<u>**CHAPTER 11**</u>

# Use of Drift Nets to Infer Fish Transport and Migration Strategies in Inland Aquatic Ecosystems

*Michal Janáč\** and *Martin Reichard*[a]

## Principles of drift nets' use

Drift nets are stationary nets designed to capture drifting organisms, i.e., those transported via water current. For the purposes of this chapter, drift is understood as the transport itself, in which along-current movement of an organism is maintained by the current alone and not at the expense of the fish's energy reserves. This will be independent of whether (1) it results from passive dislodgement and ends with passive deposition (Pavlov 1994), or (2) plays a part in an active migration strategy (Hare et al. 2005). It is worth noting that the term 'drift nets' is also used for coastal gill nets, where the nets themselves drift with the current (FAO 2013). Drifting gill nets work on a substantially different principle and this chapter deals only with stationary drift nets.

In fact, in its broadest sense, any stationary device capturing drifting organisms could be considered a drift net. Thus, nets usually towed in order to sample ichthyoplankton (plankton, ring or bongo nets) can also serve as drift nets when set in a stationary position. Both rotary screw traps, used to sample downstream migrating juvenile salmonids (e.g., Johnson et al. 2005), and anchored stow nets, used for commercial catches in tidal zones, work on similar principles to drift nets. Drift pumps (Gale and Mohr 1978; Dahms and Qian 2004), which mechanically pump water from

Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic, v.v.i., Květná 8, 603 65 Brno, Czech Republic.
[a] Email: reichard@ivb.cz
\* Corresponding author: janac@ivb.cz

the current, thereby avoiding problems with drift net clogging (see below), also serve to capture drifting organisms. However, drift pumps carry a potential bias because they may also capture non-drifting organisms present in the current.

In its basic form, a drift net consists of a frame, a tapering net attached to the frame and (optionally) a collecting jar attached to the cod end of the net (Fig. 11.1). The mouth of a drift net is installed perpendicularly to the current, such that the water and the drifting organisms flow through the net mouth. Particles carried by the current are trapped by the mesh and moved towards the cod end by current pressure. After an allotted time, the organisms collected are either picked individually from the cod end or collected in a jar, or washed from the nets into a collection jar or examination basin.

In order to ensure drift nets stay in their chosen position, they need to be anchored. Anchoring points may comprise the river bottom or banks, a boat, pontoons, bridges, piers or an anchor. In shallow water (< 1 m depth), iron rods hammered into the bottom are used both to anchor the nets and to maintain the optimal position, i.e., mouth facing perpendicular to the current. In deeper water, drift nets may be attached at a stationary point by more flexible means (e.g., by rope) using a system of weights to stabilize its position.

Although towed plankton nets had been used to sample early life stages of fish since 1828 (Kelso and Rutherford 1996), stationary sampling nets, developed for sampling drifting freshwater invertebrates, were not used for another century (Needham 1928). Subsequently, the study of drift has become a major field in macroinvertebrates studies (see Waters 1972; Brittain and Eikeland 1988; Svendsen et al. 2004 for reviews). The first studies using stationary drift nets specifically design for fish collection appear around the middle of the 20th century (e.g., Brett 1948; Wolf 1951); using drift nets only slightly modified from those for macroinvertebrates (e.g., a larger mesh size). Today's nets differ little from these, though some modifications have been proposed for specific purposes. The attachment of a flow meter, either at the mouth
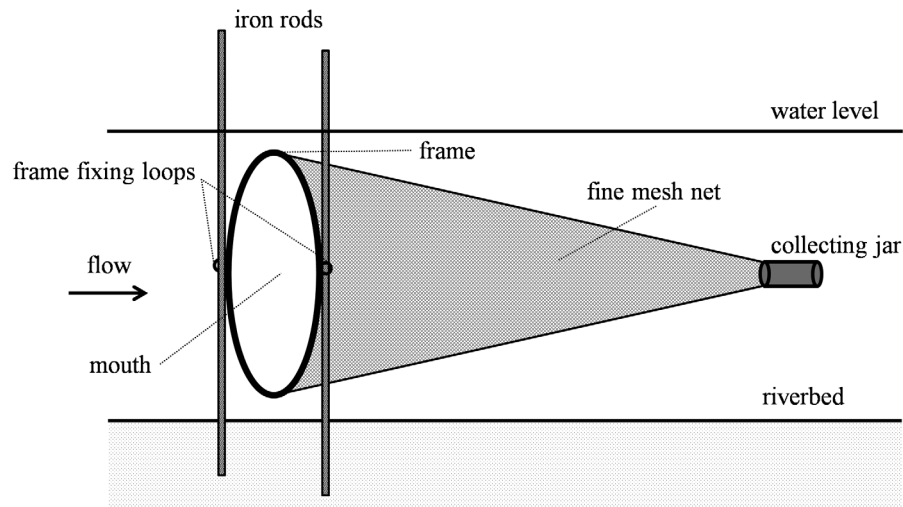


**Figure 11.1.** Schematic diagram of a basic drift net positioned in a shallow river.

or at the middle of the net, is probably the most common deviation from the basic scheme (Gale and Mohr 1978). In addition, many studies varied the shape of the net and/or the mesh size (see the subsection 'Net design'). Schmutz et al. (1997) proposed a sampler that could automatically collect six samples in temporal succession; allowing sampling over relatively short intervals without the presence of an operator. As fish drift mostly at night, this provides much appreciated relief in otherwise fatiguing work. The sampler works on the principle of six compartments rotating within a frame construction, with all nets except the lowest remaining closed during each interval (see Müller 1966 for macroinvertebrate drift samplers working on similar principles). However, the use of such samplers is restricted to shallow waters (Schmutz et al. 1997). Oesmann (2003) modified drift nets such that they can be opened and closed while under water, thereby allowing quantitative sampling at distinct depth strata. The method uses the principle of net collapse during retrieval to prevent contamination from other strata, as in the approach of Nester (1987). In order to study fish larval movements in an estuary, Graham and Venno (1968) ensured that their drift nets faced into the tidal current by attaching the nets to vanes attached to a line buoyed at the surface and anchored to the bottom. Similarly, a system of two buoys and two anchors allowed D'Amours et al. (2001) to set and retrieve multiple, vertically-stratified nets against the flow of a river. Finally, Hare et al. (2005) were able to continuously observe drifting larvae in an estuary by alternating two sets of vertically-stratified nets attached to a cable deployed from the stern of a ship.

Generally, drift nets are specifically designed to sample waters with unidirectional flow and are set at stationary points with easy access; hence they are mainly used in rivers. Several studies, however, have used anchored neuston (Lindsay et al. 1978; Hettler 1979), plankton (Graham and Venno 1968; Bradbury et al. 2004) or channel nets (Lewis et al. 1970; Hare et al. 2005) to sample ichthyoplankton drifting with ebb or flood tides in estuaries.

Despite well-developed procedures for sampling marine ichthyoplankton and the known importance of drift for young marine fish, the use of drift nets (in the sense described above) is rare in the marine environment. Most data on marine drifting fish has been obtained using towed nets as the marine environment rarely provides conditions of unidirectional flow and stationary points. Indeed, only in exceptional circumstances stationary nets are installed in seawaters, namely in polar waters where nets may be attached to the ice crust and submerged below a seal hole (Sewell et al. 2008), or the installation of plankton nets in shallow coastal-waters (e.g., reef flats; Hendler et al. 1999). Crest nets are stationary nets fixed to the substrate immediately behind the crest of a reef, which sample reef-fish larvae migrating from their nurseries (e.g., mangroves or seagrass beds) to their reef settlement areas, which may also be considered as an example of marine use of drift nets (Dufour and Galzin 1993; Nolan and Danilowicz 2008).

## How drift nets are used to infer fish movement

All that we can be confident about when sampling organisms captured in drift nets is that the organisms were being carried by the current at the time of capture. Any

information on where, when, why and how fish larvae started drifting, or where drift would have terminated if they had not been captured in the drift nets, usually remains hidden. Only through carefully designed studies, in which drift net sampling is accompanied with other sampling methods, measurement of environmental variables and/or modelling, can we infer more detailed information on movement of fish larvae. A number of different reasons have been put forward as to why fish larvae drift; however, few studies have provided definitive proof.

For example, larvae of some species that use estuaries as nursery areas might selectively (i.e., actively) use tidal streams to enter, remain in, or leave an estuary (Hare et al. 2005). Active processes are also connected with drift of freshwater fish larvae. Studies by Robinson et al. (1998), Wolter and Sukhodolov (2008) and Schludermann et al. (2012) demonstrated that at least some of the larvae being carried in a river current do not follow the same paths as passive particles, and that these larvae are capable of (1) actively leaving the current, despite their poor swimming ability, and/or (2) actively choosing currents that would distribute them to a suitable habitat.

In contrast, drift of some organisms may be part of a completely passive process. Drifting eggs, for example, are both passively dislodged and passively distributed. Eggs of lithophilic fish (fish typically spawning on fast-flow gravel beds) (Balon 1975) may be swept by the current from gravel beds and drift for hundreds of metres before becoming adhesive enough to attach to the bottom (Hofer and Kirchhofer 1996). Pelagophilic fish, on the other hand, spawn directly into the water and the eggs can drift for hundreds of kilometres. These eggs develop into larvae during the journey, whereupon some active component may be involved in its further distribution (Jiang et al. 2010). Increased water velocity during times of elevated discharge will often sweep eggs and fish larvae away from shelters, resulting in so called 'catastrophic drift'. Following passive dislodgement, catastrophic drift is also intuitively considered to result in passive distribution, though no study to date has dealt with this question. Larvae may also 'passively' enter a current as a consequence of losing orientation in darkness (Pavlov 1994) or through some other accidental means (*sensu* 'background drift' according to Brittain and Eikeland 1988).

The degree to which active processes contribute to migration of fish larvae and juveniles in most species/age groups is presently unknown. Rather, studies have tended to combine drift net sampling with knowledge of fish life-histories in order to hypothesize on the importance of drift in different fish species/age groups.

The capture of small, early-stage larvae in drift nets set below spawning grounds indicates post-hatching migration. In cases where spawning grounds cannot serve as nurseries, such post-hatching drift is hypothesized as ensuring distribution of early-stage larvae into suitable nurseries. Fast-flow gravel beds, for example, provide optimal oxygen concentrations for eggs of lithophilic fish; however, high water velocity and low food availability make this habitat less than suitable for the larvae. In this case, drift is hypothesized as ensuring movement to slower and richer river stretches (Hofer and Kirchhofer 1996). Post-hatching drift has been reported widely for numerous species, e.g., in potamodromous percids (Priegel 1970), coregonids (Naesje et al. 1986), salmonids (Bardonnet et al. 1993) and cyprinids (Persat and Olivier 1995), as well as anadromous osmerids (Bradbury et al. 2004), lampreys (Harvey et al. 2002) and clupeids (O'Connell and Angermeier 1997). Long distance

spawning migrations are common in these species and larval drift downstream is sometimes considered as compensating for the long distances travelled upstream by adult spawners.

Motivation for post-hatching drift is most apparent in amphidromous gobiids, cottids and galaxiids (Iguchi and Mizuno 1990; McDowall 2007), whose larvae hatch in freshwater. These larvae are incapable of feeding in freshwater and have very limited swimming ability; hence, it is essential that larvae of these species reach marine waters within a few days of hatching (Iguchi and Mizuno 1999).

Drift samples also commonly contain (1) newly-hatched larvae of species that attach eggs to nearshore structures, vegetation or in cavities (i.e., phytophilic, phyto-lithophilic, speleophilic or ostracophilic fish *sensu* Balon 1975) and whose spawning grounds are often close to, or identical to, their nurseries, and (2) late larvae/early juveniles (Pavlov 1994; Reichard and Jurajda 2007). Explanations for their presence vary widely and might include accidental dislodgement, high population density, or habitat shift related to ontogenetic development (Pavlov 1994; Zitek et al. 2004; Reichard and Jurajda 2007).

Drift nets, or their equivalents, are also used to track anadromous post-smoltification migrations of juvenile salmonids and the analogous movement of young acipenserids, although such movements are not completely passive (i.e., fish swim with the current) (Pavlov 1994).

Attaching a drift net to the outlet of a power-generating facility fed by a reservoir, lake or river can not only provide information on fish transfer between two water bodies but also information on young fish movement into the pelagic or benthic zones of the initial water body, depending on the vertical position of the outlet (Kelso and Leslie 1979; Baruš et al. 1986; Carter and Reader 2000). Note that this is independent of whether fish are actively following currents, as in migratory young salmonids and acipenserids (Coutant and Whitney 2000), or are passively entrained as a consequence of crossing in front of a water intake during diel vertical or horizontal migrations (Pavlov et al. 2002). Scientists often additionally record the amount of damage caused to fish by pressure changes, turbine passage or overheating when studying entrainment through power generating facilities (Cada 1991; Carter and Reader 2000).

## How to prepare samples using drift nets

### Net design and exposure time

Drift nets are designed to capture small organisms. The mesh size used is generally determined by the size of organism being studied. A very fine mesh (64 μm) was used by Iguchi and Mizuno (1990) when capturing larvae as small as 1 mm total length; however, most studies use a 400–500 μm mesh, as recommended by Schmutz et al. (1997). Though, a mesh as large as 1 mm can still effectively sample eggs and fish larvae as small as 6 mm standard length (Copp et al. 2002).

The choice of appropriate mesh size should be carefully considered. A too large mesh may damage the smallest fish or let them through (Schmutz et al. 1997), while a too fine mesh may prove effective at catching coarse Particulate Organic Matter (POM), which will lead to gradual clogging of the net. Clogging results in backflow,

which will bias drift density estimates derived from the volume of water filtered (see below). Measuring flow velocity both at the start and end of net exposure provides an adequate estimate of the net clogging effect (with visual inspection providing a rough estimate, naturally). If clogging causes considerable backflow, one can calculate the actual volume of water filtered based in water velocity change. Note, however, that water velocity in gradually clogged nets does not change linearly with exposure time (Faulkner and Copp 2001).

The effects of backflow can be reduced by lengthening the net; however, longer nets are more difficult to handle. The net:mouth area ratio rarely exceeds 6:1 (Schmutz et al. 1997), and a ratio higher than 5:1 is usually considered to provide sufficient efficiency (Kelso and Rutherford 1996; see also Gale and Mohr 1978 for inspiration on net design). Note that reducing the net mouth area (see Elliott 1970) provides the same effect of increasing relative net length, but it will also decrease the volume of water filtered.

Iguchi and Mizuno (1990) constructed their drift net with two mesh sizes, with a fine mesh at the cod end and a coarser mesh near the mouth, allowing coarse POM to be retained in the mouth of the net (Schmutz et al. 1997), while the fine mesh at the cod end would reduce the risk of fish damage.

The negative effects of clogging on drift-net efficiency can be effectively resolved in steep rivers and above weirs or waterfalls, by replacing the net with a horizontal plastic tube (Elliott 1970). This tube feeds water into a net positioned under the tube end outside of the waterbody. Thus, net clogging does not create backflow in the tube. Water volume is calculated based on tube width and exposure time. However, the use of such mechanisms is limited by the habitats in which they can be used and, to date, they were only used for macroinvertebrate drift studies (e.g., Kubíček 1966).

A range of factors, including net clogging, compel scientists to compromise on ideal sampling effort. Exposure time, for example, varies widely between studies, ranging from 10 minutes to 12 hours, with 15–30 minutes being most common in areas containing higher amounts of coarse POM. Short exposure times (lower water volume filtered) lead to an increased probability of missing less common species; while long net exposures increase the probability that captured fish will be damaged and unidentifiable (Schmutz et al. 1997) and prevents determination of diel drift patterns at fine scales (see Elliott 1970 for accompanying problems). Moreover, high volumes of water filtered increase the amount of coarse POM retained in the net, increasing both clogging and subsequent manipulation time due to the "painstaking separation of the sample from organic and mineral debris" that follows each sampling (Faulkner and Copp 2001). Although immediate separation of the sample in the field is less comfortable than sorting preserved samples in the laboratory, it is generally preferred for a number of reasons, including reduction of preservation medium used, reduction of collateral damage to animals not of interest to the study, and, most importantly, it saves time as "living, moving and naturally pigmented animals are easier to spot amongst the debris than dead animals" (Copp et al. 2002).

Based on our experience, a shallow white basin (40x30x5 cm) originally designed for photographic development is suitable for sorting samples of live drifting organisms. Aliquots are poured into the basin in volumes sufficient for detection

of small organisms, but also depending on the amount of coarse POM and water transparency. Then, fish larvae and juveniles are individually removed using tweezers. Small plastic bulb pipettes are extremely useful for removing the smallest fish larvae. The sorted fish are then sacrificed (e.g., by an overdose of anaesthetic) and preserved (4% buffered formaldehyde is widely used). Kelso and Rutherford (1996) provided a detailed discussion on preservation media for fish larvae. When captured eggs and/or larvae are too young to be identified, it is sometimes possible to hatch/raise part of a sample for later determination of more developed stages.

In general, net design and exposure time will depend on the size and density of organisms under study and on the amount of coarse POM. Final net design (shape, size, mesh size) will always represent a compromise between filtration efficiency, clogging rate, sample sorting time (Svendsen et al. 2004) and ease of net manipulation.

## Temporal aspects of sample preparation

### Seasonal aspects

The time of collection will be directly related to the assumed time of fish migration. For most fish species, drift occurs in the earliest life stages and is, therefore, a function of when fish spawn (Brown and Armstrong 1985). Indeed, inter-annual variability in drifting fish assemblages is usually attributed to variability in spawning success (Robinson et al. 1998; Reichard et al. 2002a), though some studies proposed that propensity to drift is density-dependent and can change between years within the same population (Economou 1991).

Strict seasonal patterns enable the planning of sampling campaigns with a precision of a few weeks, with higher precision attainable on the basis of river discharge and water temperature during the spawning season. Water temperature may speed up or slow down both spawning season and egg and larval development, and thus also timing of drift. Notably, drift seasonality in coregonids and salmonids may also be driven by changes in discharge rate (Naesje et al. 1986; Johnston et al. 1995). In general, the first sample of the seasonal cycle should precede the expected start of drift, with two consecutive negative sampling sessions usually taken as an indication that the drift season has come to an end.

Sampling frequency over the course of a season will depend on the aim of the study. Daily intervals (or nightly, as drift occurs mostly at night; see below) intuitively provide the most precise picture of seasonal drift pattern. Daily sampling can be too demanding, especially when studying partial spawners, which appear in drift net samples for long periods. Weekly sampling intervals (approximately) are usually chosen, representing a compromise between precision and effort, but sufficient to record the most important seasonal peaks in drift. Long-term studies that observe changes in drifting fish assemblages over the course of a whole year, for example, may set even longer sampling intervals of up to one month, usually with increased sampling frequency during the periods when drift is expected to peak.

*Diel aspects*

As larval drift occurs mostly at night, it is usually sufficient to collect samples during periods of darkness. However, further sampling may be necessary if diel movement patterns are the main objective of the study. Presence of diel drift patterns in streams is linked to water transparency, with most studies reporting no diel pattern in turbid rivers (Secchi disc transparency lower than 30 cm) (e.g., Pavlov 1994; Pavlov et al. 1995) and nocturnal drift in the vast majority of rivers with transparency higher than 30 cm (Pavlov 1994; see Reeves and Galat 2010 for review). Diel periodicity is not bound strictly to transparency, since species-specific diel patterns have been noted at the same sites (Robinson et al. 1998; Reeves and Galat 2010). Stream morphology may also play a significant role as observed by Iguchi and Mizuno (1990), which reported relaxation of otherwise strictly nocturnal goby diel drift patterns in steep, fast-flowing water courses where fish were likely unable to sustain the water current.

Whole-night, or even 24 hours, observation is tiring. Persat and Olivier (1995) and Zitek et al. (2004) suggested that a single night sample, collected during the first two hours of darkness, may be sufficient to predict drift density for the entire 24 hours. Indeed, a number of studies have reported peak drift density during the first hours of darkness (e.g., Reichard et al. 2002b). Some studies, however, have also noted a second peak just before sunrise (Brown and Armstrong 1985) or a single peak in the middle of the night (Naesje et al. 1986). In all these cases, those samples taken in the two hours after sunset appeared to be reliable predictors of overall drift density for the whole night. Note that a single sample may be insufficient where fish size is of concern, as the size of drifting fish may vary over the course of the night (Sonny et al. 2006, but consult Janáč et al. 2013b for contradictory results).

## Spatial aspects of sample preparation

*Longitudinal aspects*

Longitudinal positioning of drift nets will depend upon the purpose of the study, as in the following examples. When studying drift of young fish from a reservoir, nets are placed at, or close by, the outlet(s) (Pavlov et al. 2002). Alternatively, multiple drift nets positioned across a stream immediately before its confluence with a main stem river, lake, reservoir or the sea will provide a reasonable measure of the amount of fish contributed (Franzin and Harbicht 1992). When the aim is to document the journey of newly hatched fish to the sea, or a lake, the best results are obtained by a longitudinal series of sampling points from the uppermost spawning site to the river's mouth (Priegel 1970).

*Lateral and vertical aspects*

The majority of studies agree that riverine fish drift is observed primarily in relatively shallow zones near the shore (Reichard et al. 2004). Shallow, nearshore habitats are also the most easily accessible and usually do not demand great effort or invention

for net anchoring. It seems reasonable, therefore, to focus on these habitats when preparing drift net samples. One should be aware that spatial drift patterns can differ between species (Brown and Armstrong 1985; Pavlov 1994; Oesmann 2003), age groups (Gale and Mohr 1978; Reichard et al. 2004) and river morphology. Concerning the last topic, Pavlov et al. (2008) noted that "velocity gradients at river channel bends can drastically redistribute fish larvae drifting downstream".

There are two major patterns of vertical distribution when studying drift outside of the shallow zone, namely (1) prevalence of surface drift (Brown and Armstrong 1985; Oesmann 2003), or (2) homogenous distribution throughout the water column (Carter et al. 1986; Franzin and Harbicht 1992). Gale and Mohr (1978) and D'Amours et al. (2001) observed surface drift dominating only during the night, with bottom drift dominating during the day. Graham and Venno (1968), on the other hand, found larvae in surface nets during the ebb tide, while bottom catches prevailed during the flood tide. Notably, some studies suggest that lateral and/or vertical distribution of drifting fish in rivers is more dependent of flow velocity gradients along the transverse profile, rather than the gradient of distance from margin or surface (Copp et al. 2002; Lechner et al. 2013).

## How to interpret and analyze data obtained from drift nets

In common with the general trend in ecological studies, statistical analysis of drift has evolved greatly since the 1960's (Svendsen et al. 2004); though the tools available for basic description of drift net samples remain the same. In general, two approaches are used to describe drift net yield: drift rate and drift density (Elliott 1970).

Drift rate represents a simple count of individuals captured in a standardized net per unit time, but it is rarely used since it is highly correlated with discharge. Intuitively, drift rate will increase with increasing discharge as a larger amount of water will carry more drifting individuals. In exceptional cases, so far only observed in invertebrates, drift rate can increase with decreasing discharge in response to stream desiccation (Elliott 1970).

Drift density, expressed as the number of individuals per volume of water filtered through the net, is generally agreed to be the most useful measure for quantifying drifting fish. The volume of filtered water ($m^3$) can be easily calculated as the area of submersed net mouth ($m^2$) multiplied by flow velocity in the mouth ($m.s^{-1}$) and exposure time(s). In reality, this calculation represents no more than an approximation, as water velocity varies both spatially (within the net mouth) and temporally. However, this approximation is generally acceptable and two measurements of water velocity per sample are considered acceptable. Measurements are usually conducted at the start and end of each sample, using portable flow meters positioned at the centre of the net mouth. Occasionally, high temporal variability in current velocity may call for intermediate measurements. In such cases, flow meters permanently attached to the nets allow continuous measurement of flow velocity and more accurate calculation of filtered water volume.

For decision makers, it is often important to know the total amount of drifting fish, namely when drift is used as an early measure of year-class strength (D'Amours et

al. 2001), or when quantifying number of fish lost from a water body via entrainment into the inlet of a power-generating facility (Kelso and Leslie 1979). Estimates of total number of drifting fish are relatively rare; as they must contend with (1) spatial variability over the transverse profile of the river/outlet, which can be very high, especially in large rivers, and relatively low in reservoir outlets; (2) diel variability; (3) missing data from not sampled dates (continuous sampling is rarely conducted throughout the drift season); and (4) dependence of number of drifting individuals on river discharge.

In order to deal with high spatial heterogeneity, a pilot study should be conducted in order to reveal zones with different drift densities or, alternatively, density gradients. The subsequent full-scale monitoring study should then have drift nets situated in each of the zones observed, allowing estimation of drift density for the whole transverse profile. The total estimate is obtained by averaging the density from each zone, weighted by the proportion that each zone contributes to the total area of the transverse profile. Diel variability can be treated in a similar way, though an approximation to simple day and night densities and duration may be used. Drift density for intervening days (i.e., missing data) can be obtained by interpolation, while diel discharge values can usually be obtained from gauging stations. The following formula can then serve for calculation of total number of drifting fish over a 24 hour interval:

$$N = Q \sum_{i=1}^{n} T_i * d_i$$

where Q is the daily average discharge (m$^3$ s$^{-1}$), $T_i$ is the duration of period $i$ within 24 hours(s), $d_i$ is the drift density during period $i$ (individuals m$^{-3}$) and, commonly n is 2, corresponding to the chosen periods (day and night). Note that, even after this process, the estimate of total number of drifting fish will still have a large degree of uncertainty, due to the number of approximations involved in the process.

By sampling drifting young fish and the source assemblages of young fish concurrently (typically encountered in nearshore areas), the propensity of particular fish species (or developmental stage/size categories) to drift can be revealed. For example, Reichard and Jurajda (2007) calculated a drift index (E) based on relative abundance (RA; % of total number of fish sampled in drift or in nurseries):

$$E = \frac{(RA\ in\ drift - RA\ in\ nurseries)}{(RA\ in\ drift + RA\ in\ nurseries)}.$$

Drift indices such as these will be influenced by bias inherent in the sampling gear used to sample the source assemblages, which will usually consist of species with different habitat preferences (e.g., nearshore pelagic, nearshore demersal and shelter-seeking fish larvae and juveniles).

*Statistical treatment*

Fish abundance data obtained from drift nets will rarely follow a normal distribution. Traditionally, drift data were analyzed using ANOVA (following data transformation) or non-parametric (e.g., Kruskal-Wallis) tests. Generalized Linear Models (GLMs), designed specifically to cope with non-normally distributed data, are now widely

available and we strongly recommend that GLMs should be used to analyze abundance data from drift nets. Numbers of captured fish usually follow a Poisson distribution. However, drift density values are not integers, being standardized to volume of filtered water. In this case, the most appropriate option is using a Poisson distributed GLM on pure count data (i.e., numbers of individuals) with water volume set as an offset parameter (Zuur et al. 2009).

Data obtained from drift nets are frequently correlated, as the sampling design often involves repeated sampling over time (e.g., when assessing seasonal and/or diel patterns) using several nets distributed vertically and horizontally. Variables representing correlation structure (e.g., replicated samples from the same cross-section) often represent 'nuisance variables', which should be modelled as random factors. Several other approaches have been used to overcome the 'problem' of correlated drift net data. If a test of correlation structure undertaken prior to analysis reveals only a weak correlation, for example, data non-independence may be omitted, as outlined by D'Amours et al. (2001). Alternatively, the effect of repeated sampling can be removed by data standardization within a sampling unit (see Janáč et al. 2013a). Such approaches may raise criticism, often rightly, as they may be easily biased or be heavily dependent on subjective criteria. Overall, incorporating random factors into the model appears to be the most appropriate solution for dealing with correlated data; hence, we recommend mixed GLMs or their alternatives (e.g., GLMs with generalized estimation equations) when analyzing drift abundance data (see Zuur et al. 2009).

The effect of abiotic factors (e.g., discharge, temperature, turbidity) on drift density has traditionally been studied using correlations; but they can just as easily be studied using GLMs. In fact, as these abiotic factors are known to influence drift density, incorporating them as covariates into models dealing with drift abundance is often advisable, at least at the stage of model construction.

When size of drifting fish is of concern, two statistical approaches have commonly been applied. Some studies treat fish size as a response variable and use GLMs or traditional Kolmogorov-Smirnov tests, while others tend to categorize fish size into distinct groups and the abundance of the newly established 'pseudo-species' are compared using contingency tables or GLMs.

Multivariate methods are rarely used in the analysis of fish drift samples. However, Zitek et al. (2004) used cluster analysis to distinguish between different spawning events (repeated occurrence of the same size group in drift during a season) and the occurrence of later developmental stages; while Oesmann (2003) used canonical correspondence analysis to explain variability in drifting fish assemblages through environmental variables. Non-parametric multidimensional scaling based on ecological distance matrices (e.g., Bray-Curtis) can also be used to visualize similarities in drift assemblage between different sites or dates.

In general, it is reasonable to compare densities of drifting fish within a river (e.g., when studying seasonal or diel drift patterns or differences between sites). Inter-stream comparisons of drift density are more questionable, mainly due to low representativeness of samples taken from larger rivers where just a small proportion of the river can be sampled. On the other hand, comparisons between different streams are reasonable when comparing assemblage composition of drifting fish, fish propensity to drift or temporal and spatial drift patterns. Some studies have described drift patterns for

the entire assemblage of drifting fish (species pooled rather than separated); however, this is not a good practice as spatial and temporal drift patterns and propensity to drift have proven to be species-specific, at least in some cases (Brown and Armstrong 1985; Reichard and Jurajda 2007). Therefore, we urge that analysis should be undertaken at the species or pseudo-species level, whenever possible.

## Case studies using drift nets

Drift nets have been used to document stream fish drift worldwide, having been used in rivers of Amazonia (Pavlov et al. 1995), Australia (Humphries et al. 2002), South Asia (de Graaf et al. 1999), China (Jiang et al. 2010), Japan (Iguchi and Mizuno 1990), Russia (Pavlov et al. 1977), Europe (Zitek et al. 2004) and northern America (Gale and Mohr 1978), with most studies taking place in the latter three.

In a series of studies, the drift of young fish was monitored in large rivers of Europe, Asia and Amazonia (see Pavlov 1994 for a review). The numerous species captured during the studies documented the widespread occurrence of drift, confirming that it is not restricted to anadromous fishes but occurs also in many strictly freshwater fish, including not only potamodromous fish but also 'stationary species' with limited adult home ranges. Based on the results of these studies, Pavlov (1994) identified a range of mechanisms that influence how fish enter a current, how they react once in the current and how they orientate themselves once there. According to Pavlov (1994), drift primarily results from relaxation or reversing of various retention mechanisms (e.g., negative phototaxis, positive thigmotaxis, shelter seeking or rheoreaction) that have evolved in riverine fish larvae to keep them out of stronger currents.

Brown and Armstrong (1985) used drift nets to document drift of approximately 60 species in the Illinois River (USA). This thorough study was one of the first to describe basic seasonal, diel, lateral and vertical patterns in fish drift, and to demonstrate that drift is a function of when species spawn, a prevailing night-time drift pattern, and preferences for nearshore and surface drift. In combination with concurrent samples of resident larval fish, drift net samples suggested that some species that were abundant in the river may be able to resist drift.

Kennedy and Vinyard (1997) used drift nets to demonstrate drift avoidance in larvae of the small catostomid *Catostomus warnerensis*, hypothesizing that the species evolved 'drift resistance' in response to unreliability of habitats downstream. The almost complete absence of the species in drift nets, reinforced by direct observation of drift cessation in released larvae, supported the authors' hypothesis.

More recently, Schludermann et al. (2012) tested the hypothesis that there may be an active component in the drift of potamodromous nase *Chondrostoma nasus* larvae in the River Danube. The combination of (1) a hydrodynamic model tracing transport of passive particles, and (2) drift net samples of released larvae, marked with alizarin red, revealed that larvae were not distributed in a completely passive manner.

Priegel (1970) used drift nets to document the early life-cycle stages of the potamodromous walleye *Sander vitreus*, concluding on the necessity of larvae leaving their marsh hatching grounds for lake habitats with richer food sources within three–five days. By releasing large numbers of marked (coloured dye) walleye fry and installing

drift nets at several control points along the river, Priegel (1970) calculated the rate of drift spread, proving the ability of small walleye to drift 70 km within just two days.

Iguchi and Mizuno (1999) installed drift nets in several Japanese coastal streams at varying distances from the spawning grounds of the amphidromous goby *Rhinogobius brunneus*. Captures demonstrated that fish travelling further distances were in significantly worse condition than those travelling shorter distances. Thus, the significance of swift transport to the sea (larvae were incapable of feeding in freshwaters), and the related limited reproductive success observed in areas furthest from the sea, contributed greatly to knowledge of amphidromous gobiid life-cycles.

By installing drift nets at the inflow and outflow of a coal-fired power station cooling system, Carter and Reader (2000) estimated the density of fish entrained by the inlet canal from a nearby river, and concluded that all larvae die after passing through the cooling system. Concurrent drift net sampling in the river revealed that species composition and diel and seasonal patterns of drifting fish assemblages corresponded to those entrained at the inlet, confirming that the entrained fish larvae originated mostly from river drift.

Drift nets installed just below the outlet of a shallow, lowland reservoir allowed Janáč et al. (2013a) to monitor diel and seasonal changes in the assemblage of young fish leaving the reservoir through the turbine of a hydropower facility. The study showed that passage of non-native tubenose goby *Proterorhinus semilunaris* through the turbine allowed further downstream spreading of the species. Indeed, they estimated that approximately 0.5 million young tubenose gobies passed into the river, with only a 3% suffering significant damage.

Graham (1971) used drift nets to document the routes taken by larval oceanodromous herring *Clupea harrengus* during ebb and flood tides within an estuary. By installing two vertically stratified sets of drift nets at both the landward and seaward ends of the estuarine channel, Graham (1971) revealed differences in the vertical distribution of larvae carried by tidal currents, and thus demonstrating "a system of larval movement that retains the larvae within the estuary." The suggested retention mechanism consists of (1) up-estuary movement via flow near the bottom, (2) upward movement through the water column upon reaching the limit of up-estuary movement, (3) down-estuary movement via surface flow, and (4) descent again into the up-estuary bottom flow.

Hare et al. (2005) used drift nets to sample larvae of several fish species (mostly *Micropogonias undulatus*, *Brevoortia tyrannus* and *Paralichthys dentatus*) migrating from continental shelf spawning sites to estuarine nurseries. With the addition of extensive measurement of physical variables, the authors tested several hypotheses regarding larval ingress mechanisms, including their relative importance. Tidally driven ingress was of particularly high importance, with higher larval concentrations present during up-estuary flood tides compared to low concentrations during down-estuary ebb tides. The authors rejected several hypotheses connecting tidally driven larval flux with purely physical processes (e.g., tidal change in water column density or vertical mixing), thus supporting the hypothesis that tidally driven larval flux results from active behaviour.

In general, knowledge of larval and juvenile migration still remains relatively limited and even purely descriptive studies are desirable. Future research on

the migration of early fish life stages should include controlled experiments that test hypotheses originating from descriptive studies (Reichard et al. 2002b; Faria and Gonçalves 2010) and from individual based models (Peck et al. 2009).

## Acknowledgements

## References

Balon EK (1975) Reproductive guilds of fishes—proposal and definition. Journal of the Fisheries Research Board of Canada 32: 821–864.

Bardonnet A, Gaudin P and Thorpe JE (1993) Diel rhythm of emergence and of 1st displacement downstream in trout (*Salmo trutta*), atlantic salmon (*S. salar*) and grayling (*Thymallus thymallus*). Journal of Fish Biology 43: 755–762.

Baruš V, Gajdůšek J, Pavlov DS and Nezdolij VK (1986) Downstream fish migration from the Mostiště and Věstonice reservoirs (ČSSR) in the spring-summer period. Folia Zoologica 35: 79–93.

Bradbury IR, Campana SE, Bentzen P and Snelgrove PVR (2004) Synchronized hatch and its ecological significance in rainbow smelt *Osmerus mordax* in St. Mary's bay, Newfoundland. Limnology and Oceanography 49: 2310–2315.

Brett JR (1948) The design and operation of a trap for the capture of migrating young sockeye salmon. Transactions of the American Fisheries Society 75: 97–104.

Brittain JE and Eikeland TJ (1988) Invertebrate drift—a review. Hydrobiologia 166: 77–93.

Brown AV and Armstrong ML (1985) Propensity to drift downstream among various species of fish. Journal of Freshwater Ecology 3: 3–17.

Cada GF (1991) Effects of hydroelectric turbine passage on fish early life stages. pp. 318–326. *In*: Darling DD (ed.). Waterpower '91: A New View of Hydro Resources. American Society of Civil Engineers, New York.

Carter JG, Lamarra VA and Ryel RJ (1986) Drift of larval fishes in the upper Colorado River. Journal of Freshwater Ecology 3: 567–577.

Carter KL and Reader JP (2000) Patterns of drift and power station entrainment of 0 + fish in the River Trent, england. Fisheries Management and Ecology 7: 447–464.

Copp GH, Faulkner H, Doherty S, Watkins MS and Majecki J (2002) Diel drift behaviour of fish eggs and larvae, in particular barbel, *Barbus barbus* (L.), in an English chalk stream. Fisheries Management and Ecology 9: 95–103.

Coutant CC and Whitney RR (2000) Fish behavior in relation to passage through hydropower turbines: a review. Transactions of the American Fisheries Society 129: 351–380.

Dahms HU and Qian PY (2004) Drift-pump and drift-net-two devices for the collection of bottom-near drifting biota. Journal of Experimental Marine Biology and Ecology 301: 29–37.

D'Amours J, Thibodeau S and Fortin R (2001) Comparison of lake sturgeon (*Acipenser fulvescens*), *Stizostedion* spp., *Catostomus* spp., *Moxostoma* spp., quillback (*Carpiodes cyprinus*), and mooneye (*Hiodon tergisus*) larval drift in des prairies river, quebec. Canadian Journal of Zoology-Revue Canadienne De Zoologie 79: 1472–1489.

de Graaf GJ, Born AF, Uddin AMK and Huda S (1999) Larval fish movement in the river Lohajang, Tangail, Bangladesh. Fisheries Management and Ecology 6: 109–120.

Dufour V and Galzin R (1993) Colonization patterns of reef fish larvae to the lagoon at Moorea Island, French-Polynesia. Marine Ecology Progress Series 102: 143–152.

Economou AN (1991) Is dispersal of fish eggs, embryos and larvae an insurance against density dependence? Environmental Biology of Fishes 31: 313–321.

Elliott JM (1970) Methods of sampling invertebrate drift in running water. Annls Limnologie 6: 133–159.

FAO (Food and Agriculture Organization) (2013) Fishing Gear types. Driftnets. Technology Fact Sheets. *In*: FAO Fisheries and Aquaculture Department[online].Rome. http://www.fao.org/fishery/geartype/220/en. Accessed 5 September 2013.

Faria AM and Gonçalves EJ (2010) Ontogeny of swimming behaviour of two temperate cling fishes, *Lepadogaster lepadogaster* and *L. purpurea* (Gobiesocidae). Marine Ecology Progress Series 414: 237–248.

Faulkner H and Copp GH (2001) A model for accurate drift estimation in streams. Freshwater Biology 46: 723–733.

Franzin WG and Harbicht SM (1992) Tests of drift samplers for estimating abundance of recently hatched walleye larvae in small rivers. North American Journal of Fisheries Management 12: 396–405.

Gale WF and Mohr HW (1978) Larval fish drift in a large river with a comparison of sampling methods. Transactions of the American Fisheries Society 107: 46–55.

Graham JJ (1971) Retention of larval herring within the Sheepscot estuary of Maine. Fishery Bulletin 70: 299–305.

Graham JJ and Venno PMW (1968) Sampling larval herring from tidewaters with buoyed and anchored nets. Journal of the Fisheries Research Board of Canada 25: 1169–1179.

Hare JA, Thorrold S, Walsh H, Reiss C, Valle-Levinson A and Jones C (2005) Biophysical mechanisms of larval fish ingress into Chesapeake Bay. Marine Ecology Progress Series 303: 295–310.

Harvey BC, White JL and Nakamoto RJ (2002) Habitat relationships and larval drift of native and nonindigenous fishes in neighboring tributaries of a coastal california river. Transactions of the American Fisheries Society 131: 159–170.

Hendler G, Baldwin CC, Smith DG and Thacker CE (1999) Planktonic dispersal of juvenile brittle stars (Echinodermata: Ophiuroidea) on a caribbean reef. Bulletin of Marine Science 65: 283–288.

Hettler WF (1979) Modified neuston net for collecting live larval and juvenile fish. The Progressive Fish-Culturist 41: 32–33.

Hofer K and Kirchhofer A (1996) Drift, habitat choice and growth of the nase (*Chondrostoma nasus*, Cyprinidae) during early life stages, Vol. Birkhauser Verlag, Basel.

Humphries P, Serafini LG and King AJ (2002) River regulation and fish larvae: variation through space and time. Freshwater Biology 47: 1307–1331.

Iguchi K and Mizuno N (1990) Diel changes of larval drift among amphidromous gobies in Japan, especially *Rhinogobius brunneus*. Journal of Fish Biology 37: 255–264.

Iguchi K and Mizuno N (1999) Early starvation limits survival in amphidromous fishes. Journal of Fish Biology 54: 705–712.

Janáč M, Jurajda P, Kružíková L, Roche K and Prášek V (2013a) Reservoir to river passage of age-0 + year fishes, indication of a dispersion pathway for a non-native species. Journal of Fish Biology 82: 994–1010.

Janáč M, Šlapanský L, Valová Z and Jurajda P (2013b) Downstream drift of round goby (*Neogobius melanostomus*) and tubenose goby (*Proterorhinus semilunaris*) in their non-native area. Ecology of Freshwater Fish 22: 430–438.

Jiang W, Liu HZ, Duan ZH and Cao WX (2010) Seasonal variation in drifting eggs and larvae in the upper yangtze, china. Zoological Science 27: 402–409.

Johnson SL, Rodgers JD, Solazzi MF and Nickelson TE (2005) Effects of an increase in large wood on abundance and survival of juvenile salmonids (*Oncorhynchus* spp.) in an Oregon coastal stream. Canadian Journal of Fisheries and Aquatic Sciences 62: 412–424.

Johnston TA, Gaboury MN, Janusz RA and Janusz LR (1995) Larval fish drift in the valley river, manitoba: Influence of abiotic and biotic factors, and relationships with future year class strengths. Canadian Journal of Fisheries and Aquatic Sciences 52: 2423–2431.

Kelso JRM and Leslie JK (1979) Entrainment of larval fish by the douglas point generating-station, lake huron, in relation to seasonal succession and distribution. Journal of the Fisheries Research Board of Canada 36: 37–41.

Kelso WE and Rutherford DA (1996) Collection, preservation, and identification of fish eggs and larvae. *In*: Murphy BR and Willis DW (eds.). Fisheries Techniques. American Fisheries Society, Bethesda, MD.

Kennedy TB and Vinyard GL (1997) Drift ecology of western catostomid larvae with emphasis on warner suckers, *Catostomus warnerensis* (Teleostei). Environmental Biology of Fishes 49: 187–195.

Kubíček F (1966) Eine neue methode der quantitativen entnahme der organischen drift. Zoologické Listy 15: 284–285.

Lechner A, Keckeis H, Schludermann E, Humphries S, McCasker N and Tritthart M (2013) Hydraulic forces impact larval fish drift in the free flowing section of a large european river. Ecohydrology 7: 648–658.

Lewis RM, Hettler WF, Nelson Johnson G and Wilkens EPH (1970) A channel net for catching larval fishes. Chesapeake Science 11: 196–197, 191p191.

Lindsay JA, Radle ER and Wang JCS (1978) Supplemental sampling method for estuarine ichthyoplankton with emphasis on Atherinidae. Estuaries 1: 61–64.

McDowall RM (2007) On amphidromy, a distinct form of diadromy in aquatic organisms. Fish and Fisheries 8: 1–13.

Müller K (1966) Die tagesperiodik von fliesswasserorganismen. Zeitschrift fuer Morphologie und Oekologie der Tiere 56: 93–142.

Naesje TF, Jonsson B and Sandlund OT (1986) Drift of cisco and whitefish larvae in a norwegian river. Transactions of the American Fisheries Society 115: 89–93.

Needham PR (1928) A quantitative study of the fish food supply. NY State Conservation Department Annual Report 17: 192–206.

Nester RT (1987) Horizontal ichthyoplankton tow-net system with unobstructed net opening. North American Journal of Fisheries Management 7: 148–150.

Nolan CJ and Danilowicz BS (2008) Advantages of using crest nets to sample presettlement larvae of reef fishes in the Caribbean Sea. Fishery Bulletin 106: 213–221.

O'Connell AM and Angermeier PL (1997) Spawning location and distribution of early life stages of alewife and blueback herring in a Virginia stream. Estuaries 20: 779–791.

Oesmann S (2003) Vertical, lateral and diurnal drift patterns of fish larvae in a large lowland river, the elbe. Journal of Applied Ichthyology 19: 284–293.

Pavlov DS (1994) The downstream migration of young fishes in rivers—mechanisms and distribution. Folia Zoologica 43: 193–208.

Pavlov DS, Pakhorukov AM, Kuragina GN, Nezdolii VK, Nekrasova NP, Brodskii DA and Ersler AL (1977) Some peculiarities of downstream migrations of young fishes in the Volga and Kuban rivers. Voprosy ikhthiologii 17: 415–428.

Pavlov DS, Nezdoliy VK, Urteaga AK and Sanches OR (1995) Downstream migration of juvenile fishes in the rivers of Amazonian Peru. Voprosy ikhthiologii 35: 227–247.

Pavlov DS, Lupandin AI and Kostin VV (2002) Downstream Migration of Fish through Dams of Hydroelectric Power Plants, Vol. Oak Ridge National Laboratory, Oak Ridge, Tennessee.

Pavlov DS, Mikheev VN, Lupandin AI and Skorobogatov MA (2008) Ecological and behavioural influences on juvenile fish migrations in regulated rivers: a review of experimental and field studies. Hydrobiologia 609: 125–138.

Peck MA, Kühn W, Hinrichsen H-H and Pohlmann T (2009) Inter-annual and inter-specific differences in the drift of fish eggs and yolksac larvae in the North Sea: a biophysical modeling approach. Scientia Marina 73S1: 23–36.

Persat H and Olivier JM (1995) The first displacements in the early stages of *Chondrostoma nasus* under experimental conditions. Folia Zoologica 44: 43–50.

Priegel GR (1970) Reproduction and early life history of the walleye in the lake winnebago region. Wisconsin Department of Natural Resources Technical Bulletin 45: 1–105.

Reeves KS and Galat DL (2010) Do larval fishes exhibit diel drift patterns in a large, turbid river? Journal of Applied Ichthyology 26: 571–577.

Reichard M and Jurajda P (2007) Seasonal dynamics and age structure of drifting cyprinid fishes: an interspecific comparison. Ecology of Freshwater Fish 16: 482–492.

Reichard M, Jurajda P and Ondračková M (2002a) Interannual variability in seasonal dynamics and species composition of drifting young-of-the-year fishes in two european lowland rivers. Journal of Fish Biology 60: 87–101.

Reichard M, Jurajda P and Ondračková M (2002b) The effect of light intensity on the drift of young-of-the-year cyprinid fishes. Journal of Fish Biology 61: 1063–1066.

Reichard M, Jurajda P and Smith C (2004) Spatial distribution of drifting cyprinid fishes in a shallow lowland river. Archiv für Hydrobiologie 159: 395–407.

Robinson AT, Clarkson RW and Forrest RE (1998) Dispersal of larval fishes in a regulated river tributary. Transactions of the American Fisheries Society 127: 772–786.

Sewell MA, Van Dijken SG and Suberg L (2008) The cryopelagic meroplankton community in the shallow waters of gerlache inlet, Terra Nova Bay, Antarctica. Antarctic Science 20: 53–59.

Schludermann E, Tritthart M, Humphries P and Keckeis H (2012) Dispersal and retention of larval fish in a potential nursery habitat of a large temperate river: an experimental study. Canadian Journal of Fisheries and Aquatic Sciences 69: 1302–1315.

Schmutz S, Zitek A and Dorninger C (1997) A new automatic drift sampler for riverine fish. Archiv für Hydrobiologie 139: 449–460.

Sonny D, Jorry S, Watriez X and Philippart JC (2006) Inter-annual and diel patterns of the drift of cyprinid fishes in a small tributary of the Meuse river, belgium. Folia Zoologica 55: 75–85.

Svendsen CR, Quinn T and Kolbe D (2004) Review of Macroinvertebrate Drift in Lotic Ecosystems. Wildlife Research Program, Seattle.

Waters TF (1972) The drift of stream insects. Annual Review of Entomology 17: 253: 272.

Wolf P (1951) A trap for the capture of fish and other organisms moving downstream. Transactions of the American Fisheries Society 80: 41–45.

Wolter C and Sukhodolov A (2008) Random displacement versus habitat choice of fish larvae in rivers. River Research and Applications 24: 661–672.

Zitek A, Schmutz S and Ploner A (2004) Fish drift in a Danube sidearm-system: Ii. Seasonal and diurnal patterns. Journal of Fish Biology 65: 1339–1357.

Zuur AF, Ieno EN, Walker N, Saveliev AA and Smith GM (2009) Mixed Effects Models and Extensions in Ecology with R. Springer-Verlag, New York. 574p.