Chapter 1
Introduction

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Abstract

The unique asymmetric structure and appearance of flatfishes, their abilities to change colour to match the background and to burrow in the sediment all make them a fascinating subject of study. Following a brief history of flatfish research and its contribution to fish biology and fisheries science, the scope and contents of *Flatfishes: Biology and Exploitation* are outlined. The contents can be roughly divided into three parts with numerous links between them. The first part deals with systematics, distribution and life history stategies; the second with biology and covers development, recruitment, ecology, growth and behaviour. The final five chapters describe and discuss aspects of exploitation including the major fisheries, management and assessment and the contributions of aquacultural studies to flatfish biology. A final section on nomenclature discusses the difficulties inherent in using common and scientific names and describes the method used to ensure that there is no ambiguity in the text.

Keywords: Flatfishes; systematics; distribution; life history; ecology; growth; behaviour; fisheries; management; aquaculture

1.1 The fascination of flatfishes

Most people's first encounter with flatfishes is on a fishmonger's slab where their unusual shape makes them instantly recognizable. Flatfishes have certainly featured in the human diet for millennia. They appear in prehistoric rock carvings (Muus & Nielsen 1999), their remains are found in ancient middens (Nicholson 1998; Barrett *et al.* 1999) and they continue to make up a significant proportion of the world groundfish catch today. Gastronomy apart, the interested layman's curiosity is aroused not only by the presence of both eyes on the same side of the head and their flattened shape, but also by the remarkable ability of flatfishes to match the colour and

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pattern of their background and to bury in the sediment. The last three characters are present in some other bottom-living fishes (e.g. skates and rays, anglerfishes) but together with eye migration in the larva and the less obvious features of protrusible eyes and a dorsal fin that continues onto the head, they make the flatfishes unique.

An intriguing question is why some flatfishes have their eyes on their right side whereas in others the eyes are on the left side. Examination of the occurrence of left and right 'sidedness' within the Order Pleuronectiformes shows that although some families are predominantly left or right sided (see Chapter 2 this volume), the trait for a particular direction of asymmetry does not reflect relationships within the order. This conclusion holds true whether morphological or molecular evidence is used to deduce interrelationships (Berendzen & Dimmick 2002). Furthermore, in some species, for example the fossil *Amphistium* (Friedman 2008), the primitive *Psettodes* and the European flounder (*Platichthys flesus*) and starry flounder (*P. stellatus*), 'reversed' individuals are common. Also, in these two *Platichthys* species at least, sidedness varies geographically (Policansky 1982a, b; Fornbacke *et al.* 2002). Breeding experiments with starry flounder have demonstrated that the direction of asymmetry is predominantly under genetic control but there may also be some environmental influence (Policansky 1982a; Boklage 1984). The exact mechanism involved is unclear and remains a subject of debate (McManus 1984; Morgan 1991), although the optic chiasma may be involved (see Chapter 7, this volume). To return to the original question, inheritance of eye position suggests that there should be some selective advantage of having eyes on one or other side of the head. It seems intuitively reasonable to assume that it would be advantageous for all members of the population to have the same eye position (Policansky 1982a), particularly during mating, and in most species this is indeed the case. However, Fornbacke *et al.* (2002) have suggested that left-sided individuals of young European flounder may be favoured by less competition with the right-sided European plaice (*Pleuronectes platessa*). In addition, the two morphs of starry flounder are not simple behavioural images of one another. Differences in behaviour together with slight anatomical differences between them suggest that the morphs are not ecologically identical and that the polymorphism may be driven by competitive interactions between left- and right-sided forms (Bergstrom 2007; Bergstrom & Palmer 2007).

The ability of flatfishes to camouflage themselves against the seabed on which they lie is also a source of fascination for many. Background matching is the result of rapid nervous and slower hormonal responses to visual stimuli received by the eyes and is achieved by differential responses of the chromatophores in the skin. In this way flatfishes can match not only the general colour of their background but also its pattern, even to the extent that the sizes of the spots on a spotted background can be mimicked (Ramachandran *et al.* 1996; Healey 1999; Burton 2010).

The variety of flatfishes and their adaptations to a benthic existence also make them intriguing subjects for study by fish biologists. Flatfishes vary in adult size from a few centimetres up to 2 m or more. They are widely distributed in cold, temperate and tropical seas in depths from the intertidal zone to the continental slope, including hydrothermal vents, but seem to be absent from the deepest parts of the sea (see Chapter 3 this volume). This variation in size and habitat means that they display a considerable range of patterns in ecology and life history and in physiological and behavioural adaptations to life on and in the bottom. Their value as food has also resulted in numerous investigations of these patterns and adaptations in relation to growth, feeding, reproduction and population structure, and the application of the results to management. Yet the intraspecific and interspecific roles of flatfishes in benthic ecosystems as predators, competitors and prey are still largely unresolved, even though flatfishes may account for around a quarter of groundfish species richness and biomass in some areas such as the North Sea (Daan *et al.* 1990). In some coastal nurseries, juvenile flatfishes may numerically dominate the benthic fish fauna (e.g. Gibson *et al.* 1993).

1.2 A brief history of flatfish research and its contribution to fish biology and fisheries science

Although flatfishes feature in many early descriptive zoological treatises and several common species were given their scientific names by Linnaeus in 1758, the first detailed articles describing research on flatfishes appear in the scientific literature at the end of the nineteenth century. Much of this early research was stimulated by the need for information on the biology of the common foodfishes and was fuelled by a concern for the state of their fisheries and why catches fluctuated (e.g. Petersen 1894; Holt 1895). At that time, fluctuation in catches was considered to be due principally to changes in migration patterns but also to the possibility that stocks were being overfished, challenging the earlier assertion by T.H. Huxley that the sea was an inexhaustible resource. It was realized that basic information was lacking and this lack led to the development of numerous research programmes to collect data on age, growth and size at maturity and examine whether fishing did, in fact, have any effect on populations. It rapidly became evident that fishing could have significant effects and Holt (1895), for example, recommended the imposition of a size limit for European plaice and common sole (*Solea solea*) in the North Sea. He also considered the possibility of protected areas, close seasons, mesh restrictions and artificial propagation. He dismissed stock enhancement using reared young stages as impractical and uneconomic even though the development of rearing techniques for fishes on a large scale both in North America and Europe had been in progress for some time (Ewart 1885; Dannevig 1897; Blaxter 1975; Smith 1994). Subsequent trials indicated that Holt's opinion was correct and the emphasis in the North Sea moved to the transplantation of wild fish with some success (see Blaxter 2000 for review). Flatfishes played a significant part in the development of these conclusions following experiments in Scotland and the 'Great Fishing Experiments' resulting from cessation of fishing in the North Sea during the two World Wars (summarized by Smith 1994). In these 'experiments' it was clearly demonstrated that the population structure of North Sea plaice could be greatly altered by fishing but was also capable of recovery when fishing pressure was released.

The early studies in Europe and the United States represented the beginnings of fisheries research and contributed to the formation of bodies such as the International Council for the Exploration of the Sea (ICES) (Rozwadowski 2002) and the International Pacific Halibut Commission (Smith 1994). Much of this work is summarized in subsequent chapters in this book and it has made significant contributions to fish biology and fisheries science. Particular mention can be made of the classic early works on tagging (Petersen 1894) and colour change (e.g. Mast 1914). Beverton & Holt's (1957) seminal treatise on the dynamics of exploited populations incorporated the results of many flatfish studies and intensive investigations of flatfish movements in the North Sea (summarized by Harden Jones 1968) added greatly to our understanding of migration, a topic that continues to produce novel insights into fish behaviour (e.g. Metcalfe & Arnold 1997; Metcalfe *et al.* 2006). The development of ageing techniques for fishes owes much to studies of flatfish species (see Chapter 9 this volume) and the renewed interest in mass rearing to the juvenile stage pioneered in Europe (Rollefsen 1934; Shelbourne 1964) provided material for studies of larval behaviour and physiology that would not have been possible using wild-caught individuals (see, for example, Blaxter 1986). Studies of sex determination and the endocrine control of metamorphosis in flatfishes have also contributed significantly to our wider understanding of these topics (Borski *et al*. 2010). Mass rearing techniques, which for several species are now routine (Daniels & Watanabe 2010), also paved the way for further evaluation of the feasibility of flatfish stock enhancement, particularly in Japan, using juveniles rather than eggs and larvae. The International Flatfish Ecology Symposia (see Preface) provide a platform for the presentation and discussion of the most recent studies.

In a wider context, anatomical studies of flatfishes have contributed to discussions of evolutionary mechanisms. The origins of flatfishes were a contentious issue in early debates because intermediate stages between symmetric and asymmetric forms (i.e. those with incomplete eye migration) had not been found. Furthermore it was considered that such intermediate forms could not be adaptive. Consequently, arguments for saltatory change were invoked and even natural selection itself was attacked. However, the subsequent discovery and description of the fossils *Amphistium* and *Heteronectes*, the most primitive flatfishes currently known, showed that the attainment of asymmetry of the eyes and of cranial anatomy could indeed have been gradual (Friedman 2008).

1.3 Scope and contents of the book

The book is an overview of the biology and exploitation of flatfishes. Although necessary constraints on length mean that the coverage of each topic is not fully comprehensive, each chapter does represent a succinct summary of the 'state of the art' in its own field. Furthermore, as Hensley (1997) and several authors in this volume continue to point out, current detailed knowledge is based on only a few, mostly north temperate, species of economic interest.

The contents can be roughly divided into three parts with numerous links between them. The first part deals with systematics, distribution and life history stategies; the second with biology in the widest sense and covers development, ecology, growth and behaviour. The final five chapters describe and discuss aspects of exploitation including the major fisheries, management and assessment and the contributions of aquacultural studies to flatfish biology.

The book starts with chapters on systematics and biogeography that review our current understanding of the evolution and taxonomic diversity of flatfishes. Flatfish fossils are rare but the oldest known date from at least 45 million years ago when many lineages had already diversified. The Order Pleuronectiformes is considered to be monophyletic and over 800 species in 15 family level taxa are presently recognized, but the total species diversity for the order is unknown. The flatfish fauna of north temperate regions is generally well known but those of the tropics and deeper water are not. Tropical flatfishes are small, difficult to identify and many tropical habitats have not been well sampled. These factors, together with the growing realization that taxa formerly considered to be widespread single species may actually be species complexes, indicate that many flatfish species still await discovery. The companion Chapter 3 provides an overview of flatfish distributions by describing the global occurrence of the flatfish families and their patterns of species richness in terms of geographical region and specific environments. Although flatfishes have a virtually worldwide distribution, this distribution is not uniform; the East China Sea, for example, is particularly speciose but freshwaters, the deeper parts of the sea and high latitudes in the Southern Ocean are comparatively species poor. Consideration of the historical biogeography of the group provides an explanation of some of these patterns but, here again, incomplete knowledge of systematics and distribution prevents as yet a full picture being obtained. Clearly, much remains to be done in this field of flatfish biology. After an introduction to life-history theory, the next chapter describes the diversity in life-history traits of flatfishes and how they vary according to geographical area, habitat use patterns and functional guilds. Intraspecies variability is also examined with particular reference to phenotypic plasticity, local adaptation, cogradient variation and parental effects. Finally, anthropogenic impacts such as fishing pressure and climate change on life-history traits are discussed. Chapter 5 describes the reproduction of flatfishes and focuses on those characteristics that affect the production of offspring and their survival namely, egg size, spawning, gonad development and fecundity, onset of sexual maturity, and the energetics of reproduction and growth. The authors explore the adaptive significance of patterns of reproduction from the viewpoint that reproductive characteristics have evolved, and continue to evolve, in response to environmental conditions. They discuss these characteristics in relation to the geographical distribution of species and their implications for population dynamics and the resilience to perturbations caused by exploitation and pollution.

Most flatfish eggs and all larvae that hatch from them are planktonic. Consequently their rate and direction of dispersal after spawning is largely dependent on the characteristics of local water movements. Chapter 6 describes the types of water movement to which eggs and larvae are exposed and the physical mechanisms by which they are transported to, or conversely retained in, their appropriate nursery grounds. Most transport is assumed to be passive, especially as flatfish larvae are relatively feeble swimmers, but the ability of larvae to migrate vertically enables them to exert some control over their net direction and speed of movement. A comparison of species and genera in the same and different locations reveals remarkable variety in transport patterns, all of which are adapted to local hydrographic conditions and which link spawning grounds to nursery areas. Coupled physical and biological models can contribute greatly to the understanding of this process. The extent of variation in the success of transport to suitable nursery grounds has considerable implications for population genetics and connectivity, management and recruitment.

At the end of their planktonic stage, larvae begin the process of metamorphosis and their transition to a benthic way of life. The metamorphosis of flatfishes is characterized by the migration of one eye to the opposite side of the head and by subsequent pigmentation of the ocular side only. Chapter 7 describes the systems involved in the development and regulation of these external asymmetries and how they may have evolved. An important finding related to eye-sidedness is that the Nodal pathway, which is known to control laterality of internal organs, fixes eye-sidedness through a series of novel mechanisms. Regarding pigmentation, latent precursors that give rise to the adult-type chromatophores that confer colour to the ocular side are localized along the base of the dorsal and anal fins until metamorphosis.

Chapter 8 reviews the data and hypotheses relating to the generation, regulation and variability of recruitment and analyses three factors relevant to these processes; namely a species' range, and its average level of, and annual variability in, recruitment. Temperature is considered to be the predominant factor determining range but it is also important in determining the duration of the egg and larval stages and hence the critical distance between spawning and nursery grounds. With respect to recruitment level, the authors conclude that level is governed by two distinct processes; the effect of food availability on adult condition at spawning time and density dependent mortality of juveniles on the nursery grounds. This density dependent mortality, which results from the concentration of juveniles in two dimensions after settlement, may also be an important contributing factor to the lower recruitment variability of flatfishes compared with other groups.

A knowledge of growth rates and patterns is essential for many areas of fish and fisheries biology and flatfish growth is summarized in Chapter 9. The range of longevity within the group is large (<2 to 60 years) and a complex range of factors affect growth throughout life. Some of the earliest studies seeking methods for ageing fish were carried out on flatfishes and led to the recognition of the value of otoliths as records of past growth. Otoliths are now routinely used for ageing all stages from larva to adult but our knowledge of flatfish growth patterns has arisen from a combination of both laboratory and field studies. These studies have demonstrated the vital importance of temperature in determining growth rate but numerous other factors come into play with differing importance throughout the life history. Food supply is particularly critical in the larval and juvenile stages and there has been much discussion of the question of density dependent growth. In some areas juvenile growth rates have been used to assess the quality of nursery grounds. In the adults, growth patterns and their interpretation are strongly affected by reproduction and the effects of exploitation. The next chapter describes the distribution and dynamics of habitat use by juvenile and adult flatfishes.

In many species, but not all, there are considerable differences between the distribution of these two stages because the inshore areas where metamorphosing fishes settle are separated from the offshore feeding and spawning grounds of the adults. Particular attention is given to the 'nursery' role of these early juvenile habitats. Growth on these nursery grounds is subsequently followed by a gradual movement into deeper water. Superimposed on this gradual ontogenetic change in distribution, however, are shorter frequency variations in habitat occupation varying from tidal to annual timescales. The factors controlling these movements are for the most part unknown and although numerous studies have identified abiotic variables such as depth, salinity, temperature and substratum type, which correlate with distribution, there may not necessarily be any causal relationship between them. Instead, or in addition, gradients of abiotic factors may be used to locate areas that fulfil the requirements of the particular life history stage. Consideration of spatial scale is also relevant. Whereas large and small-scale differences in distribution may be defined by depth, salinity and temperature it is likely that biotic factors such as food availability and predator avoidance are important at smaller scales. Nevertheless, substratum type may be of greater importance in determining habitat occupation for flatfishes than for many other groups. It is certainly true that the substratum is the source of food for the great majority of flatfishes and whereas some species are piscivorous, most prey on invertebrates living in and/or in sediments.

Chapter 11 reviews the trophic ecology of flatfishes first by defining the main feeding types and the factors affecting their diet and then by examining the range and effects of flatfish predators and competitors. The evidence for intra- and interspecific competition is ambiguous but in some cases is strongly suspected. Predation on flatfishes, on the other hand is intense particularly in the youngest stages, and predators range from crustaceans through birds and mammals, not the least of which is man. These various aspects of trophic ecology are combined in a case study of Georges Bank in which the authors demonstrate shifts in abundance and species composition, potential competitive interactions and the extent of predation by and on flatfishes, which may be considerable. Nevertheless, better assessments of *in situ* competition and population-level impacts, together with a greater understanding of the impacts of changes to benthic communities, and their broader implications for flatfishes, are still required.

Chapter 12 describes aspects of flatfish behaviour in some detail. It includes a summary of locomotion but concentrates on the key activities of spawning, feeding and reactions to predators that enable fishes to reproduce, grow and survive. These activities take place at a range of spatial scales from localized foraging to long distance migrations and the chapter also includes a brief account of movement patterns that have evolved to make the most effective use of the environment. Much remains to be learnt about flatfish behaviour and recent studies have demonstrated that they spend much more of their time off the bottom than was previously realized. Finally, the significant role of behaviour in the capture and culture of flatfishes is discussed and its importance attempts to design selective fishing gear and to augment and conserve wild flatfish populations through stock enhancement.

The last section of the book is concerned with the exploitation of flatfishes. Three chapters, written in a similar format to allow comparison, describe flatfish fisheries in the Atlantic and Pacific Oceans and the tropics. Each first describes the main species involved, their relative importance and the nature of the fisheries in the region. Following a short history of flatfish exploitation, an assessment is made of their economic importance and each chapter ends with a description and discussion of management strategies, results and problems for each region. The major fisheries are in the northern hemisphere where the larger species of righteye flounders (Pleuronectidae), soles (Soleidae) and lefteye flounders (Bothidae, Scophthalmidae) are the main targets and include the largest of all flatfishes, the halibuts. In the southern hemisphere catches are smaller and consist mostly of Soleidae, Bothidae, large-tooth flounders (Paralichthyidae) and some tonguefishes (Cynoglossidae). Tropical flatfishes, in contrast to those at higher latitudes, are mainly caught as bycatch rather than in targeted fisheries and the catches are much more diverse. Here, American soles (Achiridae), tonguefishes and psettodids (*Psettodes* spp.) also feature in the catches together with smaller numbers of species from other families. In terms of total fish catches, flatfishes form a small but significant proportion in the north Pacific and Atlantic (~10 – 30%) but much less in the southern hemisphere (<2% in the south Pacific) and the tropics. Nevertheless, they can command a high price and their economic value is often relatively much higher than landings statistics would suggest.

The increasing exploitation of flatfishes led to the realization that management strategies would need to be put into place to protect stocks. Such strategies were first mooted in Europe at the beginning of the last century, somewhat later in the North Pacific and are still largely lacking in the southern fisheries and tropics. For the most part, such strategies are overseen by international bodies but in some areas (e.g. Japan) may be under more local control. Regrettably, and for a variety of reasons discussed in the three chapters, many of these management plans have not prevented stock declines. There are success stories, however, as in yellowtail flounder (*Limanda ferruginea*) and Pacific halibut (*Hippoglossus stenolepis*), where a long history of research and management by the International Pacific Halibut Commission has resulted in one of the most successful fishery management programmes in the world. Successful management requires data and that is often lacking, particularly in the southern hemisphere and the tropics. In tropical regions, landings are gross underestimates of the total catch because bycatch and the products of artisanal fisheries are not included. Landings are mostly not identified, so that catches of individual species are impossible to estimate. Locally, tropical flatfishes are becoming more important as a food source as catches of other ground fishes have declined. In these regions, solutions to overfishing and habitat destruction will not be prevented by traditional approaches to fisheries management that attempt to regulate only resources. Rather, management will have to focus on people, not fish, to find solutions.

The penultimate chapter takes an overview of assessment and management in general but necessarily concentrates on those areas (the northeastern Pacific and the North Atlantic) where most data are available. The authors first consider aspects of flatfish population dynamics that are important for assessment and management, particularly the relationship between stock size and reproductive success which they consider to be historic basis for evaluating stock dynamics and conservation targets and limits. They then illustrate how traditional approaches are changing as the exploration of the effects of environmental forcing on growth and recruitment proceeds. Finally, they present a summary of stock assessment results and harvesting policies currently in use in Europe and North America and note that many more advanced stock assessment methods have been developed in the last few years. They conclude that although many stocks continue to decline some are stable or increasing. It seems that future developments will require greater use of the precautionary approach and an emphasis on cooperation between scientists, managers and fishers, all of whom are ultimately seeking the same goal.

Apart from the need to regulate exploitation, the concern over the decline of wild stocks stimulated two other approaches to maintaining the supply of flatfishes for human consumption. First, the enhancement of wild stocks by supplementation with reared individuals and second, intensive farming. Both these approaches required the development of mass culture techniques. The final chapter in the book examines the relationships between research and developments in flatfish aquaculture and studies of the ecology and fisheries of wild populations. The benefits of knowledge exchange between studies of wild and captive populations are often overlooked, as are the synergies that have arisen from work on the same species under different conditions. Examples are presented of how additional knowledge has been acquired by drawing on work with wild and cultured populations, especially the early life-history stages, and in areas such as understanding metamorphosis, the mechanisms controlling maturation and reproduction, and the importance of population genetic structure. Significant synergies have grown out of the development of genomics tools in particular, contributing to advances in aquaculture, ecotoxicology, and a greater understanding of population structure and local adaptations.

1.4 Nomenclature

Finally, a note on nomenclature. Like most groups the scientific nomenclature of flatfishes is in continual flux and, as with many other commercial species, their common names are confusing. A few examples will make the problem clear. ‘Flounder’ is widely used as a general term for all flatfishes and is applied with epithets to a great variety of species. ‘Sole’ is similarly but more restrictively used. Common names in the English language vary notoriously from place to place as in ‘American plaice’ and ‘long rough dab’ for *Hippoglossoides platessoides*. Furthermore, species described as a ‘flounder’ or ‘sole’ may not necessarily reflect their systematic position. The ‘English sole’ (*Parophrys vetula*), for example, is neither English nor a sole. The question then arises of which system of nomenclature should be used in a book on flatfishes that is both unambiguous and reflects current systematic thinking. One approach would be to use the names used by the authors of individual chapters without any attempt to adopt a uniform system. On this basis, reference to the original publications cited would make the identity of species clear. However, this approach could lead to confusion particularly as there have been major changes in flatfish nomenclature in the past few years, some of which are reflected in recent publications whereas others are not. The approach adopted here will hopefully minimize ambiguity and maximize the readability of the text. In each chapter a species is defined at first mention by its scientific and English common name. Thereafter only the common name is used. The scientific names used are those given in FishBase (www.fishbase.org) at the time of going to press (2014), except for those members of the Pleuronectidae whose names have been recently changed following the extensive taxonomic revision by Cooper & Chapleau (1998). Common names are those given in FishBase although in some cases no common names are available. In such cases the common name used by the chapter author has been used. Two appendices are provided at the end of the book that list the scientific and common names used throughout the text and the pleuronectid scientific names used before and after Cooper & Chapleau's (1998) revision.

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