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The Dynamics of a Tephritid Seed Predator on *Tripolium vulgare* in a Stochastic and Heterogeneous Environment

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Abstract

In this thesis the factors regulating the interaction between the seed predatory fly *Paroxyna plantaginis* (Diptera: Tephritidae) and its host plant *Tripolium vulgare*, (former *Aster tripolium*, Asteraceae) are determined and evaluated. The host is patchily distributed on islands in the study area (the archipelago of Skeppsvik 63°44-48' N, 20°34-40'E) in northern Sweden. Possible factors that may cause the persistence of this system include direct density-dependent feedback processes, temporal and spatial heterogeneity, and the effect of stochasticity (chance). The impact of these forces is analysed through both pattern and process approaches, concentrating on the spatial and temporal distribution of the resource and the timing and dispersal of the fly, as well as the influence of stochasticity.

Relating attack frequencies to host density showed no strong indication of tight regulation between the specialist seed predator and its host plant (Paper I). Smaller plants and subpopulations were subject to the highest variation in attack frequency, suggesting that there is a strong element of chance influencing the risk of attack. There were, however, indications of a spatial effect at low fly densities, which seemed to break down at higher densities, implying that dispersal behaviour and strength may be related to adult fly density. The fragmented resource is more evenly used at higher attack frequencies (Paper II): an effect which may be coupled directly to fly densities (Paper III). A mismatch between the phenology of the fly and the sea aster flowering phenology seems to benefit the first flowering flower heads, which are less often attacked in a normal year (Paper III). However, it was experimentally shown that the flies compensate for the temporal and spatial unpredictability by a female-biased density-dependent dispersal (Paper IV). Density-independent water-borne dispersal during the puparia stage may also affect the dynamics of the tephritid (Paper V).

This system is an example of a highly persistent interaction, for which stochastic and spatial effects are of major importance. The density-dependent dispersal of females may act within generations in the spatially heterogeneous environment and this may be transformed from a local response to a mode of regulation that works between generations.

Key words: plant-animal interactions, population dynamics, regulation, density-dependence, stochasticity, temporal and spatial refuges, plant defence, dispersal, optimal patch use.

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Appendix

Papers I-V

This thesis is based on the following papers, which will be referred to by the corresponding Roman numerals in the text.

- I. Albrechtsen, B. R. & P. Lundberg. **Scale-dependent attack frequency of a specialist tephritid fly.** *Manuscript.*
- II. Sjöberg, M.; B. Albrechtsen, & J. Hjältén. 2000. **Truncated power laws: a tool for understanding aggregation patterns in animals?** *Ecology Letters* 3: (90-94).
- III. Albrechtsen, B. R. 2000. **Seed predation by a tephritid fly and flowering phenology. Escape through time and space.** *Ecoscience in press.*
- IV. Albrechtsen, B. R. & G. Nachman. **Female-biased density-dependent dispersal of a tephritid fly inhabiting a fragmented habitat and its implications for population regulation.** *Oikos in press.*
- V. Albrechtsen, B. R. **Asymmetry in water-borne dispersal of a tephritid and its parasitoids.** *Manuscript.*

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1. Introduction

Natural populations fluctuate in time and space due to a range of factors including: their internal dynamics, interactions with other species and variations in the surrounding environment. There is both applied and theoretical interest in population fluctuations, because knowledge of them brings us closer to an understanding of phenomena like outbreak, persistence, diversity, and extinction of species (Varley et al., 1973; Pimm, 1991; Fryxell & Lundberg, 1997; Tilman & Kareiva, 1997 and others). To understand population fluctuations it is necessary to consider the nature and strength of both inter- and intra- specific demographic processes as well as the effect of environmental variability (Lundberg et al., in press). In order to describe complex phenomena, it is often necessary to adopt a simplified approach, or to identify a relatively simple system. Specialised herbivores or parasitoids and their hosts are therefore excellent examples of systems, that may serve as suitable model system (for example Hassell & Wilson, 1997). One major challenge in population dynamics is to link the unstable dynamics that characterise closed systems to the dynamics of persistence, which is characteristic of natural open systems and spatially complex systems (Fryxell & Lundberg, 1997). The classic explanation for regulation of populations involves a range of factors, such as predator-prey dynamics with optimal patch use and prey switching, inbuilt temporal or spatial lags in coevolved or competing species, spatial regulation or non-equilibrium dynamics, and stochastic events (Begon & Mortimer, 1986)

This thesis focuses on the dynamics of the tephritid fly (*Paroxyna plantaginis*) and its host plant, sea aster (*Tripolium vulgare*). The system shares many features with those of other nonfrugivorous tephritid seed predators and may be considered representative of the interactions involving this group of specialised flies. Therefore it has all the exciting properties of spatial and temporal heterogeneity common to most tephritid systems. In the study area, the fly has no host specific enemy and the only important enemy of sea aster is *P. plantaginis*. The monocarpic host is also entirely dependent on seed production for its fitness. A high degree of natural fragmentation and environmental stochasticity adds to the interaction. This gives the system the potential of elucidating some general and important ecological problems. The tightly coupled plant-herbivore interaction provides the possibility of addressing several important questions related to the regulation and persistence of the interacting organisms. These issues include correlation's in the phenology of the specialised herbivore and its host plant; inter-seasonal changes in abundance, the link between individual behaviour and population dynamics, the potential for regulation provided by the spatial distribution and the impact of stochasticity.

Close to the northern limit of its extension, along the coast of the Gulf of Bothnia, only three herbivorous insects are known to be associated with the plant. These

include two seed predators - a tortricid lepidopteran (*Eucosma catoptrana*), a tephritid fly (*P. plantaginis*) - and a leaf mining lepidopteran (*Bucculatrix maritima*). Of the two seed predators only the tephritid seems to be important in the plant dynamics (5.2.3.). The leaf miner may, however, also have an impact on the mortality of vegetative plants, but it is not considered in this thesis.

2. Ecological background

2.1. Plant-Herbivore coevolution - aspects of plant defence

Coevolution is often thought to have led to tight interactions between specialist consumers and their resources (Thompson, 1999). Avoidance strategies between plants and their herbivores may have evolved as active defence mechanisms (involving the production of secondary compounds or physical armaments), or passive escape in time and space strategies (Feeny, 1976; Rhoades & Cates, 1976; Belsky et al., 1993).

Flowering phenology may therefore have evolved as a defence against seed predators (Zimmerman, 1980; Rathcke & Lacey, 1985; Brody, 1997) It is further hypothesised that monocarpic plants without a seed bank - like sea aster - are likely to suffer most severely from seed predators and get the highest reward from escaping seed predation compared to long lived plant species or species with a seed bank (Louda & Potvin, 1995).

Safeguarding certain flowers on a plant from seed predation may involve a phenological lag or flowering displacement (Campbell, 1991; English-Loeb & Karban, 1992; Eriksson, 1995; Biere & Honders, 1996), seed predator behaviour which protects certain flowers heads (Paper III), or a mismatch in the timing between flowering and oviposition phenologies, for example due to climatic, density or spatial factors (Ågren & Willson, 1992; Ehrlén, 1996, Paper III). If certain types of flower heads on sea aster plants consequently escape attacks from the tephritid fly, this may be considered a systematic escape from the seed predator, which may be interpreted as a preservative for the systems persistence, and may possibly have developed through coevolution.

2.2. Tight dynamics and the stability paradigm

The population dynamics of parasitoid-host systems, including those of seed predatory tephritid flies on Asteraceae plants, may be considered a true interaction. This means that in theory - and in the absence of other actors - the interacting species might have the potential to regulate each other's populations. This implies that in theory the population numbers may be expected to reach an

equilibrium (Andrewartha & Birch, 1954; Varley et al, 1973; Begon & Mortimer, 1986; Fig. 1).

Equilibrated populations are no longer thought to be the rule in nature. Populations rather exhibit *stationarity* around a certain population size or density (Dennis & Taper, 1994; Turchin, 1995) previously described as stochastic equilibrium (May, 1973) or convergence in distribution (Chesson, 1982). The basic challenge, however, remains: all natural populations must necessarily be regulated (Sinclair & Pech, 1996). On the other hand the regulatory power of a system may work so fast that it is difficult to identify the regulating process (Murdoch & Swarbrick, 2000). Most populations, however, show less stable dynamics far away from equilibrium (Pimm, 1991), and one reason for this may be that many populations rarely experience strong regulation due to environmental stochasticity (den Boer & Reddingius, 1996).

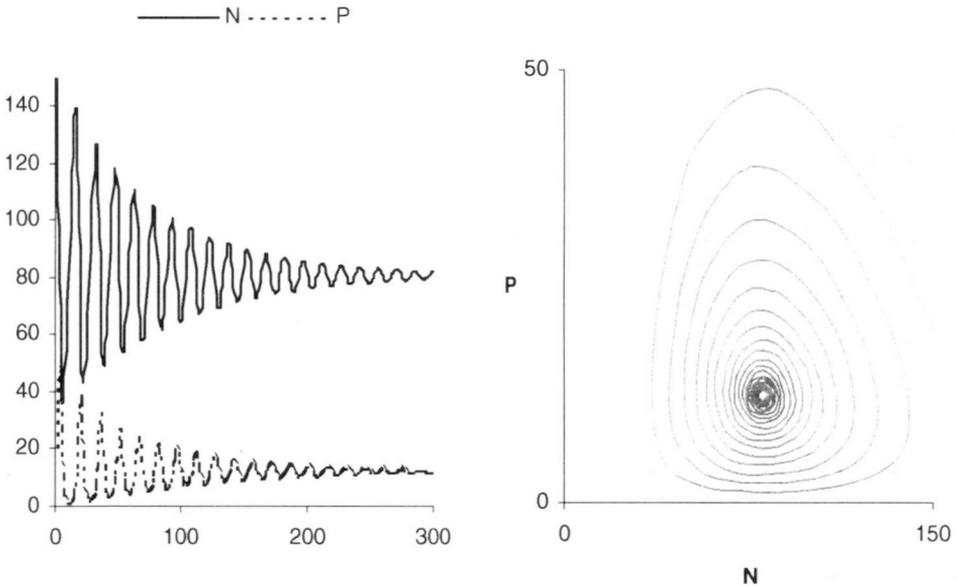


Fig. 1. The idea of regulation exemplified by the Nicholson-Bailey model (after Varley et al., 1973; p. 62-66). This model describes a parasitoid (P)-host (N) system with density-dependent mortality acting on the host. The model ran for 300 generations whereupon the two interacting populations reached a situation of coexistence, establishing an equilibrium or 'steady state'. The model is, however, very sensitive to parameter setting. In this example the parasite's area of discovery is 0.031, host mortality is 0.12, and the reproductive value is 2.

Knowledge of the relative importance of stochastic and deterministic factors in population fluctuations is crucial in ecology (Royama, 1992; Turchin, 1995; Gurney & Nisbeth, 1998; Grenfell et al., 1998). One major problem is how to detect and measure regulation. It is generally accepted that regulation cannot occur in the absence of density dependence, i.e. there has to be a negative feedback on population growth when density becomes sufficiently high (Murdoch & Walde, 1989; Hanski, 1990; Godfray & Hassell, 1992; Turchin, 1995, 1999; Sinclair & Pech, 1996). The measurement of direct density-dependence and its strength therefore becomes essential when evaluating possible regulatory processes. Turchin (1995) concludes that the density-dependent effect is characterised by a return tendency, which causes the population to always return to its long-term stationary probability distribution of densities. He further lists three general conditions that have to be fulfilled for regulation to occur: the return tendency must be of the right sign, it has to be strong enough to counteract disruptive effects of density-independent factors, and the lag with which it operates must not be too long.

The presence of density-dependent patterns and processes alone is not a proof of regulation, but they do provide hints of possible regulating factors in investigated systems. However, few quantitative studies have been performed measuring and evaluating the strength of specific density-dependent processes in order to relate them to other density-dependent and density-independent factors (Harrison & Cappuccino, 1995; Turchin, 1995; Turchin 1999). In addition time-lags will disconnect a tight dynamic (Begon & Mortimer, 1986). This implies that the lag in the generation time from seed to seed set of sea aster should provoke a fluctuation in the dynamics of the interaction with the seed predator. A time lag that might be detected in a time series.

2.3. How to detect regulation - pattern approaches

Time series like the one presented in figure 1 have been the most commonly used instruments for detecting regulation in populations, but they have significant shortcomings. For instance, a time series of 30 years or more is needed in order to detect regulation (Harrison & Cappuccino, 1995), and repeating fluctuations in a time series do not necessarily help identify the process causing the dynamics. The repeating population patterns often assumed to have been caused by biological processes may equally well be caused by other forces like heterogeneity, resulting in escape in time and space, or the impact of environmental stochasticity (Bjørnstad et al., 1999; Lundberg et al., in press). Further, the population variability of one species will often increase the longer we monitor a population (Pimm, 1991 p. 91). This means that the assumed condition of stationarity (Turchin, 1995) may not be met. However, if the between-year dynamics of *P. plantaginis* and *T. vulgare* follows coupled dynamics - like the Nicholson-Bailey model in figure 1 - it could be interpreted that this is a regulated

system. Variability in the generation time of sea aster should on the other hand result in a less coupled dynamics.

Another pattern approach (the " $CV^2 > 1$ -rule") has been used for analysing parasitism frequency in relation to the density of the host (Pacala & Hassell, 1991; Taylor 1993). According to this rule a general criterion for regulation is that the coefficient of variation from regression exceeds unity. This analysis further allows for a partition of the coefficient into a density-dependent component and a density-independent component (Pacala & Hassell, 1991). A variant of this approach is used in Paper I. However, the static nature of the data can be problematic in this approach, because it gives no insight into the temporal population dynamics that led to the pattern (Taylor, 1993). This problem is especially important when the data are highly variable (as in my study system, Paper I). Such variability not only causes poor fits in the data, but can also be interpreted as indicating that density-independent regulation has a strong influence (Pacala & Hassell, 1991). This is by definition difficult, as regulation should always include density-dependence (see above). In Paper I we used equations of the functional response family to assess whether attacks depend on plant density. Further, by considering the data according to the spatial hierarchy of the study system (Nielsen & Ims, 2000), critical scales may be defined at which important population processes may take place (Levin & Pacala, 1997; Bjørnstad et al., 1999; Paper I).

Recently, evaluation of the frequency distribution of group sizes (so-called truncated power law or TPL-analysis, Bonabeau & Dagorn, 1995) has been proposed as a means of linking consumer density to spatial resource use (Paper II). In this paper we further suggested a way of determining unique values for the TPL. TPL-analysis is another pattern approach that fails to provide insight into the processes that created identified patterns. It does, however, provide a novel way of comparing use of resources relative to their abundance. This approach allows for more direct analyses of the larval distribution relative to characteristics of the resource abundance. Comparing the distribution of groups of tephritid larvae with the distribution of their sea aster resource will indicate to which extend the resource is used, and how the consumer is limited by the resource distribution.

In all the three above-mentioned methods of interpreting patterns, temporal and spatial heterogeneity is considered. The use of all patterns demand that the data must be collected from the same place at comparable time intervals (reducing the effect of irrelevant population variables, such as shifts due to daily temperature changes or to differences in habitat quality).

2.4. Population dynamics in space - dispersal as a key issue

The importance of dispersal for persistence has long been recognised in spatial population ecology (Huffaker, 1958; Fryxell & Lundberg, 1997; Tilman & Kareiva, 1997). The development of metapopulation theory reinforced the interest in dispersal (Hanski & Simberloff, 1997) and by introducing the concept of connectivity (which is defined as a combination of the distance between subpopulations and the dispersal range of the focal organism) Harrison (1991) clarified the distinction between subdivided populations from non-equilibrium populations to patchy populations (Fig. 2, Harrison & Taylor, 1997).

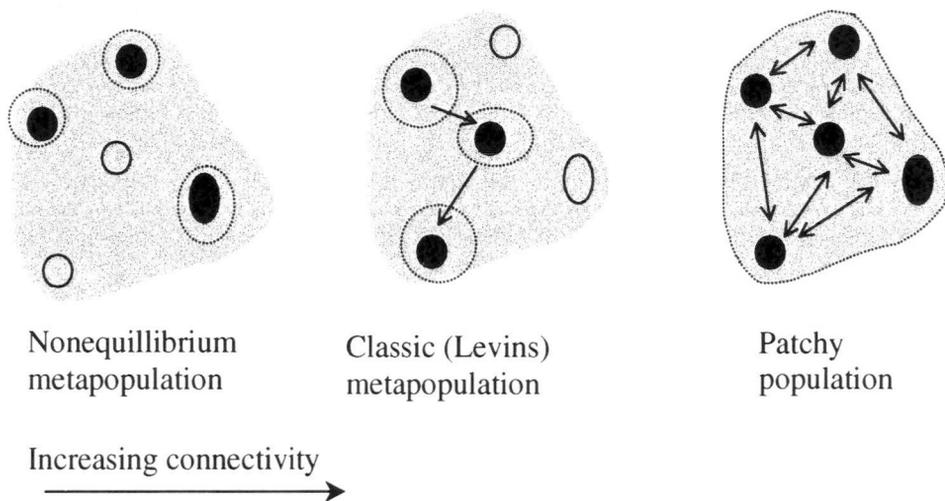


Fig. 2. Relationships among the main types of subdivided populations after Harrison & Taylor (1997). Occupied habitat patches (filled circles); vacant habitat patches (empty circles); boundaries of local populations (dotted lines); dispersal (arrows). Mainland-island populations and intermediate cases combining the different features do not differ qualitatively from these three basic types.

Understanding the dispersal of individuals across space is a challenge in the ecological analysis of heterogeneous and subdivided populations (Kareiva, 1990, 1994; Fryxell & Lundberg, 1997; Tilman & Kareiva, 1997). Dispersal is generally thought to be costly and mechanisms that trigger emigration comprise social pressure (including crowding), the presence of predators and resource depletion (Ims & Yoccoz, 1997). Dispersal can explain more than simply the synchrony of patchy subpopulations. It is also suggested to have a stabilising effect, either directly (Gadgil, 1971; Gurney & Nisbet, 1998) or by transforming local dynamics within years to a global regulation dynamic between years (Hassell 1987; Paper I). Stabilising dispersal implies that it should be density-dependent. Empirical studies by Denno & Peterson (1995) and Midtgaard (1999) suggest that

insect emigration is unrelated to density, but other studies indicate that both emigration (Romstöck-Völkl, 1990; Denno & Peterson, 1995; Herzig, 1995) and colonisation (Ohgushi, 1995) are density-dependent processes. The empirical studies, however, often hinge on indirect measurements (for example wing-dimorphism), and have not always been experimentally supported. Furthermore, such investigations may not cover the entire dispersal event (Ims & Yoccoz, 1997) and the strength of the process is not considered (Turchin, 1995).

In paper IV an attempt is made to decide the power of dispersal in *P. plantaginis*. A density-dependent pattern of dispersal is a precondition for possible spatial regulation in this system, and if the strength of dispersal varies between sexes their behaviour will have different consequences for the population dynamics. This study was, however, limited to a one species measurement, and in order to evaluate the generality of the results, similar measurements for other species are needed.

2.5. The foragers dilemma - to leave or to stay

Denno & Peterson (1995) suggested that foragers primarily leave their patch due to depletion. This was also considered the primary cause for leaving patches in the models of optimal oviposition theory by Haccou et al. (1997). The classic issue considered in optimal foraging and oviposition theory is when an animal should leave its patch. The optimal time may be calculated using the marginal value theorem (Charnov, 1976), or derivatives of this (Haccou et al., 1997). These models, however, provide an average assessment of the most optimal decisions, and they do not touch upon the mechanism of patch leaving or, rather, what triggers the individual decision (Green, 1984). For oviposition decisions in tephritids, olfactory signals from the host and host-marking pheromones may be critical cues letting a female know when to leave a patch (Roitberg et al., 1984). Oviposition may also depend on the egg-load (Mangel & Roitberg, 1989; Fletcher & Prokopy, 1991) and host plant quality (Price et al., 1994).

2.6. Tephritid-Asteraceae as a model system

Flies of the tephritid family are easily recognised by their distinct wing patterns and spectacular dancing displays. Members of this group of mostly specialised phytofagous flies also show highly complex mating and oviposition behaviour. Further, they seem outstanding in their ability to track their host plant, regardless of how unpredictable it may appear in time or space. This implies that the flies may have dramatic population dynamics, possibly explaining why Tephritidae include both pest species and species that have been selected as possible bio-control agents of weeds (Díaz-Fleischer & Aluja, 2000).

The nonfrugivorous tephritids (Tephritinae) are specialist exploiters of vegetative structures and inflorescences, mostly those of the Asteraceae family (Zwölfer, 1983; Drew & Yuval, 2000). This subfamily is considered the most recently evolved tephritid group, originating from drier savanna regions (Drew & Yuval, 2000). Insertion of the eggs into the plant tissue serves multiple purposes: it protects the offspring against desiccation, predators and parasites, and it may also be a way of escaping competition (Headrick & Goeden, 1998; Díaz-Fleischer et al., 2000).

Among the benefits of using the present system is the low level of human disturbance, characteristic of economically unimportant systems in a marginal areas like the shore of the Gulf of Bothnia. The studied sea aster-tephritid system is naturally fragmented and can therefore give us information on how the plant-herbivore dynamics work across space. As further advantage is that this system can be easily handled, allowing the experimental manipulation of both plants and flies. It is also very easy to find both the flies and the plants: the plant grows in sparsely vegetated areas, adult flies are direct observable, and infested flower heads are easily defined and recognised.

3. Questions addressed

To understand the dynamics between this tephritid and its sea aster host plant the following questions were addressed:

1. *Are the dynamics of the plant and the seed predator coupled in a way that indicates between-year regulation of the system?*

To consider this issue, data on the dynamics of sea aster and *P. plantaginis* on one island over eight years are presented and discussed. Other attack patterns are also considered (Paper I and Paper II).

2. *Can temporal and spatial mechanisms enable the host plant to escape attacks from the tephritid seed predator?*

To answer this question the within-plant risk of flower heads being attacked was analysed in relation to the sea aster flowering phenology (Paper III). Further, the impact of variability in the generation time of sea aster is discussed.

3. *Is the emergence of adult flies linked to the prolonged presentation of flower buds characteristically seen in the host plant?*

Here the focus is on the emergence of adult flies, how synchronously they emerge and whether their emergence depends on collection site, sex or weight of the puparia.

4. *Is the dispersal behaviour of the fly an advantageous adaption to the spatial distribution of its resource?*

Addressing this question involves the consideration of the range of the active dispersal (including effects of the size of the nearest neighbour patch and distance to it), the nature (density-dependence) and strength of dispersal (Paper IV), and mortality during active and passive dispersal (Paper V).

4. Materials and Methods

4.1. Study system

4.1.1. The study area

The tephritid system was studied in the archipelago of Skeppsvik in the Gulf of Bothnia in northern Sweden ($63^{\circ}44-48'N$, $20^{\circ}34-40'E$; for a detailed description, see Ericson & Wallentinus, 1979). This archipelago contains about 100 islands within an area of 20 km^2 (Fig. 3). The islands form chains in a north-south orientation, due to ice movements during the last ice age and ongoing elevation of the land. A combination of variations in wind (including autumn storms), fluctuating water levels (up to 250 cm in a normal year) and ice cover (from November to April) creates a natural disturbance gradient within the archipelago.

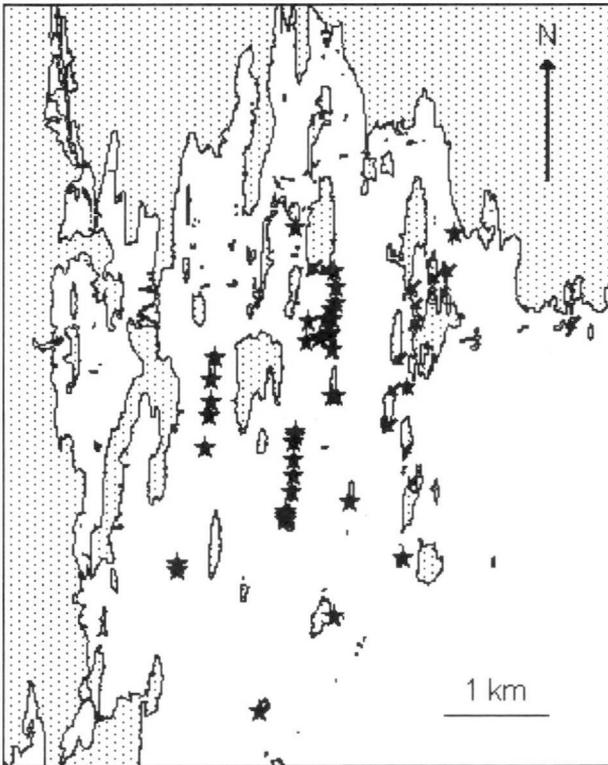


Fig. 3.

Skeppsvik Archipelago, in the Gulf of Bothnia, Sweden ($63^{\circ}44'-48'N$, $20^{\circ}34'-40'E$). Stars indicate islands with populations of sea aster and tephritid flies in one or more of the studied years. The south-eastern parts are more exposed to wave and wind action than the sheltered parts in the north-west.

4.1.2. The host plant

Tripolium vulgare, Besler ex. Nees (Asteraceae, former *Aster tripolium*) is a native, monocarpic species growing on coarse- to fine- grained pebbled seashores. In the study area germination takes place in early summer in connection with prolonged low-water level periods (Lars Ericson, personal communication).

Flowering stage is reached during the third year (only very rarely during the second year on more wave-washed sites where inter-specific competition is reduced). In the middle part of the archipelago, flowering usually starts after the third or fourth year - or even later. The longer time depends upon increased inter-specific competition (Albrechtsen & Ericson, unpublished) Flowering starts in mid June and continues throughout August. Seed mature in late August- September and seed disperse with strong storms during autumn. Due to frequent water level changes (Fig. 4) the plants are often partly submerged. Many plants also experience drought due to periods with low water levels.

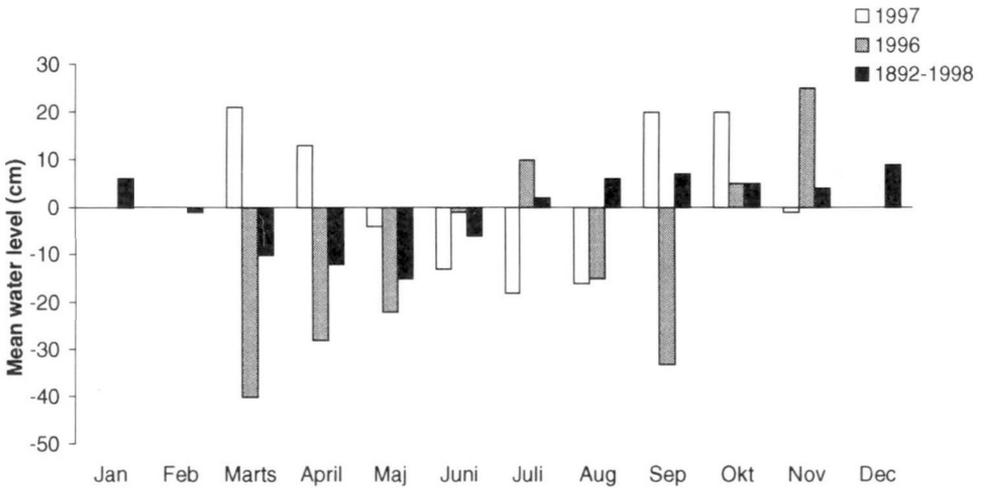


Fig 4. Monthly mean water level at the mareograph station, Ratan c. 20 km north of the study area, shown as deviation from zero line, corrected for land uplift. The mean is shown as a mean of 100 years and for two of the study years.

4.1.3. The seed predator

The tephritid seed predator (*Paroxyna plantaginis* Haliday) is a univoltine, monophagous fly. It belongs to the nonfrugivorous specialist tephritids that are closely associated with their host plant (type IIIb; Zwölfer, 1983). Tephritids in this group often oviposit in immature plant tissue, which provides a relatively long-lived substrate, and oviposition sites are often chosen based on the size or stage of the host flower head (Straw, 1989; Völkl et al., 1993; Zwölfer & Arnold-Rinehart, 1994). The longevity of adult nonfrugivorous tephritids is relatively short (generally up to about one month) and the lifetime fecundity is between 50 and 150 eggs per female (Zwölfer, 1983)

P. plantaginis usually lays one egg in each flower head. However, in plants where more than 85 % of the flower heads are infested two - and in rare cases three - larvae have been found in single flower heads. A slight swelling of the flower

head indicates the presence of a larva or puparium. At the end of the season, the puparium usually drops out of the flower head, and previously infested receptacles can be identified by the presence of the empty puparial chamber. Thus, flower heads that are or have been infested can easily be recognised. The presence of one larva in a flower head severely reduces the seed set (Paper III).

Little is known about adult fly feeding in these nonfrugivorous species, compared to the economically more significant frugivorous species. The nonfrugivorous tephritinae are, however, autogamous, which means that they are not dependent on finding protein for egg development. This has led to questions about whether the adults feed at all (Drew & Yuval, 2000). However, my studies showed beyond doubt that adult *P. plantaginis* do feed, as I observed them ingesting pollen from flowering herbs, especially *Juncus gerardii*.

4.2. Methods

4.2.1. Population dynamics of *T. vulgare* and *P. plantaginis*

Attack frequencies were obtained by counting the total number of flower heads, and relating this number to the number of attacked flower heads per plant. In some cases the frequencies were also scaled up to the stand and island level (Paper I).

The number of flower heads on a plant varies greatly, hence, the use of attack frequencies, is a standard method for evaluating this sort of data (for example Roitberg et al. 1984; Pacala & Hassell, 1991; Taylor, 1993; Hassell & Wilson, 1997). However, use of such frequencies introduces systematic bias when entering high and low frequencies, as there is a floor (zero) and a ceiling (one) for the range of possible frequencies. This bias is expressed in skew residuals, for example in regression analysis, and can be adjusted by transforming the data. In the analyses I used the arc sin transformation whenever necessary (Sokal & Rohlf, 1995).

Another problem arising from the use of attack frequencies appears when working at different scales. At any scale the attack frequency may be calculated as the proportion of infested flower heads relative to the total number of flower heads. This expresses a per capita probability (or risk) of being infested at the focal scale, the resulting attack frequencies will, however, vary between scales.

4.2.2. The host's escape in time and space

Plants were followed through four years from one-year seedlings to flowering time and a minimum time to flowering was obtained. The variation in generation time is important because it imposes variability in the time lag whereby the fly and the host plant dynamics may interact.

The effect of within season flowering phenology on the risk of attack was analysed by a simple model using data obtained from Paper III. The model expresses the average realised seed set for a flower head (S_{real})

$$S_{real} = S_{pot} \cdot P_c \cdot (1 - A_r) \cdot A_s \quad \text{Eq. 1}$$

where S_{pot} is the potential seed set related to the flower head age in a model plant, P_c is the per seed chance of selfing, A_r is the per flower head risk of attack by *P. plantaginis* and A_s is the per seed chance of surviving an attack (for parameter settings see appendix A).

This model was also used to determine the impact of the tortricid seed predator in the study area.

4.2.3. Extended emergence of flies

Relationship between the fly and flowering phenology is treated in Paper III. Data on fly emergence were achieved from puparia collected for the dispersal study presented in Paper IV. The emergence history provided further insight into the emergence phenology of the flies.

4.2.4. The fly's adaptation to spatial resource heterogeneity

To determine the within-season effect of distance from the nearest neighbour on the risk of attack, sea aster plants were transplanted in 1992 and 1994 to islands with increasing distance from natural populations. Within-year transplantation's were performed with plants that were about to flower as indicated by the size of the vegetative rosette early in the growing season (Gray, 1997). The plants were planted individually in pots (0.5 l.) filled with a 1:1 mixture of commercial soil and gravel. The pots were placed out-door and covered with fibre cloth until they could be transplanted on islands.

Further information to help understand the fly's adaptation to a fragmented resource was obtained from the investigations into patterns of attack presented in Papers I and II, and through experimental studies of dispersal presented in Paper IV. The impact of passive transport of the puparia was also discussed in relation to data given in Paper V.

5. Results

5.1. Population dynamics of *T. vulgare* and *P. plantaginis*

Sea aster often shows major changes in population size, and colonisation and extinction events frequently occur. It is not unusual that sea aster suddenly appear on an island, persist for a few years and then disappears (Albrectsen and Ericson, unpublished). Throughout the study period, 19-42 islands out of 100 were

occupied by flowering *T. vulgare*. The population sizes within-islands also fluctuated widely but showed correlated variation among islands. The level of attack by *P. plantaginis* also appeared to be correlated among islands, although a high degree of stochastic (density-independent) variation was always present (Paper I), and though the northern and sheltered parts of the archipelago generally seemed to be most heavily attacked (Paper III).

The dynamics on one island through eight years is presented in Fig. 5. In 1996, three years after the year with the lowest frequency of attacks, a peak of flower head numbers appeared on this island, a trend that was observed throughout the entire archipelago. However, the population of attacked flower heads did not increase to the same extent, suggesting that the flies could not keep track with the increased number of flower heads. This conclusion is repeated in the tendency of the attack frequency to decrease that year.

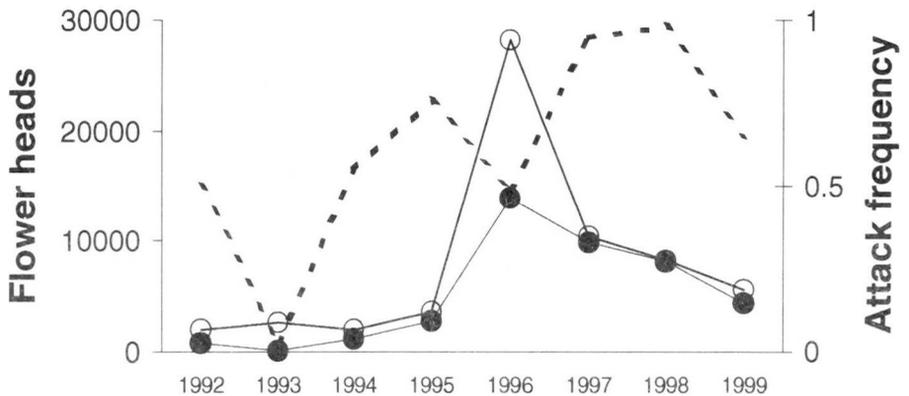


Fig. 5. The dynamics of *T. vulgare* flowering and attacks by *P. plantaginis* on the island Södra Teklaredd. Total number of flower heads (open circles); occupied flower heads (closed circles); attack frequency (dotted line). The number of individual flowering plants and the total number of flower heads were highly correlated ($r = 0.996$). The figure presents direct counts apart from in 1998, when the attack frequency was estimated from a sample of 50 individuals.

In Paper II we used the TPL analysis to show how the distribution of infested flower heads will change from a scenario with many plants with few larvae attacks under low attack conditions to an attack pattern which approaches the distribution of flower heads on the plants in high attack years. This indicates that the flies spread out eggs to many plants rather than concentrate them on a few (den Boer and Reddingius, 1996).

5.2. The host's escape in time and space

Time lags in the time from seed to flowering sea aster should provoke a fluctuation in the dynamics with the univoltine tephritid fly. In addition variability in the generation time of the host plant should detach the interaction between the two species.

5.2.1. Evidence of time lags

A putative direct connection between the year of least frequent attacks (1993) and the peak year of flowering plants (1996) suggests there is a three-year time lag between seed set and flowering. This time lag accords with own unpublished data on seedling, survival, growth rate and the time until flowering is reached. This study shows considerable differences between various parts of the archipelago. In the outer, wave-washed part, flowering usually occur during the 3rd year (and rarely in the 2nd or 4th year), while the vegetative period may last for four to more than eight years in the inner part. Here flowering is usually not reached until the 4th or 5th year (Albrechtsen & Ericson, unpublished). The subpopulations that experience short generation times grow in the more exposed parts of the archipelago. They grow faster probably because of better nutritional conditions but the plants also experience higher mortality since exposure increases. On the other hand, in the inner part of the archipelago the competition from other plants may be so high that single plants will not reach maturation, although their mortality is reduced compared to expose plants. If seedlings in certain parts of the archipelago only establish from seeds from other parts of the archipelago source-sink dynamics of the host plant may be significant.

5.2.2. Mismatch of phenologies as a host refuge

The information on flowering phenology and attack risk presented in Paper III indicates that early flower heads set more seeds and have a lower risk of tephritid attacks. This information may be used to quantify the potential higher seed set in early flower heads in a simple model (eq 1.). The data behind the model includes information from transplanted sea aster plant that had flower heads with fewer seeds compared to plants from naturally growing populations.

The potential seed set is related to the flower head age in a model plant, the per seed chance of selfing, and the per flower head chance of escaping attack by *P. plantaginis* (details are given in Appendix A). Further this exercise provides the possibility of balancing the attacks by the tortricid butterfly *Phalonidia affinitana* (that attacks the earliest flower heads in the central branch) and the expected advantage of early flowering with respect to attacks by *P. plantaginis*.

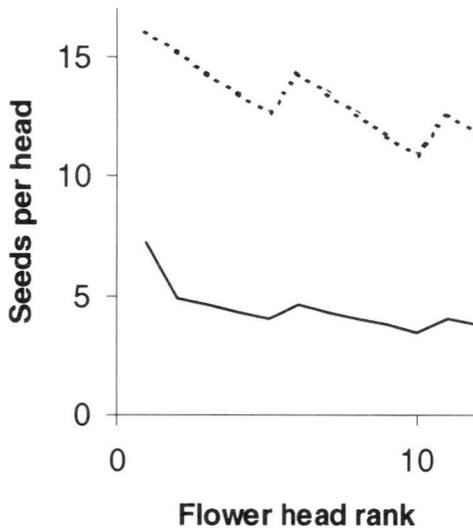


Fig 6. Potential (dotted line) and realised (solid line) seed set of *T. vulgare* in relation to flowering rank. The main factor causing a higher realised seed set is the higher seed set combined with the lower attack risk for the first flowering head.

The highest realised seed set is found in the first flower heads (on average 7.22 seeds, Fig. 6.). This indicates that early flowering may be beneficial, primary because of the higher potential seed set. However, quantitatively, the most important reason appears to be the lower risk of attack for the first flower head. In the model the attack risk is illustrated by a step function, where the lateral flower heads are clumped into a common average risk of attack. This risk may, however, vary with age of the flower head. Further, the attack risk assessments are calculated for a certain year and may vary between years, as may the suggested higher realised seed set of early flower heads. The escape of early flower heads from attacks may indicate a displacement of the flowering time. However, the flowering is extended in time, which is usually considered a sign of resource limitation rather than an evolutionary adaptation.

5.2.3. Importance of other seed predators

A tortricid butterfly (probably *Eucosma catoptrana*, Svensson 1993), which is thought to be of minor importance in this system, always attacks the earliest flower heads in the central branch of *T. vulgare*. To verify that this seed predator is really of minor importance the model may be used to calculate the attack level

at which *E. catoptrana* would balance the benefit bestowed by the early flower heads at the investigated attack level by *P. plantaginis*. At an average attack frequency by *E. catoptrana* of 0.36, the average realised seed set in the remaining first flower heads will balance the realised seed set of the tortricid-free second ranked flower heads (the first on the second branch, which on average set 4.60 seeds). No such high frequencies of tortricid attack frequency were found in any patch or survey year: the highest frequency of *E. catoptrana* - attacked plants being less than five percent. This supports the idea that *E. catoptrana* was not of major importance in this system during the study period.

5.3. Extended emergence of flies

The emergence history of flies of 1724 puparia collected for the dispersal experiment (Paper IV) showed an interesting asynchrony (Fig. 7). The puparia were collected from 25 patches on 18 islands with puparia weights spanning from 0.00052 to 0.01054 g normally distributed (Shapiro-Wilk *W* test; $w = 0.951$, $P < 0.55$) around a mean weight of 0.0061 g. The puparia were set to emerge under 18 hour day and 6 hour night conditions (21°C/15°C) in four emergence groups (2 groups with $N = 100$ and 2 groups with $N \sim 750$). Of these, 1310 puparia corresponding to 76 % successfully emerged. The majority (1289) of the emerging insects were *P. plantaginis* flies, and the remaining 21 were hymenopterous parasitoids representing seven species (one *Andilea convexa* (Walk.), one *Merismus splendens* (Graham), one *Pteromalus candui* (Szel.), six *P. glabriculus* (Th.), eight *P. intermedius* (Walk.), one *P. semotus* (Walk.), and three *Trichomalopsis arzoneae* (Boucek)). Puparia that did not develop into adults were dissected, and no parasitoids were detected in them. The emergence success and low number of parasitoids is consistent with emergence results from smaller numbers of puparia collected in the study area in 1993, 1994, 1997 and 1998.

Puparial weight affected the emergence success (logistic regression $P < 0.0001$) and the probability of a successful emergence exceeded 50 percent when a puparium weighed more than 0.0042 g (including parasitised puparia). Among the hatched tephritid flies 1280 were sexed, and 50.7 percent were female, a proportion indistinguishable from a 1:1 ratio (Goodness-of fit test: $\chi^2_1 = 0.2531$; $P = 0.61$; $N = 1280$). The sex ratio did not change between hatch groups ($\chi^2_3 = 1.804$; $P = 0.61$; $N = 1280$).

Generally females were heavier (mean \pm se, 0.007363 ± 0.00005 g) than males (0.006034 ± 0.00004 g), which were heavier than dead puparia (0.004511 ± 0.00010 g), which were, in turn, heavier than parasitoid infected puparia (0.003710 ± 0.00015 g). The emergence time was not affected by weight (**females:** $R^2 = 0.0008$; $F_{649} = 0.5089$; $P = 0.48$, **males:** $R^2 = 0.000371$; $F_{631} = 0.2326$; $P = 0.63$). It was, however, extended in time (Fig.7.), and females emerged approximately one day later than males (Table 1).

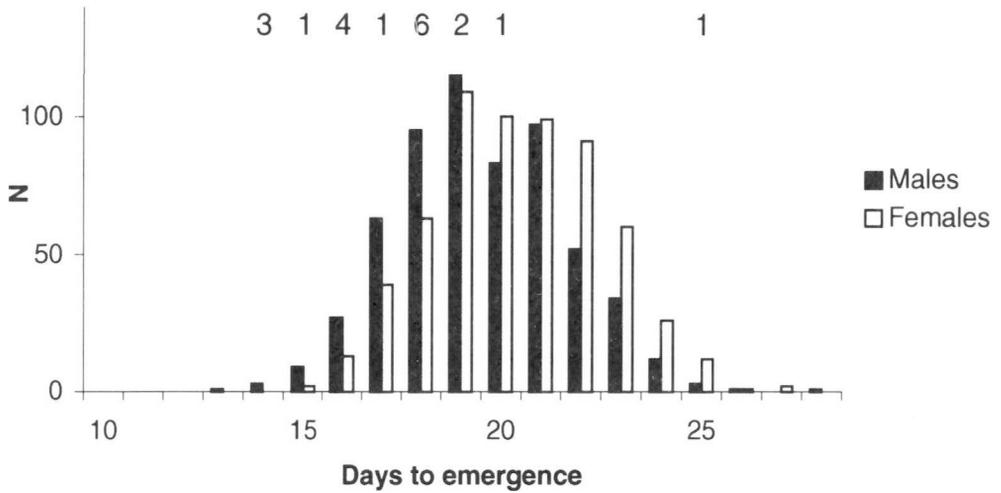


Fig. 7. The history of flies that emerged from puparia under conditions described in Paper IV. Both males and females emerged over an extended period the time of emergence was not coupled to either weight, or patch of collection. The numbers in the upper part of the figure refers to the number of parasitoids emerging from the puparia. In total, seven different species of parasitoids emerged from 21 puparia out of 1310 successful emergences.

Analysing time of emergence

Model $R^2 = 0.17$, $F_{5,1219} = 48.89$, $P < 0.0001$, $N=1220$

Source	df	SS	F	P > F
Patch	1	5.36	1.37	0.24
Sex	1	204.71	26.12	0.0001
Sex*Patch	3	17.64	0.19	0.83

Table 1. ANCOVA model summarising the effect of sex and patch of puparia collection on the time to emergence of adult flies. This was analysed for the two main emergence groups. An insignificant difference in time to emergence occurred between the two treatments and the emergence success was not affected significantly (two-tailed $\chi^2_{1219} = 4.479$, $P > 0.21$).

5.4. The fly's adaptation to spatial resource heterogeneity

5.4.1. The range of adult dispersal

Transplantation experiments were conducted in 1992 and 1994, to analyse the activity of flies relative to the size and distance of natural populations. Groups of 12 plants were transplanted to six (1992) and eleven (1994) islands, respectively. Islands free of natural populations of sea aster were used when possible.

The most distant transplant groups of 1994 could, however, not be analysed, since one group of transplants was partly washed into the sea by wave action, and grazing Canada geese (*Branta canadensis*) destroyed two other groups. A fourth group turned out to be less distant than initially thought because a population, of a single flowering sea aster, was discovered on a nearby island, which had been free of sea aster in 1993. This reduced the expected distance to nearest flowering sea aster for this patch from 1.7 to 0.6 km. Consequently, the average surveyed distance for the successful groups of transplants and the nearest natural population did not differ between 1992 and 1994 (paired t-test: $R^2 = 0.017$, $t_{12} = 0.45$, $P = 0.66$).

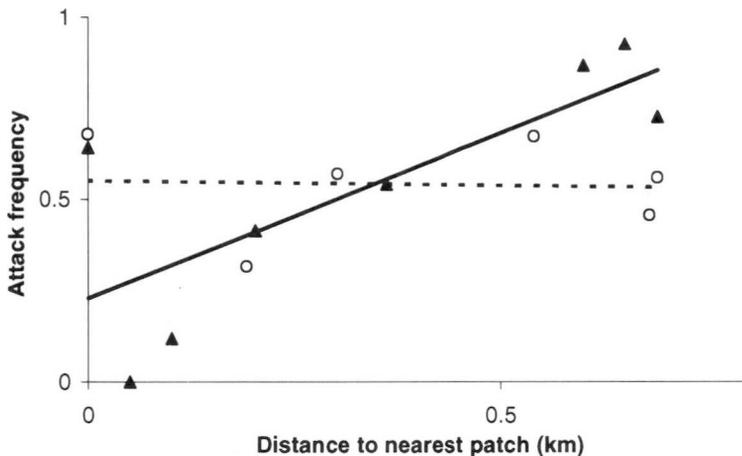


Fig. 8. Attack frequency of *P. plantagin*is on plants transplanted to aster-free islands related to the distance from the nearest natural population of *T. vulgare*. Circles represent data from 1992 (broken line, $R^2 = 0.007$) and triangles represent data from 1994 (solid line, $R^2 = 0.62$).

The attack frequency (arcsine transformed) in the transplanted groups was analysed with respect to size and distance from the nearest neighbouring population. The attack frequency on transplants increased with increasing distance from the nearest population according to the data gathered in 1994. This was, however, not the case for the transplants in 1992 (Fig. 8.). There was no

significant effect of the yearly overall attack frequency on the local attack levels ($R^2 = 0.0005$, $t_{13} = 0.08$, $P = 0.93$). Therefore, the data were pooled. For the pooled results, the size of the nearest natural patch had no effect on the attacks of the transplants ($R^2 = 0.08$, $t_{13} = 1.01$, $P = 0.34$), and neither did the attack frequency observed at nearest neighbouring patch ($R^2 = 0.08$, $t_{13} = 0.24$, $P = 0.81$). Indeed, there was no significant effect when including both of these factors and their interaction (ANOVA: $R^2 = 0.36$, $F_{13} = 1.28$, $P = 0.35$).

5.4.2. Female-biased density-dependent dispersal

To determine the dispersal characteristics, marked flies were released at three different densities in artificial host patches (Paper IV). The individual histories of recaptures were noted as well as migration between patches and invasion by unmarked flies. The loss of marked flies relative to initial density and sex was analysed using maximum likelihood estimation. Females generally had the highest loss rate. When comparing a density-independent model with a density-dependent model of the loss rate, the density-dependent model proved to be more accurate four times out of six for the females, but not once for the males. A female-biased invasion rate also suggested that female dispersal was density-dependent.

During the dispersal experiment in 1997 (Paper IV) unmarked flies invaded the artificial plots from a distance of more than 1.5 km. This was documented by observing unmarked flies entering artificial patches and by mapping the natural populations closest to the experimental area. Moreover, the flies appeared to arrive at the artificial patches right after the daily sea breeze had peaked, suggesting that long-distance dispersal of this fly is assisted by the prevailing wind (Fig. 9).

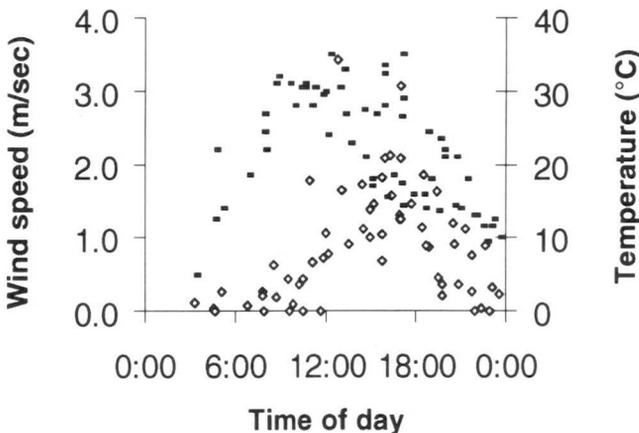


Fig. 9. Daily wind speed (diamonds) and air temperature (bars) measured in July 1997. The relatively high temperature over the mainland relative to the sea generates a southern sea breeze, peaking in late afternoon.

6. Discussion

This study was an attempt to define population regulating factors between a tephritid fly and its spatially distributed sea aster host plant and to evaluate the relative influence of biotic and abiotic forces. In the absence of other biological actors of major impact to the system, a tight coupling between the fly and the plant was expected.

High proportions of the available flower heads were generally attacked throughout the study period, indicating that the fly may be capable of reducing the size of its host plant population. There is no strong indication of a tight dynamics from the time series approach, one of the reasons being that the time series was too short (Harrison & Cappucino, 1995). On the other hand, the data suggest that the sea aster population will increase with a time lag of three years after a low attack year. The eruptive growth of flowering aster plants in 1996 agrees with sudden population peaks of flowering sea aster, which are known from long term observations in the study area (Lars Ericson, personal communication). This corresponds with the hypothesis by Louda & Potvin (1995) suggesting a high impact of seed predators on monocarps. If so, what we see is essentially an example of generally strong suppression performed by the seed predator on the host plant, which may be relaxed following single years when the flies have experienced adverse conditions, for example due to bad weather conditions.

The frequency of parasitoids emerging from the puparia was very low and also extremely variable. This supports the hypothesis that no specialist parasitoids exist in this study area and that the flies are subject to bottom-up limitations. The study of attack frequencies at different scales, however, showed that seasonal attacks are generally very variable except during years with extremely high densities. A hierarchy of scales (plant, stand and island) was suggested for evaluating this data, but no clear scale that determines crucial regulation processes could be found within this system. Much larger distances should obviously be considered, in order to determine the scale at which important processes concerning the fly dynamics take place (Harrison & Taylor, 1997; Levin & Pacala, 1997; Bjørnstad et al, 1999; Nielsen & Ims, 2000). Variability in attack frequencies on smaller plants seemed to guarantee the persistence of the host plant (Paper I). In addition, the attack patterns indicated that the fly may be regarded as a pandemic species in the archipelago, i.e. having generally high attack frequencies.

From truncated power law analyses we can follow how the distribution of attack groups on plants changes with the attack density indicating that the females spread out their eggs to many plants rather than concentrate them on a few (Paper II). The TPL analysis may be generally used to describe frequency distribution of group sizes in animals: insects, fish, grey seal, buffalo etc. (Perry & Taylor, 1985; Bonabeau & Dagorn, 1995; Paper II). Moreover this approach show a means of

relating the resource distribution to its use by a focal species (Paper II) rather than being an indication of the environmental dimensionality of a system as suggested by Bonabeau & Dagorn (1995).

Even if the seed predatory fly may reach attack frequencies close to one a drop in the sea aster population may not be observed. This may be due to the variation in the generation time of the sea aster, which varies from three to more than eight years of vegetative growth prior to the flowering event. Such time lags imply delayed density-dependence which cause destabilisation (Begon and Mortimer, 1986) and the variability in the time lag further decouples an apparent tight dynamic. This may also explain why the high number of flowering plants did not collapse three years after a high attack level was reached.

A study of the flowering phenology was performed to determine the possibility of a plant defence strategy of passive escape in time (Feeny, 1976; Rhoades & Cates, 1976; Belsky et al., 1993) in the form of flowering phenology (Zimmerman, 1980; Rathcke & Lacey, 1985; Brody, 1997). Early flower heads did escape seed predation to a higher degree than later flower heads in a one-year experimental study (Paper III). When presented in an appropriate state of flowering the flies actually attacked the early flower heads to the same extent, which excluded the possibility of a systematic escape caused by the fly oviposition behaviour. In addition, fly abundance is highest in the beginning of the flowering event, when head anthesis is the most advanced flowering stage. Therefore, the best explanation for the escape of early flower heads was a mismatch in phenologies.

The onset of flowering varies between years due to temperature and water level conditions. Of specific importance in the study area is that high water levels in the middle of the summer may reduce the availability of flower heads. This introduces an element of temporal unpredictability from the fly's point of view. The time-extended emergence of the flies may be seen as a perfect adaptation to an environment, which is also very unpredictable. The emergence experiment was performed under higher than natural temperature conditions, which means that the true emergence period is considerably more extended in time. This probably means that the flies emerge throughout the entire bud production period, that could not have been covered by the average lifetime of an individual (Zwölfer 1983; Headrick & Goeden, 1998).

One conclusion was clear from the transplantation of sea aster to distant islands: the flies frequently move long distances. The distance from the nearest natural patch data showed an unexpected increase in attack with distance for the 1994 data. From transplantation studies in 1996 it appeared that the populations in the inner archipelago generally seemed to be more heavily attacked (Paper III), probably due to the prevailing wind conditions. The three transplant groups, which got most heavily attacked in 1994 were also located either on such inner

islands or on the northern, sheltered end of an island. This indicates that wind effects may be more important for the observed attack pattern than patch size or distance between patches. Obviously both abiotic and biotic factors are important for the invasion of species at distances far beyond their usual dispersal range, but within the typical dispersal range their consequences for population dynamics are questionable.

Though no finite scales could be defined that are critical for population processes it was indicated in Paper I, that the strength and range of dispersal will vary with adult fly density. Long-range movements in tephritids are common between oviposition and feeding site, and a high turnover rate has been noted in several systems (Solbreck & Sillén-Tullberg, 1986; Dempster et al., 1995; Eber & Brandl, 1996). In Paper IV the mechanism behind this general pattern is suggested to be density-dependent dispersal, which was shown for the female flies. The strengths of such regulating dispersal processes have, however, seldom been measured (Turchin, 1995). This limits the present study to a between sex comparison. Observations of a female-biased dispersal have, however, been recorded in other tephritid flies (Jones et al., 1996; Jorge Hendrichs, personal communication), and the female-biased dispersal may be of general importance. For example in relation to the sterile male technique used to biological control economically important tephritid species.

Dispersal is a risk spreading strategy which may be initiated to escape for example resource depletion, intra- and inter-specific competition and local enemies (den Boer, 1986; Ims & Yoccoz, 1997). Empirical studies suggest that depletion may trigger emigration in sap feeders (Denno & Peterson, 1995). Tephritid evolution in terms of resource utilisation is thought to have been selected towards an avoidance of competition for resources either by distinct niche separations or by oviposition-detering substances left by females in occupied flower heads (Headrick & Goeden, 1998). Pheromone deterrents are known to influence dispersal distance in frugivorous female tephritids (Roitberg et al., 1984). On the other hand, both a high density of infested fruits and a high egg load may incline the female to oviposit under sub-optimal conditions (Mangel & Roitberg, 1989; Price et al., 1994). This is consistent with the observation that the pattern of one larva per infested flower head, which is typical of the infection by the nonfrugivorous *P. plantaginis* under light attack densities, breaks down under heavy attack conditions. The low parasitoid frequency supports the idea that the larvae of the fly are well protected in the flower head of its host and that parasitoids may not be able to attack *P. plantaginis* under normal circumstances, but rather attack fly larvae under sub-optimal conditions (Price & Clancy, 1986; Price, 1988) for example caused by crowding (Paper V).

Depletion of unoccupied flower heads in the right stage for oviposition is therefore likely to explain the density-dependent dispersal in *P. plantaginis*. This indicates that the females may adopt a pre-emptive competition strategy for egg-

laying substrates, while the more territory males (with weaker and probably density-independent disappearance patterns) tend to adopt a more sit-and wait strategy. In this system the active dispersal may further be a necessity considering the risk of passive dispersal of puparia to distant aster-free islands (Paper V). The less successful precondition for passive drift of parasitised puparia compared to unparasitised ones further indicate a prey-biased asymmetry where the parasitoid may be spatially out of regulatory reach (Trumper & Holt, 1998).

7. Conclusion

In conclusion, the fly may permanently suppress the seed production and by that also limit the population size of its host plant. The fragmented distribution of sea aster does not seem to be a limiting factor for the fly, due to an efficient density-dependent dispersal of the female flies. Sometimes the fly population may however be reduced, for example due to bad weather conditions, which releases the host plants population that may show eruptive population growth. Single plants and flower heads may on the other hand escape attack due to chance events and position. This system certainly supports the idea that strong density-dependence may be important for the regulation of a host population and that highly stochastic events may be important in the interaction. The stochastic effects in this system are probably also important for the persistence of the system. The density-dependent dispersal of females may be triggered by resource depletion and act within generations in the spatially heterogeneous environment. In that way the density-dependent effect may be transformed from a local response to regulation that is effective between generations.

Long time series and studies of the regulating power (for example by exclusion experiments) are needed to determine the true impact of *P. plantaginis* on *T. vulgare*, these studies should be supplemented with studies aiming to decide if sea aster is seed limited. It would also be interesting to combine the dispersal characters and fly density to the distribution patterns that were detected for this system. In addition, it might further be interesting to relate the strength of density-dependent dispersal for this species to that of other species, for example an outbreak species or a species threatened because of habitat fragmentation. To determine the maximum distance of dispersal for this tephritid fly much larger distances should be considered, and to decide the importance of passive dispersal and winter mortality, direct studies on the fate of the puparia are necessary.

Appendix A.

The average realised seed set (S_{real}) related to flower head age as presented in Fig. 6.

$$S_{real} = S_{pot} \cdot P_c \cdot (1 - A_r) \cdot A_s$$

where S_{pot} is the potential seed set related to the flower head age in a model plant, P_c is the per seed chance of selfing, A_r is the per flower head risk of being attacked by *P. plantaginis* and A_s is the per seed chance of surviving if attacked.

Assumptions:

1. P_c , A_r , and A_s will not depend on the age of the flower head.
2. The distribution of the attack risk (A_r) is modelled as a step function distinguishing the first flowering flower head from all the others on a plant.

Calculating the elements of the model:

S_{pot} was estimated from 86 plants as the maximal number of ovules for the first five flower heads on a plant. The information concerning the average difference in seed set for the first five flowering heads was used to mimic the seed set in a model plant with 12 flower heads grouped into branches (b) of 5+5+2 flower heads, aged (a) within the branches. The values of average seed set in terminal and lateral flower heads from (Paper III) were used for the parameter settings. Hence,

$$S_{pot} = 16.92 - 0.87a - 1.73b$$

P_c was calculated from a study of bagged flower heads, and an average frequency of 0.69 was obtained. The attack risk (A_r) was 0.3 for the first flowering terminal flower heads and 0.5 for the later flowering lateral heads. The chance of a seed surviving in an attacked flower head (A_s) was estimated to 0.07.

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