, with nudibranch abundance quickly declining after the loss of ample prey resources (Figure 2a). This seasonal pattern was also found by Lambert (1991) at an adjacent subtidal site. A similar decline in prey resources and consequently *D. frondosus* abundance observed in Casco Bay, Maine suggests a general trend for coastal waters south of Penobscot Bay.

Areas north-east of Penobscot Bay showed a trend of seasonally stable hydroid abundance allowing for the persistence of *Dendronotus* populations. The hydroid abundance at Eastport had a similar seasonal pattern as York, although thecate hydroid populations and a low number of *D. frondosus* survived in low abundance throughout the year (Figure 2b). Spawn masses were found during the summer months when both hydroid and nudibranch abundance were the highest (Figure 3b). West Quoddy Head had no measurable seasonal fluctuation in hydroid abundance (Figure 2c). The highest number of *Dendronotus* sp. were found in September (Figure 2c), directly following the summer spawning period (Figure 3c). These were also the smallest individuals found at this site, suggesting that they were new recruits to the area. Conversely, the lowest number of nudibranchs was found during the period of spawning in the summer. A measurement of total biomass may have been more indicative of reproductive potential of the population for *Dendronotus* sp. (Todd and Doyle 1981), while *D. frondosus* shows a distinctly different trend with highest numbers of adults concurrent with spawning periods.

Research with other opisthobranchs suggests that geographical patchiness and temporal persistence of prey selects for larval stages with reduced dispersal potential, such as lecithotrophy (Goddard 1996) or capsular development (Miles and Clark 2002). This study suggests that suitable habitats for *Dendronotus* spp. are separated by several months in a seasonally unstable environment south of Penobscot Bay. These geographical and temporal barriers may be bridged by the relatively long planktonic period of *D. frondosus* (Figure 5; Sisson 2004) resulting in the colonization of new hydroid communities. Data from the two sites in the northern Gulf of Maine indicate a seasonally constant abundance of hydroid prey (Figure 2), allowing *Dendronotus* sp. to persist despite minimal larval dispersal (Figure 5; Sisson 2002b).

Clark and Goetzfried (1978) hypothesize that these differences in prey abundance might result in the selection of species with different larval types. In this model, shorter planktonic larval periods (e.g. lecithotrophy versus planktotrophy or direct development versus lecithotrophy) are selected for when food resources are abundant and constant. They predicted that the increased availability of food for adults increases reproductive output in the form of larger eggs. These eggs have a longer capsular period, corresponding with a shorter planktonic phase after hatching. This allows for a continued exploitation of the resource and a shorter egg-to-juvenile period, thus resulting in increased fitness for the organism. Other models (Todd and Doyle 1981; Havenhand 1993) have shown that a
decrease in the “egg-to-juvenile” (premetamorphic) period can enhance adult fitness by selecting for larger adults with a higher reproductive potential.

In some areas north of Penobscot Bay, such as at Eastport, seasonally abundant food resources are available to *D. frondosus*. The next step for testing Clark and Goetzfried’s model (1978) would be to show variability of egg size and an increase in egg size among populations that are longer lived on a constant food supply, possibly resulting in larvae with a shorter planktonic period. Preliminary results indicate that planktotrophic larvae with a more developed larval gut hatch from spawn masses deposited by larger *D. frondosus* individuals collected in Eastport, potentially resulting in an abbreviated planktonic development.

Nudibranchs in the genus *Dendronotus* often have contrasting developmental characteristics. *Dendronotus frondosus* has a reported circum-boreal distribution and common occurrence in a variety of hydroid communities (Robilliard 1970), which may provide a unique system for life history comparisons such as this study. Natural history data on this species complex in the Gulf of Maine have generated a hypothesis for the relative importance of selective agents in determining their biogeographical distribution and factors potentially involved with their evolutionary divergence, especially larval characteristics.

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