Chapter 7

Age and growth

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7.1 Introduction

Flatfishes are very accessible in the wild and hardy in the laboratory, thus many of the early studies of fish growth used flatfishes, especially plaice (Pleuronectes platessa) in the Atlantic and a number of species in the Pacific. As the science of fisheries developed, so did the need to quantify the population structure and growth characteristics of the different flatfish species. In fact, the importance of ageing fishes and determining their growth rate was realised early in the last century (Allen 1916).

Much of the early information on the aging and growth of flatfishes (primarily plaice) is referenced in Wimpenny (1953), Graham (1956) and Beverton & Holt (1957). Prior to the 1950s researchers had gained a fairly good understanding of the methods. A clear pattern of summer and winter growth was recognised in the otoliths, which were first used in the late 1800s. Other bony structures such as opercular bones, the pectoral girdle and the concave faces of the vertebrae exhibited seasonal growth patterns (Cunningham 1905) but these were not as distinctive as those on the otoliths. The observation that a pair of rings may not delimit 1 year’s growth led to early verification studies based on marginal increment analyses. Experimental work on plaice and flounder (Platichthys flesus) showed that the seasonal pattern on both otoliths and scales was primarily driven by seasonal changes in water temperature rather than by variations in food availability. The use of otoliths for age estimation of flatfishes was not universal. Species differences slowly became apparent and methodological refinements followed.

Direct measurements of the growth of flatfishes were afforded by series of tagging and transplantation experiments, and laboratory or enclosure experiments (Johnstone et al. 1921). In all cases it was apparent that there was considerable variability in individual growth rates and that growth rates varied between areas. The widespread sexual dimorphism in growth with females growing faster and reaching larger sizes than males was also recognised (e.g. Johnstone et al. 1921; Bigelow & Schroeder 1953; Bagenal, 1955).

The effects of gear selectivity and ontogenetic behavioural changes of flatfishes on the accurate estimation of age structure and growth rates were recognised, especially with the offshore movement of larger juvenile plaice from the nursery grounds and a general offshore movement with size and age. The possibility that fishing pressure could make major changes to the age structure and growth of commercially exploited flatfish populations was mentioned by Jones (1958), citing the prevalence of Rosa Lee’s phenomenon in plaice.
The transplantation experiments in the late 1800s and early 1900s were the first comprehensive studies on the manipulation of plaice growth rates. Transplantations from low to high productivity areas (Jutland coast to the shallow Limfjord (Anonymous 1909) or from the English coastal region to the Dogger Bank) resulted in an enhanced growth rate. However, anthropogenic effects were not well studied and only a few studies demonstrated the influence of contaminants on growth rates (e.g. Dilling et al. 1926).

Beginning in the 1950s more studies focused on growth during the juvenile stages, especially on nursery grounds. These studies were motivated by the drive to understand recruitment and the increasing interest in ecology. Also, the development of modern mariculture depended primarily on experimental work with flatfishes. These studies confirmed previous findings and provided new information on growth during the larval stages. The rapid advances in methodology and general understanding of subcellular biology from the early 1970s onward allowed very rapid advances to be made into new approaches to the study of age and growth in fishes.

7.2 Age estimation

7.2.1 Larvae and juveniles

Age estimation studies of larval flatfishes are confined to rather few species, despite the value of determining the age of larvae for recruitment studies. The otoliths of juvenile flatfish have a number of characteristics that provide valuable information. There are usually one or two increments close to the core of the otolith that indicate hatching, or other events soon after hatching. The otolith is nearly spherical during larval development, but becomes more hemispherical close to metamorphosis.

The majority of validation studies have confirmed that primary increments are formed daily in the otoliths of larval and juvenile flatfish. Experimental studies have supported the use of primary increment counts to estimate age for wild larvae of plaice (Hovenkamp 1990), common sole (Solea solea) (Amara et al. 1994), flounder (Bos 1999), and the greenback flounder (Rhombosolea tapirina) and longsnout flounder (Ammotretis rostratus) in Australia (Jenkins 1987). However, winter flounder (Pseudopleuronectes americanus) (Casas 1998), turbot (Psetta maxima) (Geffen 1982) and summer flounder (Paralichthys dentatus) (Szedlmayer & Able 1992) have exhibited non-daily increment formation during the larval stage. Specific developmental events can be recorded as distinct otolith features and this enables the estimation of individual age at different stages during early life history. Such developmental events include hatching (e.g. in plaice; Karakiri & von Westernhagen 1989), and mouth opening (e.g. in sole; Lagardere & Troadec 1997) or first feeding (e.g. in California flounder (Paralichthys californicus); Kramer 1991).

During metamorphosis the shape of the otolith changes dramatically. Accessory growth centres are formed at points on the surface of the otolith, and these tend to shape the growing otolith into the flattened rectangular shape characteristic of the adults. The formation of the growth centres is clearly associated with metamorphosis but the exact timing seems to differ among species. For example, in thickback sole (Microchirus variegatus) accessory growth centres form before the migrating eye has crossed the midplane (dorsal edge) but in sole the
growth centres do not form until after the eye has crossed the midplane (Amara et al. 1998). In plaice, the first of the accessory growth centres forms at the end of stage 4 (Ryland 1966) when the body is already flattened and the eye has completed migration (Modin et al. 1996). In Dover sole (Microstomus pacificus) the growth centres form when the eye migration begins (Markle et al. 1992). In windowpane (Scophthalmus aquosus) the formation of the accessory growth centres begins after the migrating eye has crossed the midplane and continues until the end of metamorphosis (Neuman et al. 2001). The otoliths of juvenile greenback flounder, however, do not seem to form accessory growth centres, even after settlement (May & Jenkins 1992). Disruptions in increment formation have been associated with metamorphosis in some species (Campana 1984; Jenkins 1987; Lagardère & Troadec 1997), and age estimations covering this period may have higher associated errors. During metamorphosis and for a short period afterwards the otoliths are asymmetrical, both in shape and in size, and this asymmetry may also affect age estimation (Sogard 1991). Increments formed within the accessory growth centres may not represent daily growth, and it is not clear whether the otolith surface in the areas between growth centres continues to accrete daily increments. However, once the individual growth centres expand and come into contact with one another, new material is once again accreted over the whole surface. In most species examined, the post-metamorphic, post-growth centre, otolith increments are formed daily and thus age estimates derived from these counts are considered valid (Table 7.1). Counts of the primary increments in the post-metamorphic area of juvenile flatfish otoliths can give valuable information about the timing and patterns of settlement. Separate settlement cohorts of different ages were identified in plaice (Al-Hossaini et al. 1989) and common sole (Amara & Lagardere 1995).

### 7.2.2 Adults

Age estimation in flatfish is primarily accomplished using otoliths. In fact, the work that is most commonly cited as the first example of age estimation using otoliths is a study of plaice (Reibisch 1899). In the majority of species examined the otoliths display clear and

| Table 7.1: Validated otolith age estimates for larval and juvenile flatfishes |
|-------------------------|-----------------------------|------------------------|
| Species                | Comments                                   | References              |
| Starry flounder        | Disrupted increments during metamorphosis | Campana 1984            |
| (Platichthys stellatus)|                                           |                        |
| Plaice                 | Larvae                                     | Karakiri & von Westernhagen 1989 |
|                        | During metamorphosis                        | Modin et al. 1996       |
|                        | Juveniles                                   | Al-Hossaini & Pitcher 1988 |
| Winter flounder        | Larvae                                     | Casas 1998              |
|                        | Juveniles                                   | Sogard 1991             |
| Common sole            | Low contrast increments during metamorphosis| Lagardère & Troadec 1997|
| Dover sole             | Larvae                                     | Butler et al. 1996      |
| Greenback flounder and | Disrupted increments during metamorphosis  | Jenkins 1987            |
| long-nose flounder     |                                           |                        |
| (Ammotretis rostratus) |                                           |                        |
| Summer flounder        | Larvae                                     | Szedlmayer & Able 1992  |
| Fringed flounder       | Juveniles                                  | Reichert et al. 2000    |
| (Etropus crossotus)    |                                           |                        |
unambiguous increments, a factor that led to the early acceptance of their use as an accurate method of age estimation. Notable exceptions are yellowtail flounder (Limanda ferruginea) and summer flounder, which are aged using scales (http://www.nefsc.noaa.gov/fbi/speciestbl.html; Penttila & Dery 1988). Difficulties in age estimation using otoliths sometimes occur in species such as plaice (Nash et al. 1992), long rough dab and winter flounder (Penttila & Dery 1988) because the first annulus is missing or indistinct. Some warm-water or short-lived species also lack an easily interpreted otolith annulus pattern for age estimation, e.g. wide-eyed flounder (Bothas podas) (Nash et al. 1991; Reichert 1998) and some tropical cynoglossids (Terwilliger & Munroe 1999).

7.3 Growth of larvae

The potential value of flatfishes in the aquaculture industry has stimulated detailed studies of larval growth, and the factors influencing growth rates, for many species. In contrast, the studies of larval flatfish growth in nature are relatively few. Prior to the 1980s most studies of larval growth consisted of studying changes in mean size or in length frequency distributions over time. Because the growth estimations were crude, there was little attempt to relate growth rates to physical or biological variables. Shelbourne (1957) was probably the first to estimate the effect of food supply on larval growth, by comparing the size of plaice larvae in ‘good and bad plankton patches’. Larval growth rates, determined from laboratory and field observations, are often slow during the yolk-sac stage, but rapid from first feeding until metamorphosis.

7.3.1 Variation in growth

Individual variation in growth rates is a significant feature of larval and juvenile flatfishes (Mollander & Mollander-Swedmark 1957; Shelbourne et al. 1963; Chambers et al. 1988; Bertram et al. 1997; Benoit & Pepin 1999a). Within sibling groups there is usually little variation in size at hatching, and variability in yolk-sac utilisation is also limited. Thus, most of the variation in growth rate is probably attributable to differences in food acquisition and metabolism. Differential growth rates in settling and juvenile flatfishes may be key factors to understanding mortality patterns in natural populations (Chambers & Leggett 1992; FitzHugh et al. 1996; Amara et al. 1997). These same growth features of flatfish populations cause problems in commercial aquaculture and significant effort has been invested in reducing individual variation in growth (Bengtson 1999; Klokseth & Oiestad 1999; Gavlik et al. 2002). In aquaculture systems the production of uniform cohorts of juveniles can improve feeding regimes and reduce the need for handling and grading, and reduce harassment within groups (Bengtson 1999; Burke et al. 1999; Dou et al. 2000).

7.3.2 Factors affecting larval growth

The size at hatching for flatfish varies considerably between species, and this variation generates very different patterns of feeding and larval growth rates. Larvae at hatching range from 2–3 mm in turbot to 15 mm in Atlantic halibut (Hippoglossus hippoglossus). Even between
closely related Pleuronectidae, newly hatched plaice larvae are five times larger than flounder. Accompanying these differences are differences in the amount of yolk-sac at hatching, yolk utilisation efficiencies and differences in mouth size. There are also differences in the development of the mouth at hatching. Some species can feed immediately but others hatch without functional mouths. Yolk-sac utilisation and growth on an endogenous food supply extends from less than 1 day in tropical cynoglossids, to months in the case of Atlantic halibut. Yolk utilisation efficiencies can be high, especially in cold-water species (Houde & Zastrow 1993). Flatfish larvae continue to increase in length until shortly before the end of the yolk-sac period (Ehrlich & Blaxter 1976; Howell 1980; Fukuhara 1990).

Here four factors that can affect larval growth rates have been highlighted, namely food, temperature, density and maternal effects (see Table 7.2). In general, there is a positive relationship between food levels and growth rate but there are instances where growth does not appear to be affected by prey concentrations. Food quality is also an important factor for some species, but some species appear to be very resilient to food quality and this probably distinguishes some warm-water species from cold-water species. Temperature also has a profound effect on growth rates over both temporal and spatial scales. Tracking changes in the thermal history of larvae has been undertaken using Sr/Ca ratios in the otoliths but this method is not always reliable (Toole et al. 1993). The density of individuals can cause the development of size variation in larvae, presumably through changes in growth rate. Often the differences in growth rate are caused by differences in food acquisition. Around metamorphosis various behaviours and/or cannibalism come into play. The last factor is maternal effects. The term ‘maternal effects’ is used to group together a set of influences that are not strictly genetic, but relate to the effects of maternal condition and age on the amount and quality of yolk and the size of larvae at hatching. In general, larger eggs produce larger larvae, often with more yolk reserves and better feeding success and survival. Most flatfish are serial spawners (Chapter 4), and the interval between ovulations can be as short as 24 hours in species such as common sole (Child et al. 1991), Senegalese sole (Solea senegalensis) (Dinis et al. 1999), the New Zealand turbot (Colistium multidinnis) (Tait & Hickman 2001) or as long as 3 days in turbot (Howell & Scott 1989; McEvoy & McEvoy 1992), Atlantic halibut (Olsen et al. 1999) and plaice (Nash et al. 2000). Smaller females seem to produce smaller eggs, and egg size often decreases over successive spawnings.

### 7.4 Growth during metamorphosis

During metamorphosis flatfish larvae often spend the majority of their time in the water column, feeding on planktonic prey (Jenkins 1987; Grover 1998; Fernandez-Diaz et al. 2001). The developmental changes associated with metamorphosis may take priority over somatic growth, especially growth in length (Osse & Van den Boogaart 1997). These same developmental changes may also temporarily impair the ability of larvae to capture prey and thus reduce food consumption (Wyatt 1972; Keeffe & Able 1993) and growth. Although relatively few studies address this question specifically, declines in growth during metamorphosis have been measured in both laboratory and field studies (Table 7.3).

The relationship between larval growth rate, size and metamorphosis has received considerable attention in both laboratory and field studies. In several species it is clear that
<table>
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<th>Factor</th>
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<th>Species</th>
<th>Location</th>
<th>Reference</th>
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<tbody>
<tr>
<td>Food</td>
<td>Growth rate affected by prey concentration</td>
<td>Growth rates of many flatfish larvae seem to respond quickly to changes in food availability</td>
<td>Various</td>
<td>Laboratory</td>
<td>Wyatt 1972; Houde &amp; Schekter 1980; Bisbal &amp; Bengtson 1995; Rabe &amp; Brossen 2000</td>
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<td></td>
<td></td>
<td></td>
<td>Various</td>
<td>Field</td>
<td>Shelbourne 1957; Wyatt 1972; Lyczkowski &amp; Richardson 1979; Grover 1998</td>
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<td></td>
<td>Demonstration of growth compensation with food levels</td>
<td></td>
<td>Summer flounder</td>
<td>Laboratory</td>
<td>Bisbal &amp; Bengtson 1995</td>
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<td>Flathead sole</td>
<td>Laboratory</td>
<td>Haldorson et al. 1989</td>
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<td></td>
<td>Growth rate not affected by prey concentration</td>
<td></td>
<td>Witch</td>
<td>Laboratory</td>
<td>Rabe &amp; Brown 2001</td>
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<td></td>
<td>Growth rates affected by food quality</td>
<td>Some species are resilient to changes in nutritional quality (highly unsaturated fatty acid (HUFAs) composition) of the food</td>
<td>Plaice, Japanese flounder, southern flounder (Paralichthys lethostigma), Atlantic halibut</td>
<td>Laboratory</td>
<td>Dickey-Collas &amp; Geffen 1992; Alam et al. 2001; Denson &amp; Smith 1997; Hamre et al. 2002</td>
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<td></td>
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<td>Some species dependent on specific fatty acids, more vulnerable to poor feeding conditions</td>
<td>Japanese flounder, turbot, summer flounder, yellowtail flounder, Atlantic halibut</td>
<td>Laboratory</td>
<td>Estevez et al. 1997, 1999; Baker et al. 1998; Copeman et al. 2002; Olsen et al. 1999</td>
</tr>
<tr>
<td>Temperature</td>
<td>Temperature has a significant on growth rate</td>
<td>Warm-water species</td>
<td>Lined sole (Archipus bilineatus), southern flounder, summer flounder</td>
<td>Laboratory</td>
<td>Houde 1974; Burke et al. 1999; Gibson &amp; Johnston 1995; Johns et al. 1981</td>
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<td></td>
<td></td>
<td>Seasonal and inter-annual variations in temperature</td>
<td>Common sole, plaice</td>
<td>Field</td>
<td>Amara et al. 1994; Hovenkamp 1989; Hovenkamp &amp; Wite 1991</td>
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<td></td>
<td>Over latitudinal gradients differences in growth rate of a species may also be due to genetic or feeding conditions</td>
<td>Various</td>
<td>Field</td>
<td>Miller et al. 1991; Minami &amp; Tanaka 1992; Chambers et al. 1995</td>
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Density

Development of size variations within populations

Assumed to be the result of behavioural differences in prey detection and capture, leading to differential food acquisition. Harassing or aggressive behaviours and cannibalism are frequently observed during metamorphosis and settlement.

Various

Laboratory

Wyatt 1972; Rabe & Brown 2000, 2001; Mollander & Mollander-Swedmark 1957

Harassing or aggressive behaviours and cannibalism are frequently observed during metamorphosis and settlement.

Various

Laboratory

Houde 1977; Takahashi 1994; Daniels et al. 1996; Dou et al. 2000; King et al. 2000

Maternal effects

Size of eggs varies which influences the size at hatching and growth rate of larvae

There is some influence of egg size on egg development times, and eggs that hatch earlier produce smaller larvae with larger yolk-sacs. Growth rates of individual larvae are often affected by their size at hatching and amount of yolk reserves.

Maternal effects have been shown to influence growth and survival past the larval period.

Yellowtail flounder, plaice

Laboratory

Benoit & Pepin 1999b; Fox et al. 2003

Winter flounder, American plaice, yellowtail flounder

Laboratory

Chambers & Leggett 1992; Walsh 1994; Benoit & Pepin 1999b

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<td>Maternal effects</td>
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<td></td>
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<td></td>
<td>Winter flounder, American plaice, yellowtail flounder</td>
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metamorphosis is a size-related event, yet in others it seems to depend more on larval growth rate rather than absolute size. In some species there is a sharp size threshold for metamorphosis resulting in a fairly synchronised settling and uniform post-settlement size distribution (Fernandez-Diaz et al. 2001). In other species the size threshold for metamorphosis or settling is broader (Gavlik et al. 2002). Within a species, environmental conditions that affect larval growth rate may also affect growth during metamorphosis and the pattern of metamorphosis. Burke et al. (1999) reported that higher temperatures increased larval growth rate and resulted in more synchronised settlement in summer flounder. Poor feeding conditions resulted in slower larval growth followed by smaller size at metamorphosis in the Senegal sole, and metamorphosis was also less synchronised (Fernandez-Diaz et al. 2001).

In general, the variation in size at metamorphosis is greater than the variation in age at metamorphosis, at least for most of the experimental data on flatfish species reviewed by Chambers and Leggett (1987). The same is true of common sole (Boulhic et al. 1992; Amara & Lagardere 1995) and arrowtooth flounder (Reinhardtius hippoglossoides) (Bouwens et al. 1999) larvae collected in the wild. Higher temperatures leading to increased larval growth rates result in metamorphosis at larger sizes in most species examined (Benoit & Pepin 1999a), although in some species, such as Japanese flounder, Paralichthys olivaceus (Seikai et al. 1986), length at metamorphosis increased for slower growing larvae. Growth rate and size at metamorphosis are often uncoupled in plaice, and larvae may grow quickly and metamorphose at a small size or grow slowly and metamorphose at a larger size (Hovenkamp & Witte 1991).

In the wild, flatfishes may be particularly vulnerable during metamorphosis, although one study showed that the escape response of winter flounder was not worse during metamorphosis (Williams & Brown 1992). The most dramatic example of growth disruption associated with metamorphosis is in Dover sole. In this species metamorphosis may extend to 1 year in duration, during which time there is no apparent growth in length or weight (Markle et al. 1992; Butler et al. 1996). Kramer (1991) used size-at-age data to confirm that the growth rates of California halibut were lowest immediately after metamorphosis. These patterns lead to wide size distributions in post-settlement fish, presumably because those individuals that complete metamorphosis first resumed feeding and growth first, and often at a higher rate on the new food. Information about growth during the period of metamorphosis is vital for models of settlement and mortality. The growth of plaice decreases around the time of metamorphosis and settlement in many experimental studies. This is usually attributed to

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<tr>
<td>Common sole</td>
<td>Field (Bay of Biscay)</td>
<td>Boulhic et al. 1992</td>
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<tr>
<td>Dover sole</td>
<td>Laboratory and field, based on otolith ageing</td>
<td>Butler et al. 1996</td>
</tr>
<tr>
<td>Plaice</td>
<td>Laboratory, confirmed with protein metabolism, RNA/DNA</td>
<td>Christensen &amp; Korsgaard 1999</td>
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<tr>
<td>Senegalese sole</td>
<td>Laboratory, confirmed with biochemical measures</td>
<td>Fernandez-Diaz et al. 2001</td>
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<tr>
<td>Starry flounder</td>
<td>Laboratory, confirmed with otolith pattern</td>
<td>Campana 1984</td>
</tr>
<tr>
<td>Windowpane</td>
<td>Laboratory and field, based on otolith ageing</td>
<td>Neuman et al. 2001</td>
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<tr>
<td>Winter flounder</td>
<td>Laboratory, latency period defined</td>
<td>Berger et al. 1997</td>
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<tr>
<td>Witch</td>
<td>Laboratory</td>
<td>Bidwell &amp; Howell 2001</td>
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Table 7.3 Evidence of decrease in growth rate associated with metamorphosis
poor feeding either because of the type of prey offered, or to changes in behaviour (Neave 1985), or to the inability to process visual information and thus feed effectively. In the case of turbot visual acuity reaches its maximum after metamorphosis, whereas in plaice the eye is fully developed before metamorphosis (Neave 1984). Individuals in metamorphic stages often have the lowest indication of food consumption in field studies (Grover 1998; Lagardère et al. 1999). There is no evidence that flatfishes can control their growth rate directly in order to manipulate settling in response to favourable conditions such as substratum (Gibson & Batty 1990). However, Markle et al. (1992) discuss the possibility of delayed metamorphosis in Pacific Dover sole. Reduction in growth during metamorphosis is a concern in aquaculture where focus is usually on obtaining maximum growth rates. However, it may be advantageous to manipulate growth and development so to produce more uniform cohorts after settlement (Gavlik et al. 2002).

7.5 Growth on the nursery grounds

Flatfish nursery grounds vary between species, with different characteristics such as depth range, salinity and substratum. In principle flatfish nursery grounds are the areas occupied, starting at or shortly after settlement, for a time through the juvenile phase. Metamorphosis and the learning of new behaviours associated with a benthic mode of life may increase the vulnerability of flatfishes at the start of the nursery ground stage. After metamorphosis juvenile flatfishes generally grow rapidly relative to the rest of their lifespan. Nursery grounds generally provide a partial refuge from predation and a highly productive area that promotes growth. The duration of the nursery ground phase varies between species.

Very rarely do nursery grounds provide the ideal situation with ample prey and little to no competition for food, resulting in maximal growth of the juveniles. Variability in numbers of juvenile flatfishes settling on the nursery grounds, the amount and quality of available prey, and environmental conditions such as temperature all contribute to variation in growth rate of juvenile flatfishes on the nursery grounds. One of the major problems associated with measuring the variability in growth rate on the nursery grounds relates to continued arrival of new fishes while those already present are growing. Using mean size from samples tends to underestimate the growth in this case. To combat this problem, the primary otolith increments have been used to estimate age and hence growth rate and these in turn revealed the presence of sub-cohorts and different growth rates associated with the sub-cohorts (e.g. Al-Hossaini et al. 1989; Hovenkamp 1991; Karakiri et al. 1991; May & Jenkins 1992; Sogard & Able 1992; Dau 1994; Modin & Pihl 1994). At the end of the nursery ground phase the growth rates estimated from mean size also tend to be inaccurate as larger fishes begin emigrating to deeper water. Direct growth measurements can be made using tagging techniques (Nash et al. 1992, 1994). Both otolith and tagging studies have revealed large individual variability of growth rates on nursery grounds.

7.5.1 Growth models/growth experiments

The growth rates of post-metamorphic flatfishes have been studied intensively for aquaculture purposes, and especially for ecological studies seeking to test hypotheses about density
dependence and food limitations in nursery areas. In many species the plasticity of growth rates, showing both compensatory and depensatory growth patterns, has inhibited the development of clear models of juvenile growth. However, experimental work on growth and metabolism has established a variety of models that often serve to highlight patterns that may occur in the wild.

Laboratory studies designed to examine the relative effects of temperature and food availability suggest that growth rate is very sensitive to fluctuations in feeding conditions (Malloy et al. 1996). When food is not limiting, juvenile flatfishes may continue to grow at a wide range of temperatures (Fonds et al. 1995). This is likely to be the result of adaptation to variable shallow nursery ground conditions, but is also observed in species with offshore nursery grounds (Hallaraker et al. 1995). Food consumption and growth efficiencies were size-related in plaice and flounder, and the response of these variables to temperature was also size-dependent such that smaller fish grew faster at higher temperatures than did larger fishes (Fonds et al. 1992). In Atlantic halibut growth rate declined as juveniles became larger (Hallaraker et al. 1995).

7.5.2 Maximum achievable growth and evidence for deviations from maximum growth

The search to define maximum achievable growth on nursery grounds has been fuelled historically by the desire to be able to link juvenile growth with recruitment success (van der Veer et al. 1994; Chambers et al. 1995). However, Rogers (1994) did not find a link between growth in juvenile common sole and subsequent recruitment. In this case, other factors – such as an algal bloom altering the nursery ground feeding conditions – may have been responsible for low growth rates that did not translate into survival to recruitment.

Density-dependent effects on growth have been suggested for a number of species: English sole (Parophrys vetula) (Peterman & Bradford 1987), plaice (Steele & Edwards 1970; Zilstra et al. 1982, Poxton et al. 1983; Modin & Pihl 1994) and four spotted megrim (Lepidorhombus boscii) (Landa 1999). A re-examination of some of the plaice data suggested that the variation in growth was similar to that predicted by a model based on water temperature and maximum feeding rates and differences could be explained by settling dates (Bergman et al. 1988; van der Veer et al. 1990).

More recently, comparative growth studies have been initiated to help distinguish between good and poor settlement areas, based on the assumption that good sites will produce good growth. The maximum growth/optimal feeding conditions (MG/OFC) hypothesis assumes optimal food conditions where there is no competition for food and hence no density-dependent effects on growth (van der Veer & Witte 1993). Under these circumstances, the maximum growth is determined solely by the ambient water temperature. Conflicting evidence has been presented for whether food is ever a limiting factor on nursery grounds and whether density-dependent effects on growth are visible. Van der Veer et al. (2001) demonstrated that growth of flounder and sole in the Dutch Wadden Sea was dependent on the prevailing water temperatures and was not food limited. Neither dab (Limanda limanda) nor common sole in the Kattegat had growth rates that were food limited (Pihl 1989). Van der Veer et al. (1990) analysed a number of different 0-group plaice populations and concluded that differences in sizes of fish at the end of the nursery ground phase (August) reflected differences in thermal
regime and growing season but did not support the suggestion of density-dependent effects due to food limitation. Studies on winter flounder (Sogard et al. 2001) and southern flounder, Paralichthys lethostigma (Kamermans et al. 1995) also failed to find clear evidence of food-limited growth rates. In contrast Berghahn et al. (1995), working with plaice in the Wadden Sea, demonstrated variability in growth rate with food quality and quantity and van der Veer & Witte (1993) showed a positive correlation between growth of plaice and food abundance. They also showed that where food abundance was at a similar level the presence of Arenicola, the preferred prey, resulted in higher growth rates. Juvenile southern flounder grew faster in areas of historically lower abundance (Guindon & Miller 1995). On winter flounder nursery grounds, more prey was available over coarser sediments resulting in higher growth rates (Sogard 1992). Other factors such as periodic or sustained disruptions to normal behaviour patterns (Moore & Moore 1976; Gibson 1994; Geffen & Nash 1995); habitat quality (Able et al. 1999), day length (Poxton et al. 1983), salinity (Gutt 1985; Malloy & Targett 1991) and dissolved oxygen (Phelan et al. 2000) have also been shown to affect growth rates. While this does not argue for or against density-dependent effects it does point out that a number of other factors besides temperature will affect growth rates.

The reason for the rather inconclusive evidence for density-dependent growth effects on nursery grounds may be that it is only rarely, due to over-exploitation, that settlement on the nursery grounds is high enough to invoke competition for food. Prime nursery grounds should have relatively high 'carrying capacities' through relatively high productivity. How often nursery grounds such as the Wadden Sea reach their carrying capacity is unknown.

One further factor complicating growth rates on nursery grounds is the effect of latitude. A species may not respond to the same set of physiological variables in the same way throughout its range. In Atlantic halibut, the optimal temperature for growth was lower for high latitude fish compared with low latitude fish, compensating for the shorter growing season (Jonassen et al. 2000). In turbot the growth performance of the high latitude population was superior to the lower latitude populations (Imsland et al. 2000).

7.5.3 Growth compensation/depensation

Compensatory growth can occur when there is a negative relationship between age and growth rate, i.e. the growth slows with size. In this case the smaller fishes exhibit increased growth rates and catch up in size with the larger fishes (Ricker 1975). Under growth depensation variance of size distribution increases with time due to differential growth rates between individuals (Magnuson 1962). While there are numerous studies that demonstrate individual variability in growth rate of juvenile flatfishes on nursery grounds there are no definitive field studies that show that this is the result of behavioural hierarchies. Laboratory-based studies show the formation and maintenance of size variation in groups of juvenile flatfishes (Purdom 1974; Hallaraker et al. 1995; Carter et al. 1996). However, Bertram et al. (1993) found negative correlations between larval and juvenile growth rates in winter flounder, which challenges the notion that size variation is maintained over the early life history stages.

The common pattern on nursery grounds is an increase in mean length, an associated increase in standard deviation of length and a reduction in coefficient of variation with time (van der Veer et al. 1994). There are spatial variations within large nursery grounds and between species but the pattern is remarkably similar between species and over geographic zones.
(temperate to tropical). Variability in size during the months after metamorphosis or settlement may be partially due to variations in settling date. The variation in size toward the end of the summer could be partially due to the length of time an individual had been on the nursery ground. However, Fitzhugh et al. (1996) determined that variability in growth rate rather than birth date of southern flounder was the primary cause of the variability in length.

The variability in growth rates between individuals may be genetic but is more likely to be due to differences in food consumption and temperature regimes. Food quantity and quality and temperature vary over the nursery grounds (van der Veer et al. 1994) and that can lead to variation in growth rates. However, some species can attain similar growth rates over wide geographical areas (Bolle et al. 1994).

7.6 Growth of adults

Growth in adult fishes is governed by different constraints than in the juvenile phase because reproduction is a significant competitor for energy. As in juvenile populations, food levels, thermal regimes, habitat size and quality, genetics and anthropogenic effects should all affect adult growth rates and in addition have an influence on the age structure of a fish population. Although there is ample information on the age and growth of specific populations, few laboratory or field experiments have examined the factors that influence the growth of adult flatfishes.

The method used to measure growth rates depends on the level of resolution required. Changes over years are usually measured as population changes in length-at-age, and are reliant on good age estimation techniques. Seasonal changes in growth rate and individual growth rates are measured using different techniques, including tagging, back-calculation and biochemical methods. Population growth rates are usually represented as von Bertalanffy, Gompertz or other growth curves (see Ricker 1975). In adult populations back-calculation of length-at-age, to estimate the growth trajectory of an individual, is also used (see for example, Rijnsdorp & van Leeuwen 1992; Millner & Whiting 1996). Length-at-age data can be problematic, especially in exploited populations, as gear selectivity or avoidance can bias the estimate of mean length-at-age and thus lead to incorrect growth curves. Fishery-derived data can similarly be biased due to the selectivity of the fishery as a whole.

In flatfish populations in general there is a sexual dimorphism with females growing larger than males (Terwilliger & Munroe 1999; see also Chapter 4). Allied to the greater maximum size, females generally live longer (e.g. Bowering 1989; Chen et al. 1992; Vassilopoulou & Ondrias 1999). Notable exceptions to the females being larger than males are stone flounder Platichthys bicoloratus (Dou 1995) and the wide-eyed flounder (Nash et al. 1991).

7.6.1 Factors affecting adult growth rates

One of the main factors that has been assumed to affect growth is density, mediated through variation in food supply (Beverton & Holt 1957), although studies of marine fishes have often failed to show density-dependent growth (Rijnsdorp 1994). This apparent lack of density-dependent growth may be due to high levels of exploitation resulting in population densities that are below a threshold for these effects to come into play. Globally, many species exhibit
increased growth rates with increasing levels of exploitation. Exploitation may reduce popula-
tion size sufficiently to increase food availability. However, Rijnsdorp (1994) also points 
out that other factors could be involved in the changes in growth rate. These potential factors 
were categorised as direct, indirect (on the food availability) and artificial effects. Changes 
in growth rate could be due directly to changes in temperature, oxygen or food availability. 
Indirect effects on food availability could result from (1) natural changes in the ecosystem, 
(2) fishery-induced changes giving a relaxation of density-dependent growth, (3) shifts in the 
composition and abundance of food or shifts in community or inter-specific food competi-
tors or (4) changes in food abundance due to eutrophication or pollution. Artificial changes 
in apparent growth rate were considered sampling artefacts from changes in fishing gear or 
in age estimation techniques. Examples of the factors and effects on growth rate in flatfishes 
are summarised in Table 7.4.

7.6.2 Trade-off between growth and reproduction

The difference in the growth rates of maturing and non-maturing female plaice supports the 
general concept that growth and reproduction are activities that compete for limited resources 
(Rijnsdorp 1993b; see also Chapter 4). Recruit spawners have to build up energy reserves 
but do not have to recover from depleted body condition from the previous year’s spawning. 
Reproduction will thus have its maximum effect on somatic growth after the first reproduc-
tive season. Annual differences in growth rate can affect the length and age at first maturity, 
as in plaice (Rijnsdorp 1989) and American plaice, *Hippoglossoides platessoides* (Morgan 
& Colbourne 1999).

As growth, maturation and egg production are closely related processes it is difficult to 
disentangle the influence of age at first maturity, age or size-related variability in somatic 
growth and fecundity/egg size relationships. There is ample evidence that juvenile growth 
is a major factor in the transition to maturity. Maturation is a growth-dependent process and 
individual growth rate influences the allocation of available energy between egg production 
and somatic growth in adults. Rijnsdorp (1990) proposed that during the growing season 
adult fishes set a fixed energy reserved to be used for reproduction, and any surplus energy 
is shifted to somatic growth. Deteriorating feeding conditions means a shut off of somatic 
growth first then an effect on the size-specific reproductive output.

7.7 Longevity

Flatfishes follow the general trend among fishes with longevity greater in larger sized species 
and those with deeper water distributions (Fig. 7.1). This general pattern is likely to reflect in-
teractions between temperature, food availability and energetics. Maximum ages range from 
60 years in the Pacific Dover sole (Munk 2001) to 1.5 years in the fringed flounder (*Etropus 
crossotus*) (Reichert 1998). In contrast the solenette (*Buglossidium luteum*) is thought to live 
up to 10 years (Nottage & Perkins 1983), the blackcheek tonguefish (*Symphurus plagiusa*) 
only about 5 years (Terwilliger & Munroe 1999), and *Tarphos oligolepis* as little as 2 years 
(Minami & Tanaka 1992). Maximum ages can vary widely between populations within spe-
cies, especially those that have wide distributions. For example, American plaice populations
Table 7.4  Factors that can affect adult growth rates

<table>
<thead>
<tr>
<th>Factor</th>
<th>Response</th>
<th>Comment</th>
<th>Species</th>
<th>Location</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Food</td>
<td>Increased growth rate with increased food availability</td>
<td>Due to spatial variability in food quality and abundance, Related to beam trawl effort</td>
<td>Dab, common sole and plaice</td>
<td>Southern and central North Sea</td>
<td>Rijnsdorp &amp; van Beek 1991; Henderson 1998</td>
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<td></td>
<td></td>
<td></td>
<td>Common sole</td>
<td>North Sea</td>
<td>De Veen 1976</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>Dab</td>
<td>North Sea</td>
<td>Henderson 1998</td>
</tr>
<tr>
<td>Temperature</td>
<td>Growth rates vary with temperature</td>
<td>Complex effect of temperature and length of growing season, No correlation between temperature and growth rates, Changes in growth due to unspecified oceanographic conditions</td>
<td>Plaice</td>
<td>North Sea</td>
<td>Rijnsdorp &amp; van Leeuwen 1996</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>English sole</td>
<td>NE Pacific</td>
<td>Sampson &amp; Al Jufaily 1999</td>
</tr>
<tr>
<td>Habitat</td>
<td>The quality and quantity of available habitat affects the growth rate</td>
<td>Sediment characteristics affect growth, Due to higher energy expenditure associated with a higher branchial sodium, potassium and ATPase activity</td>
<td>English sole</td>
<td>NE Pacific</td>
<td>Sampson &amp; Al Jufaily 1999</td>
</tr>
<tr>
<td></td>
<td>Salinity: reduced growth rates at lower salinity</td>
<td></td>
<td>Paralichthys orbignyanus</td>
<td>Brazilian waters</td>
<td>Sampio &amp; Bianchini 2002</td>
</tr>
<tr>
<td>Stock/genetics</td>
<td>Stock or genetic effect on growth rate</td>
<td>Geographical differences in growth, Potential for broodstock selection, Effects of fishing pressure on the genetic variability</td>
<td>American plaice</td>
<td>Atlantic and Mediterranean</td>
<td>Vassilopoulou &amp; Ondrias 1999</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Common sole</td>
<td>Atlantic and Mediterranean</td>
<td>Exadactylos et al. 1998</td>
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<td></td>
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<td>Plaice</td>
<td>Atlantic</td>
<td>Rijnsdorp 1993a</td>
</tr>
<tr>
<td>Anthropogenic</td>
<td>Positive effects on growth rate</td>
<td>Eutrophication and beam trawling effects</td>
<td>Plaice</td>
<td>North Sea</td>
<td>Rijnsdorp &amp; van Leeuwen 1996</td>
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<tr>
<td>effects</td>
<td></td>
<td></td>
<td>Common sole</td>
<td>Bristol Channel Laboratory</td>
<td>Horwood 1993</td>
</tr>
<tr>
<td></td>
<td>Negative effects on growth rate</td>
<td></td>
<td>English sole</td>
<td>Laboratory</td>
<td>Johnson et al. 1998</td>
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</tbody>
</table>
Fig. 7.1 Longevity of flatfishes. (a) Maximum ages and lengths reported for species from five flatfish families. (b) Maximum ages and depth distributions reported for species from five flatfish families. (c) Pattern of longevity in relation to depth and latitudinal distribution. Data for all graphs from Minami & Tanaka (1992), Terwilleger & Munroe (1999), FishBase (Froese & Pauly 2002) and Munk (2001).
show strong latitudinal trends in longevity (Walsh 1994), as do megrim (Lepidorhombus whiffiagonis) (Vassilopoulou & Ondrias 1999), witch (Glyptocephalus cynoglossus) (Albert et al. 1998) and several North Pacific species (Munk 2001).

Differences in inter- and intra-specific longevity have been ascribed to latitudinal differences (see Fig. 7.1), as well as to the effects of temperature, food availability and life history strategies. The pattern of commercial exploitation is probably the most significant factor that causes local differences in longevity both between species and between populations (Rijnsdorp 1993a; Albert et al. 1998). In the early 1900s there were frequent reports of plaice of 20–30 years old, as estimated from otolith readings. Although one 40-year-old female common sole was captured in 1999 (Anonymous 1999), maximum ages in the catches of most exploited flatfish species are often in decline (Millner & Whiting 1996).

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