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REVIEWS

The biology and ecology of tropical marine sardines and herrings in Indo-West Pacific fisheries: a review

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Abstract Tropical sardines and herrings (Family Clupeidae) form important fisheries resources in the Indo-West Pacific region. However knowledge of their biology and ecology is largely scattered across diverse localised studies. In addition, their challenging taxonomy due to numerous, morphologically similar species, coupled with data collected from dispersed, often small-scale and mixed species fisheries, creates difficulties for comparing species-level research and fisheries statistics across the region. This review considers four main groups of tropical marine clupeid species important for Indo-West Pacific fisheries—*Sardinella* (subg. *Sardinella*) species ('Round-bodied Sardinellas'), *Sardinella* (subg. *Clupeonia*) species ('Flat-bodied Sardinellas'), *Amblygaster* species ('Tropical Pilchards'), and *Herklotsichthys* and *Escualosa* species ('Tropical Herrings')—and collates and synthesises existing knowledge on early life history, reproduction, trophic biology, habitat associations and population dynamics. Most research on tropical clupeid biology and ecology in the Indo-West Pacific is concentrated on the Round-bodied Sardinellas (*S. longiceps* and *S. lemuru*) from a few major fishery locations; other species-groups have been studied sporadically across their distributions. Characteristics such as maximum size, life span, size at first maturity and some habitat associations are generally similar within species-groups and differ between groups. However differences within the same reported species highlight the importance of continued work to improve taxonomic identification. There remain substantial gaps in knowledge on all species-groups. Regular critical review of specific research topics, such as reproductive parameters and population dynamics, would assist to standardise methods and terminology used, enable consolidation and comparison of findings, identify local research agenda, and help build and improve research on these important tropical species.

Keywords Clupeidae · *Sardinella* · *Amblygaster* · *Herklotsichthys* · *Escualosa* · Indo-West Pacific · Fisheries

Introduction

Clupeoid fishes—sardines, herrings, anchovies and their relatives (order Clupeiformes, suborder

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Clupeoidei)—form the basis of some of the world's largest fisheries in both temperate and tropical regions (FAO 2018). While most research efforts have focused on the large single species stocks in productive temperate and upwelling regions (e.g. Checkley et al. 2017; Ganias 2014), the importance of these fisheries in tropical areas has steadily increased. Over 2 million tonnes of tropical and subtropical sardines from the *Sardinella* genus are now caught annually, making this group the fourth largest contributor to global marine capture production in 2016 (FAO 2018).

Clupeoid production in the largest tropical region, the Indo-West Pacific (IWP),[1] has steadily increased over the past 60 years (Fig. 1a). In the last decade (2008–2017) this region accounted for around half *Sardinella* production and 13% of marine clupeoid production globally. In contrast, production in temperate and upwelling areas has remained fairly constant albeit with high annual variability (FAO 2018; FAO 2019a). Tropical clupeoids are caught by both small-scale and larger-scale fisheries, which provide livelihoods for hundreds of thousands of fishers and post-harvest workers (e.g. FAO 2018; Kripa et al. 2018; Rola et al. 2018). Many tropical clupeoid fisheries are predominantly for human consumption, providing a relatively cheap and affordable source of protein and micronutrients (e.g. Roeger et al. 2016; Rola et al. 2018). Furthermore, the population of the IWP region is projected to increase around 29% over the next 30 years to reach over 3.8 billion people by 2050 (United Nations 2019).[2] Ensuring the sustainability of these fisheries into the future is therefore of critical importance.

Knowledge of fish biology and ecology is part of the basic information required for fisheries management (Sadovy de Mitcheson 2009). Research efforts on the biology and ecology of tropical clupeoids are numerous, particularly on the most abundantly caught *Sardinella* species. However most are localised studies with few recent attempts to compare and/or synthesise existing knowledge across the region. Previous reviews of tropical clupeoid biology and ecology are useful but dated (Longhurst 1971); predominantly focussed on the smaller, short-lived sprats and anchovies (Dalzell 1993); were limited to comparison of a few species on a particular aspect of biology (Milton et al. 1994b); or mainly considered only fisheries landings fluctuations and management (Kripa et al. 2019). Similarly, tropical species have received little attention in recent reviews on general clupeoid biology and ecology (e.g. Ganias 2014).

The IWP region has the highest diversity of clupeoid species (Lavoué et al. 2014; Whitehead 1985) with representatives from all six currently recognised families contributing to marine production: Clupeidae (sardines, herrings, shads and allies), Engraulidae (anchovies), Pristigasteridae (longfin herrings),

Fig. 1 **a** Reported clupeoid (order Clupeiformes, suborder Clupeoidei) marine capture production by family in the IWP (FAO fishing areas 51, 57 and 71) from 1950 to 2017, and contribution to global marine clupeoid landings and total IWP marine landings. Data from FAO (2019a) with reported 'Clupeidae' reclassified to exclude families Dussumieriidae (round herrings, *Dussumieria* spp.) and Spratelloididae (sprats, *Spratelloides* spp.) as per recent taxonomic revisions (references in text). **b** Average annual IWP clupeoid landings from 2008 to 2017 by family (left); and within the Clupeidae family (marine species only) based on the species-groups used in this review (right). Data from FAO (2019a) with some disaggregation of 'Clupeoidei (not specified)' and '*Sardinella* spp.' landings based on species compositions reported in national statistics for Philippines (BFAR 2008–2017), India (CMFRI 2008–2017), Malaysia (DOF 2008–2017) and Australia (Mobsby and Koduah 2017). 'Round-bodied Sardinellas' comprise *S. longiceps* (dark blue) and *S. lemuru* (light blue). 'Flat-bodied Sardinellas' comprise species reported as *S. gibbosa* (dark green); 'other sardines', i.e. non-*S. longiceps*, reported to include *S. gibbosa*, *S. fimbriata*, *S. albella*, *S. dayi*, *S. sindensis* and *S. melanura*, as well as *Amblygaster* spp. (Bennet et al. 1992) (mid-green); and predominantly '*S. fimbriata*', recently redescribed in the Philippines as *S. pacifica* (Hata and Motomura 2019b) (light green). 'Tropical Pilchards' comprise separately reported *A. sirm*. 'Tropical Herrings' comprise separately reported *Herklotsichthys quadrimaculatus*. Landings of *Escualosa* spp. and marine Gizzard Shads (*Nematalosa* and *Anodontostoma* spp.) are not separately reported. 'Sardinops (temperate)' comprises landings of temperate species *Sardinops sagax* from cooler parts of FAO fishing areas 57 (i.e. south Australia) and 51 (i.e. South Africa) and are not considered further in this review. For further details, refer to Online Resource 1 ▶

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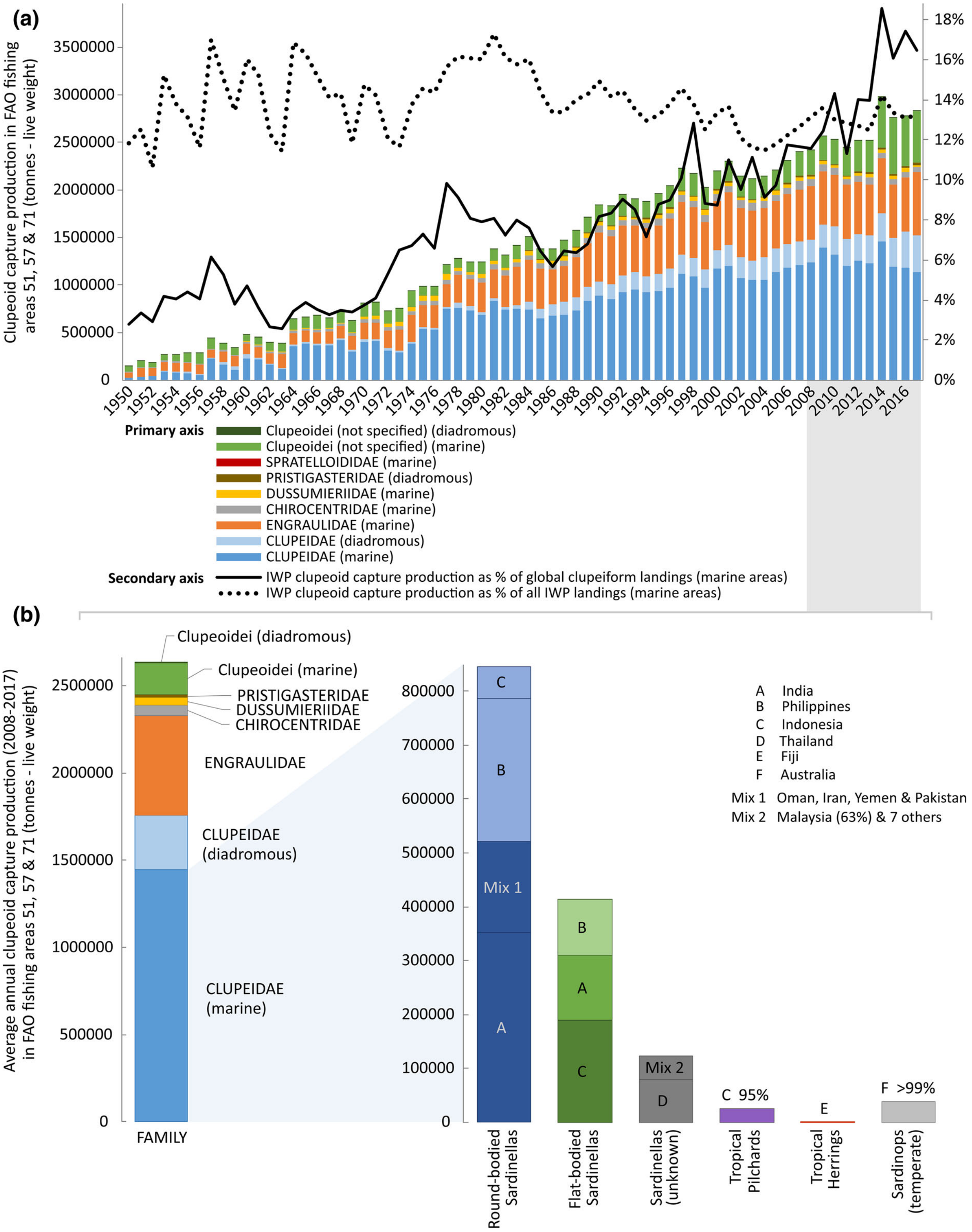
[1] The IWP encompasses the region from the south-east tropical coast of Africa, east along the southern continental margin of the India-Eurasia landmass, to the tropical South China Sea, Hawaii, Micronesia, Polynesia and north-eastern Australia (as per Lavoué et al. 2013). For analysis of fisheries production statistics, FAO fishing areas 51, 57 and 71 have been used as per Whitehead (1985), which are all considered tropical areas (FAO 2018).

[2] Based on the populations of countries with coastline in FAO fishing areas 51, 57 and 71, estimated to be just over 3 billion in 2020 and projected to reach 3.88 billion in 2050 based on the medium fertility variant (United Nations, 2019).


(a)
Clupeoid capture production in FAO fishing areas 51, 57 & 71 (tonnes - live weight)
0
500000
1000000
1500000
2000000
2500000
3000000
3500000
0%
2%
4%
6%
8%
10%
12%
14%
16%
18%
1950
1952
1954
1956
1958
1960
1962
1964
1966
1968
1970
1972
1974
1976
1978
1980
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
2012
2014
2016
Primary axis
Clupeoidei (not specified) (diadromous)
Clupeoidei (not specified) (marine)
SPRATELLOIDIDAE (marine)
PRISTIGASTERIDAE (diadromous)
DUSSUMIERIIDAE (marine)
CHIROCENTRIDAE (marine)
ENGRAULIDAE (marine)
CLUPEIDAE (diadromous)
CLUPEIDAE (marine)
Secondary axis
IWP clupeoid capture production as % of global clupeiform landings (marine areas)
IWP clupeoid capture production as % of all IWP landings (marine areas)
(b)
Average annual clupeoid capture production (2008-2017) in FAO fishing areas 51, 57 & 71 (tonnes - live weight)
0
500000
1000000
1500000
2000000
2500000
Clupeoidei (diadromous)
Clupeoidei (marine)
PRISTIGASTERIDAE
DUSSUMIERIIDAE
CHIROCENTRIDAE
ENGRAULIDAE
CLUPEIDAE (diadromous)
CLUPEIDAE (marine)
FAMILY
0
100000
200000
300000
400000
500000
600000
700000
800000
C
B
Mix 1
A
B
A
C
Mix 2
D
C 95%
E
F >99%
Round-bodied Sardinellas
Flat-bodied Sardinellas
Sardinellas (unknown)
Tropical Pilchards
Tropical Herrings
Sardinops (temperate)
A India
B Philippines
C Indonesia
D Thailand
E Fiji
F Australia
Mix 1 Oman, Iran, Yemen & Pakistan
Mix 2 Malaysia (63%) & 7 others

Chirocentridae (wolf herrings), Dussumieriidae (round herrings) and Spratelloididae (sprats or small round herrings) (Egan et al. 2018a; Fricke et al. 2020a; Lavoué et al. 2017; Lavoué et al. 2014). This review attempts to collate and synthesise existing knowledge on the biology and ecology of tropical marine IWP members of one clupeoid family, Clupeidae, which comprise the majority of reported marine clupeoid landings in the region (around 67%; Fig. 1b). While both marine and diadromous species contribute to marine capture production, I focus on species that complete their life cycle in the marine environment, which account for the majority of Clupeidae production in the region (over 80%, FAO 2019a). This review was motivated by a need to find up-to-date information on tropical clupeid biology and ecology as a starting point for understanding tropical clupeid resources in a data-poor context, Timor-Leste, where these species form an important component of small-scale fisheries landings (López-Angarita et al. 2019) but for which there is little or no documented information.

There are three parts to this review. First I outline some of the challenges and uncertainties associated with identifying and reporting at the species-level within this family and propose six groups of tropical clupeid species as a basis for structuring the review. The second section provides a review of existing literature on early life history, life history traits, trophic biology, habitat associations and movement, and interannual variability of the four species-groups most important for marine IWP fisheries. In the final section, I summarise these findings and identify areas for future research and improvement.

Tropical clupeids in IWP marine fisheries

There are currently 191 valid species in the Clupeidae family. Almost half (around 92 species) occur in the tropical IWP region, of which 44 species from 6 genera (*Sardinella, Amblygaster, Herklotsichthys, Escualosa, Nematalosa* and *Anodontostoma*) occur in marine, and marine and brackish habitats[3] (Fricke et al. 2020b). However species-level identification within these genera is challenging and problematic due to close morphological similarities between species, many of which overlap in distribution (Dalzell 1993; Whitehead 1985). As a result, species have been frequently and repeatedly misidentified, particularly within some genera and subgenera—e.g. members of *Sardinella* (subgenus *Clupeonia*) (Stern et al. 2016). This, together with revisions to species taxonomy and described species distributions (e.g. Hata and Motomura 2019b), makes species-level information difficult to compare or synthesise, and past studies potentially unreliable (Stern et al. 2016; Whitehead 1985).

Given these issues with identification and taxonomy, it is unsurprising that official marine fisheries production statistics for the IWP record only seven marine Clupeidae species categories[4]: *Sardinella longiceps, Sardinella lemuru, Sardinella gibbosa, Sardinella* spp.*, Amblygaster sirm, Herklotsichthys quadrimaculatus* and *Sardinops ocellatus*[5] (FAO 2019a). These species categories largely reflect differences in national reporting: for instance, *S. gibbosa*, *S. lemuru* and *A. sirm* landings are only reported from Indonesia and *H. quadrimaculatus* landings only from Fiji, despite the occurrence of these species in fisheries across the region (as discussed below). All clupeid landings from the Philippines and Thailand are reported as *Sardinella* spp.; while India reports *S. longiceps* landings separately and aggregates other clupeid landings in an aggregated Clupeoidei category. Some countries report all clupeid landings in this aggregated Clupeoidei category (e.g. Sri Lanka); while others aggregate all clupeoids in total marine fish landings (e.g. Timor-Leste) (FAO 2019a, see Supplementary Materials).

At the national level, collecting disaggregated production statistics on the many small-scale, dispersed and mixed species fisheries in the region is inherently challenging and probably impossible at a species-level for the Clupeidae family. Identification

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[3] A further 11 species from 6 genera (*Anodontostoma, Clupanodon, Herklotsichthys, Hilsa, Nematalosa* and *Tenualosa*) occur in freshwater, brackish and marine habitats; and 37 species from 17 genera occur in freshwater, and freshwater and brackish habitats (Fricke et al. 2020b).

[4] Excluding *Dussumeria* and *Spratelloides* genera, which are now considered to be in separate families; and also excluding diadromous species.

[5] These *Sardinops* landings are only reported from cooler waters in the southern parts of FAO fishing areas 57 (south Australia) and 51 (South Africa). *Sardinops* spp. are not considered tropical species (Whitehead 1985) and are not considered further in this review.

and reporting is confounded by local common names and assigned scientific species names. For example, there are instances where the same local common name is used for several clupeid species, reflecting their close morphologies (Widodo and Burhanuddin 1995; Willette et al. 2011), as well as different location-specific common names for a single species (see FishBase for examples, Froese and Pauly 2021). Mixed species landings, typical of tropical clupeid fisheries (Bennet et al. 1992; Whitehead 1985), may be habitually aggregated and recorded under a single local name that may differ by location (e.g. as described in Pet 1997). While the use of local names in itself may not always be problematic (and can even be beneficial in community-based monitoring programs, Cohen et al. 2014), incorrect assigning of scientific species names and/or not acknowledging when local names relate to several species, can result in inaccurate descriptions of fishery species composition (Willette et al. 2011).

Members of the same clupeoid genus often share general similarities in biology (Whitehead 1985). Therefore, to deal with these multiple sources of uncertainty in both the scientific literature and fisheries reporting, I have delineated six groups of tropical clupeids based primarily on current scientific taxonomic classification aggregated at either genus or subgenus level:

1. *Sardinella* (subg. *Sardinella*) spp. or the 'Round-bodied Sardinellas' species-group (as used in this review) currently comprises three closely-related species (all marine), two of which occur in the IWP—*S. longiceps* and *S. lemuru* (Fricke et al. 2020b). The subgenus is distinguished by the presence of nine pelvic-fin rays (i8). *S. longiceps* has a longer head and more gill rakers (Stern et al. 2018) and occurs throughout the Western Indian Ocean, from eastern Africa to India (Fricke et al. 2020b; Whitehead 1985). It forms large fisheries in India, particularly off the south-west coast (Rohit et al. 2018) as well as Iran and Oman (FAO 2019a; Piontkovski et al. 2014). *S. longiceps* is the most well-studied of all tropical clupeids, with a long history of research particularly in India (e.g. Jayaprakash and Pillai 2000; Nair 1973; Rohit et al. 2018). *S. lemuru* has a shorter head and fewer gill rakers, and is morphologically indistinct from the Atlantic species, *S. aurita* (Stern et al. 2018). It is found throughout the eastern Indian Ocean (Myanmar to Western Australia) and western Pacific (Java Sea to southern Japan, Fricke et al. 2020b). Large fisheries occur in the Philippines, particularly off the Zamboanga Peninsula (Rola et al. 2018), and in the Bali Strait in Indonesia (Merta et al. 2000). Biological studies have taken place in Indonesia (e.g. Merta et al. 2000), the Philippines (Willette et al. 2011) and Western Australia (Gaughan and Mitchell 2000).
2. *Sardinella* (subg. *Clupeonia*) spp. or the 'Flat-bodied Sardinellas' species-group currently comprises 18 marine species from the IWP[6] and two Atlantic species; there is also a freshwater species, *S. tawilis* (Fricke et al. 2020b). The subgenus is distinguished by the presence of 8 pelvic-fin rays (i7). Species within this group have been frequently misidentified due to highly similar morphology and overlapping distributions, including in museum voucher specimens and genetic databases; most species are distinguished only by a combination of ventral scute counts, gill raker counts and scale characteristics (Stern et al. 2016; Whitehead 1985). Recent work has been carried out to resolve some of these taxonomic issues (Stern et al. 2016) although new species continue to be described (Hata and Motomura 2019a; 2019b; 2019c). Some species are reported to occur throughout the IWP, such as *S. gibbosa*, while others have more localised distributions, such as *S. marquesensis*.[7] Described distributions for some species, such as *S. albella* and *S. fimbriata*, are confounded by past misidentifications and recent taxonomic revisions (Hata and Motomura 2019b; Stern et al. 2016). Flat-bodied Sardinellas form fisheries throughout the IWP, including in India, Thailand, Indonesia and Philippines (Bennet et al. 1992; Devaraj and Martosubroto 1997; Willette et al. 2011).

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[6] Marine IWP species included in the Flat-bodied Sardinella species-group: *S. albella*, *S. alcyone*, *S. atricauda*, *S. brachysoma*, *S. dayi*, *S. electra*, *S. fijiensis*, *S. fimbriata*, *S. gibbosa*, *S. goni*, *S. hualiensis*, *S. jussieui*, *S. marquesensis*, *S. melanura*, *S. pacifica*, *S. richardsoni*, *S. sindensis* and *S. zunasi* (Fricke et al. 2020b).

[7] *S. gibbosa* occurs from south Africa, east Africa to Philippines, Taiwan and northern Australia, while *S. marquesensis* is endemic to Marquesas Island (Fricke et al. 2020b; Whitehead 1985).

Fisheries are often mixed species, with different species compositions in different locations (e.g. India, Bennet et al. 1992). Local common names often refer to multiple species from this species-group – e.g. 'tembang' or 'tamban' (Indonesia, White et al. 2013) and 'tunsoy' (Philippines, Willette et al. 2011); in India, these species (together with *Amblygaster* spp.) are collectively called 'lesser sardines'. Biological studies have been carried out in India (e.g. Bennet et al. 1986; Nair 1973), the Philippines (Willette et al. 2011), Indonesia (Pet et al. 1997; Potier and Nurhakim 1995) and northern Australia (Williams and Cappo 1990). However species-level identity in past studies is often uncertain, even in those that may have been taxonomically rigorous at the time.

3. *Amblygaster* spp. or the 'Tropical Pilchards' species-group currently comprises four species, all found only in the IWP, in marine, or marine and brackish, habitat: *A. sirm*, *A. leiogaster*, *A. clupeoides* and *A. indiana* (Fricke et al. 2020b). Species are morphologically similar but distinguishable by features such as spots, gill raker counts and pelvic scute characteristics (Mary et al. 2017; Whitehead 1985). *A. indiana* is recently described from the west coast of India (Mary et al. 2017); the other three species are reported to be widespread throughout the IWP (Fricke et al. 2020b; Whitehead 1985). Fisheries (mainly reported as *A. sirm*) are noted in Sri Lanka, India, Thailand (Devaraj and Martosubroto 1997), the Philippines (Willette et al. 2011), Solomon Islands (Roeger et al. 2016) and New Caledonia (Conand 1991). These species closely resemble *Sardinella* spp., particularly Round-bodied Sardinellas, as reflected by some shared local common names—e.g. for *S. lemuru* and *A. sirm* ('lemuru' in Indonesia, Widodo and Burhanuddin 1995). In India, *Amblygaster* species are grouped as 'lesser sardines' together with Flat-bodied Sardinellas (e.g. Bennet et al. 1992). Biological research (generally *A. sirm*) has been carried out in most fishery locations—e.g. Sri Lanka (Jayasuriya 1989) and Malaysia (Rahman 2017); as part of tuna baitfish research in Kiribati and New Caledonia (Conand 1991; Milton et al. 1994b; Rawlinson 1993) and north-eastern Australia (Williams and Cappo 1990).
4. *Herklotsichthys* spp. and *Escualosa* spp. or the 'Tropical Herrings' species-group currently comprises 12 *Herklotsichthys* species and two *Escualosa* species.[8] All are found only in the IWP, in marine, or marine and brackish, habitat; *H. koningsbergeri* and *H. gotoi* also occur in freshwater (Fricke et al. 2020b). Most *Herklotsichthys* species can be distinguished by various flank and fin markings, although there are close similarities with some *Sardinella* species. *Escualosa* species resemble juvenile *Sardinella*, *Amblygaster* and *Herklotsichthys* species, but can be distinguished by a silver stripe on the flank and an almost rectangular second supramaxilla (Whitehead 1985). *H. quadrimaculatus* and *E. thoracata* are distributed throughout the IWP, while other species are known from part of the region[9] (Fricke et al. 2020b; Whitehead 1985). *H. quadrimaculatus* is reported in fisheries in Thailand, Indonesia (Devaraj and Martosubroto 1997), Sri Lanka (Deepananda et al. 2016), Kiribati, Solomon Islands, Papua New Guinea, Palau (Dalzell 1993), Japan (Oka and Miyamoto 2015) and Philippines (Willette et al. 2011). *E. thoracata* is caught in fisheries in India (Abdussamad et al. 2018), Thailand (Munroe et al. 1999) and Philippines (Willette et al. 2011). Most biological research on *Herklotsichthys* spp. has been carried out as part of tuna baitfish research in the Pacific region in the 1980–1990s (Milton et al. 1994b; Rawlinson 1993) as well as in some fishery locations (e.g. Sri Lanka, Deepananda et al. 2016) and ecological studies in Hawaii (Williams and Clarke 1983) and Australia (Robertson and Duke 1990; Thorrold 1988; Williams and Cappo 1990). Biological research on *Escualosa* spp. has been conducted in India (e.g. Abdussamad et al. 2018) and northern Australia (Cappo 1995b; Robertson and Duke 1990).

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[8] Marine IWP species included in the Tropical Herring species-group: *H. blackburni*, *H. castelnaui*, *H. collettei*, *H. dispilonotus*, *H. gotoi*, *H. koningsbergeri*, *H. lippa*, *H. lossei*, *H. ovalis*, *H. punctatus*, *H. quadrimaculatus* and *H. spilura*; *E. elongata* and *E. thoracata* (Fricke et al. 2020b).

[9] Western Indian Ocean: *H. spilura*, *H. punctatus* and *H. lossei*; Western Pacific Ocean: *H. ovalis*, *H. dispilonotus* and *E. elongata*; or off Australia (*H. castelnaui*, *H. blackburni*, *H. collettei*, *H. lippa*, *H. gotoi* and *H. koningsbergeri*) (Fricke et al. 2020b; Whitehead 1985).

5. *Nematalosa*, *Anodontostoma*, *Clupanodon*, *Hilsa* and *Tenualosa* spp. or the 'Gizzard Shads and Shads' species-group comprises eight marine or brackish species, nine species found in marine and freshwater, and four freshwater species; all occur only in the IWP (Fricke et al. 2020b). The marine *Nematalosa* and *Anodontostoma* species have various distributions—some widespread, others more localised—and may contribute to some local fisheries (Fricke et al. 2020b; Whitehead 1985). The diadromous *Nematalosa*, *Anodontostoma* and *Tenualosa* species contribute to important fisheries in the IWP, particularly *T. ilisha* in Bangladesh (FAO 2019a). This species-group is not considered further in this review; recent reviews are available for *T. ilisha* (e.g. Hossain et al. 2019).
6. Freshwater species from 16 genera, including *Sardinella*, *Nematalosa* and *Tenualosa* noted above, also occur in the IWP region. Given the focus on marine clupeids, this species-group is not considered further in this review.

Based on these species-groups, the Round-bodied Sardinellas (*S. longiceps* and *S. lemuru*) accounted for over half (58%) the IWP region's reported annual marine clupeid production in the last decade (2008–2017), while Flat-bodied Sardinellas accounted for almost a third (29%; Fig. 1b). Separately recorded Tropical Pilchard landings (recorded as *A. sirm*) accounted for 2% of production, and Tropical Herrings (recorded as *H. quadrimaculatus*) for $< 0.01\%$ (Fig. 1b). These latter two groups are likely underrepresented due to aggregation of some landings with Round-bodied Sardinellas and Flat-bodied Sardinellas (Devaraj and Martosubroto 1997). Other marine clupeids—*Escualosa* spp. and marine Gizzard Shads (*Nematalosa* and *Anodontostoma* spp.)—are not reported separately in global production statistics.[10] Actual volumes caught of all species-groups could be several times higher due to unreported catches and underreporting in official statistics (e.g. Buchary et al. 2011; Derrick et al. 2017).

The following sections focus on the first four of these species-groups, and use these groups as a framework to synthesise and compare existing information on the biology and ecology of these fishes.

Early life history

The life of most clupeids—temperate and tropical—commences as a pelagic egg, hatches as an endogenous feeding larva, develops into an exogenous feeding larva and then a juvenile, which develops reproductive structures to become a mature adult. Few studies have been carried out on the early life stages of tropical sardines in the IWP and these have been limited to only a few species, predominantly Round-bodied Sardinellas and Tropical Herrings. Like many marine fishes, tropical clupeid eggs are pelagic, transparent, spherical and small in size: 1–1.4 mm in diameter for *S. longiceps* (Nair 1959; Rohit et al. 2018). The warm temperature of tropical waters means that embryonic and subsequent larval development is usually rapid. Eggs of the Round-bodied Sardinellas, *S. longiceps* and *S. lemuru,* have been observed to hatch within 24 h (Gaughan and Mitchell 2000; Nair 1959). In laboratory studies, newly hatched *S. longiceps* larvae were 2.1–2.75 mm total length (TL) and completed yolk sac absorption within 2–3 days, by which stage the mouth was well-formed and larvae were actively swimming. Larvae commenced exogenous feeding within one day after yolk sac absorption, otherwise died (Kuthalingam 1960; Nair 1959). Fin development started around 16 days after hatching (11.3 mm TL) and was completed in 30 days; metamorphosis into juvenile form was complete after around 40 days (28.7 mm TL) (Kuthalingam 1960). In the Tropical Herring species-group, *H. quadrimaculatus* larvae of 17 mm standard length (SL), captured from the wild, were estimated to be around 30 days old based on otolith aging, and were 30 mm SL juveniles by 60 days (Williams and Clarke 1983). Similarly, in *H. castelnaui*, the major fins (dorsal, anal and caudal) had developed in larvae 12 mm SL aged between 8 to 18 days, and metamorphosis was estimated to take place 45–50 days after hatching, around 20 mm SL; however larval growth rates were found to vary between cohorts separated by as little as 2 weeks (Thorrold and Williams 1989).

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[10] All shads and gizzard shads (*Nematalosa*, *Anodontostoma* and *Tenualosa* species) that are separately reported in global marine fishery production statistics are diadromous (FAO 2019a).

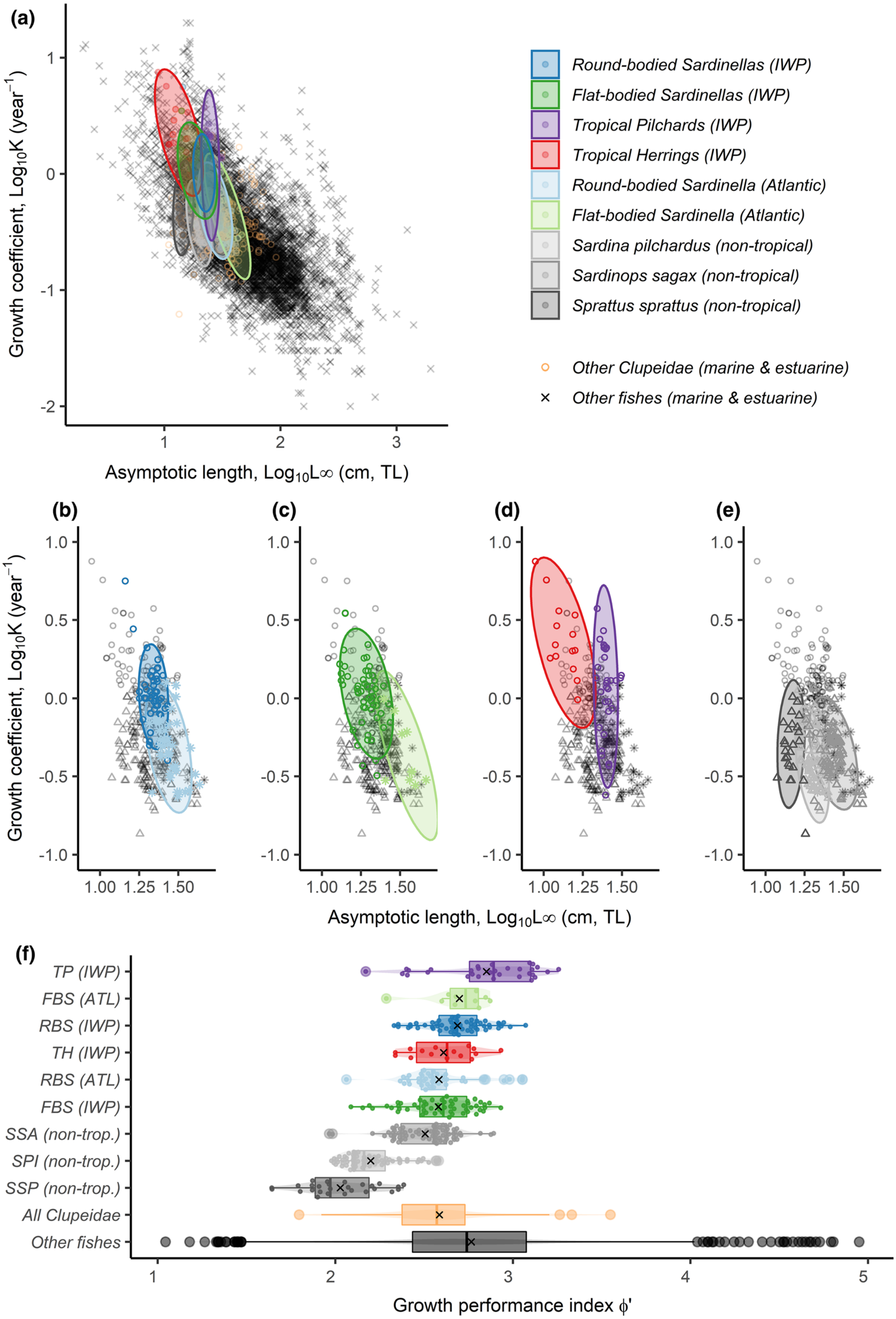
Age, growth and reproduction

There have been numerous past studies on the age, growth and reproduction of some tropical clupeid species in the IWP. However estimates for age-based life history parameters vary widely, and there is little or no data available for many species. Age estimates have largely been obtained from length-frequency analyses; some studies have used increment counts from otoliths, and a couple have counted scale or vertebrae rings. Most previous studies have applied the classical von Bertalanffy growth function (Beverton and Holt 1957) to length-at-age data, while a few have used the re-parameterised Francis (1988) equation (Milton and Blaber 1993; Milton et al. 1993) or various two-stanza models to account for differences in juvenile and adult growth (Oka and Miyamoto 2015; Williams and Clarke 1983). While detailed analysis of methods and models used to determine growth parameters is beyond the scope of this review, work in this area would be valuable to guide and standardise methods used in future studies across the region.

To describe and compare age and growth of tropical IWP clupeids for this review, growth parameters of the von Bertalanffy growth function (L_∞, K and t_0) were obtained from the FishBase database (Froese and Pauly 2021) and other published studies (see Online Resource 2: Figs. S2.1–S2.3 and Tables S2.1–S2.4). Despite being highlighted as a difficulty in an early comparative review on clupeid growth (Beverton 1963), studies have continued to use several methods of fish length measurement (i.e. total, fork and standard lengths), at times not specified length type used and have rarely provided conversion factors. For this review, lengths were converted to total length (in cm), where necessary, based on species-specific parameters provided in FishBase (Froese and Pauly 2021); this may have introduced some small inaccuracies. Comparing the growth curves of fishes is not straightforward, given growth relates to both size and time, and since fishes differ in maximum size and longevity (Pauly 1991). As such, I have used two measures based on the von Bertalanffy growth parameters to describe and compare growth patterns within and between species and species-groups: the growth performance index ϕ' and auximetric grid concept, as used in other comparative fish studies (e.g. Frisch et al. 2016; Murua et al. 2017). The auximetric grid is a double logarithmic plot of asymptotic length (L_∞) and growth rate coefficient (K), where paired L_∞ and K observations of closely related fishes (i.e. populations of the same species or species within the same genus) tend to form ellipse-shaped clouds representing the 'growth space' occupied by a given species or genus (Pauly 1991; Pauly and Binohlan 1996; Pauly et al. 1996). On average, the negative slopes of such ellipses—reflecting the inverse relationship between L_∞ and K, i.e. that smaller fish tend to have higher values of K and vice versa—have been shown to be a constant around -2. Thus similarities and differences in growth patterns can be described by the y-intercept or the growth performance index ϕ', defined as $\phi' = \log_{10} K + 2 \log_{10} L_\infty$ (Munro and Pauly 1983; Pauly and Munro 1984). Regardless of differences in maximum or asymptotic size and age, fishes with the same value of ϕ' have a similar pattern of growth, while those with a higher ϕ' value exhibit faster changes in size over their lifetime (Murua et al. 2017).

Tropical IWP clupeids have small bodies (commonly from 8 to 24 cm TL) and short life-spans (generally from around 1 to 4 years). As such, they

Fig. 2 **a** Auximetric plot comparing growth of tropical marine ▶ IWP clupeid species-groups, *Sardinella* species from the Atlantic Ocean and three non-tropical clupeids (coloured circles and 95% data ellipses) with other marine and estuarine clupeids (orange circles) and other marine and estuarine fishes (black crosses). **b to e** Auximetric comparison of Round-bodied Sardinellas from the IWP (dark blue) and Atlantic (light blue, b); Flat-bodied Sardinellas from the IWP (dark green) and Atlantic (light green, c); IWP Tropical Herrings (red) and Tropical Pilchards (purple, d); and three non-tropical clupeid species (grey, e) in closer detail. Symbols indicate region: IWP (circle), Atlantic (asterisk) and non-tropical (triangle). **f** The growth performance index ϕ', defined as $\phi' = \log_{10} K + 2 \log_{10} L_\infty$, of tropical marine IWP clupeid species-groups compared with *Sardinella* species from the Atlantic Ocean, selected non-tropical clupeids, all marine and estuarine members of the Clupeidae family (based on one mean value per species) and other marine and estuarine fishes (based on one mean value per species). Black crosses within the box plots indicate the mean value. Data and data sources for all separately plotted clupeid species-groups are provided in Online Resource 2. Where necessary, L_∞ estimates were first re-expressed as total length (TL) based on species-specific length–length equations in FishBase. Parameters for other marine and estuarine clupeids and other fishes were obtained from FishBase (records for all fishes were extracted via R package 'rfishbase' from FishBase v19.04, where asymptotic length was measured in total length and species' habitat was recorded as 'neritic', 'oceanic', 'coral reef' or 'estuaries', Froese and Pauly 2021)


(a)
Growth coefficient, $\mathrm{Log_{10}K}$ (year^{-1})
1
0
-1
-2
1
2
3
Asymptotic length, $\mathrm{Log_{10}L\infty}$ (cm, TL)
Round-bodied Sardinellas (IWP)
Flat-bodied Sardinellas (IWP)
Tropical Pilchards (IWP)
Tropical Herrings (IWP)
Round-bodied Sardinella (Atlantic)
Flat-bodied Sardinella (Atlantic)
Sardina pilchardus (non-tropical)
Sardinops sagax (non-tropical)
Sprattus sprattus (non-tropical)
Other Clupeidae (marine & estuarine)
Other fishes (marine & estuarine)
(b)
(c)
(d)
(e)
Growth coefficient, $\mathrm{Log_{10}K}$ (year^{-1})
1.0
0.5
0.0
-0.5
-1.0
1.00 1.25 1.50
Asymptotic length, $\mathrm{Log_{10}L\infty}$ (cm, TL)
(f)
TP (IWP)
FBS (ATL)
RBS (IWP)
TH (IWP)
RBS (ATL)
FBS (IWP)
SSA (non-trop.)
SPI (non-trop.)
SSP (non-trop.)
All Clupeidae
Other fishes
1
2
3
4
5
Growth performance index ϕ'

tend to have small L_∞ and high K values, and therefore occupy the upper-left region in the auximetric plot compared to other marine and estuarine fishes (Fig. 2a). As a group, tropical IWP clupeids are smaller in maximum length than some temperate clupeids (e.g. *Sardinops sagax)*, but similar to others (e.g. *Sardina pilchardus* and *Sprattus sprattus*). They are generally shorter-lived and K values tend to be higher, as reflected in the auximetric plots (Fig. 2; see Online Resource Figs. S2.1–S2.3 for individual species). This is consistent with patterns observed in tropical species across taxa (Pauly 1998). Interestingly, IWP clupeid species tend to be smaller, shorter-lived and have higher K values than their closely related Atlantic counterparts (Fig. 2b, c), possibly due to the broader latitudinal distribution of the two Atlantic species (as depicted in Whitehead 1985) and therefore exposure to a wider range of water temperatures. However the growth performance index values (ϕ') of these species-groups is similar between regions. Overall, the ϕ' values of tropical clupeid species-groups (means from 2.58 to 2.85) fall within the interquartile range of values observed in other marine and estuarine fishes (Fig. 2f), suggesting tropical clupeids reach their (small) maximum body size at rates generally similar to other fishes. (In contrast, some large pelagic tuna species have mean ϕ ' values over 4, i.e. they grow exceptionally fast to reach their large body sizes (Murua et al. 2017).) All tropical clupeid species-groups have higher growth performance than the three selected temperate clupeids, although mean ϕ' for *Sardinops sagax* (2.51) is nearer the tropical clupeids than the other two temperate species (2.03 and 2.20; Fig. 2f). It should also be noted that estimates of ϕ' for all species-groups and individual species (for which there were several observations) range widely, perhaps indicating some discrepancies in sampling and/or methods used to determine growth parameters across studies (Fig. 2f, Online Resource Fig. S2.1).

Tropical IWP clupeids typically reach maturity within 4 to 12 months (see species-group descriptions below). The general relationship between length at first maturity (L_m) and asymptotic length (L_∞) is proportional, i.e. species with shorter maximum lengths tend to mature at smaller sizes (Fig. 3), and fairly consistent across species groups. The average L_m/L_∞ ratio is 0.69 for Flat-bodied Sardinellas, 0.71 for Tropical Herrings and 0.74 for Round-bodied Sardinellas and Tropical Pilchards. A classic review by Beverton (1963) presented a similar average ratio of 0.64 for *Sardinella* spp., and 0.76 for temperate clupeids. From broad comparisons of temperate and tropical clupeids, length at first maturity often exhibits a latitudinal trend within genera, species and populations, with larger lengths occurring at higher latitudes (Ganias 2014). Data on Tropical Herring *H. quadrimaculatus* appears to be consistent with this trend (Milton et al. 1994b); however, it is not evident in other IWP species-groups (see Online Resource 3: Table S3.1) possibly due to methodological differences between studies or the narrow range of latitudes being considered (given the focus on tropical species in this review).

In both temperate and tropical species, females produce many eggs in proportion to body mass, which are broadcast to the water column, probably in spawning aggregations, and externally fertilised (Ganias et al. 2014; Milton et al. 1994b). In general, clupeid populations closer to the equator and in upwelling areas spawn over a longer period than in cooler waters (Ganias et al. 2014). In the tropical IWP, some species and populations spawn year-round with one or two periods of peak activity, while others may exhibit more restricted spawning seasons (Table 2). Extended periods of spawning increases the chances of at least some larvae encountering favourable environmental conditions (Fréon et al. 2005; Ganias et al. 2014).

Like many temperate clupeids, tropical IWP clupeid life history strategies are generally consistent with ‘opportunistic strategists’, which tend to be short-lived with small body size and size at maturation, relatively low individual fecundity, high growth rates, small eggs and little to no parental investment (King and McFarlane 2003; Winemiller and Rose 1992). Based on life history-based classification of tropical small pelagic fishes used in tuna baitfish fisheries in the Pacific, species from all four IWP clupeid species-groups are categorised as ‘Type 2 species’—moderately sized (10–24 cm) with an annual life cycle, reaching sexual maturity by 12 months of age. These are distinguished from the smaller (7–10 cm), short-lived (< 1 year) ‘Type 1’ clupeoids, which comprise the small anchovies (e.g. *Encrasicholina* spp.) and sprats (*Spratelloides* spp.); and the larger (20–35 cm), longer lived (3–5 years) ‘Type 3’ species such as small mackerels (*Rastrelliger* spp.) and round scads

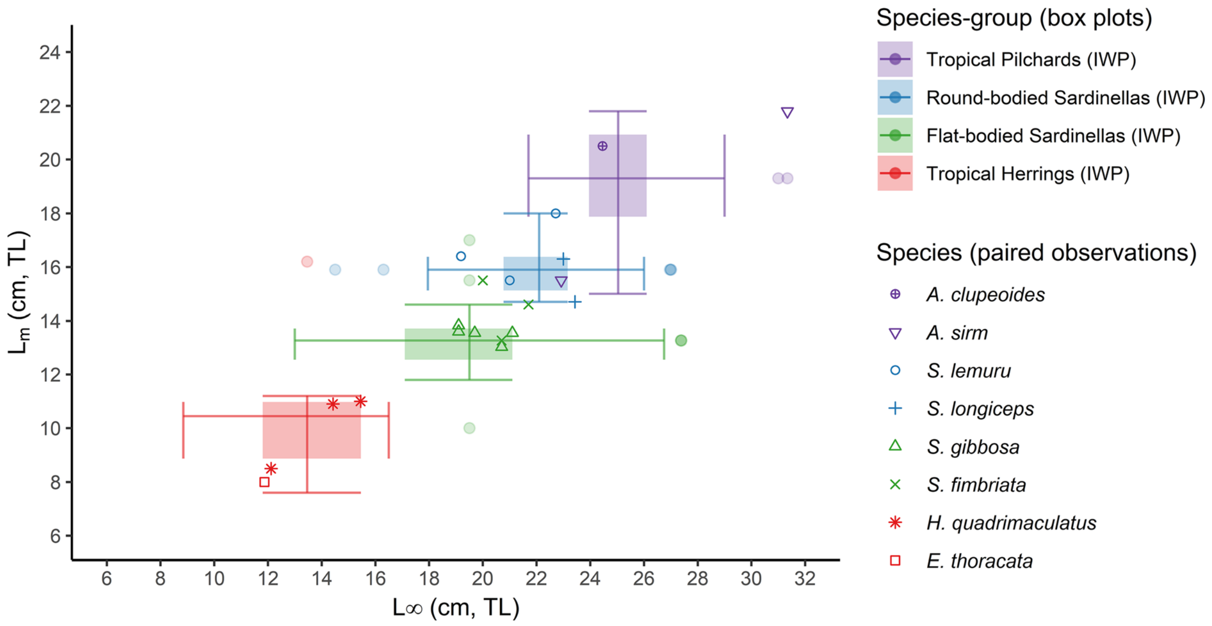


Fig. 3 Relationship between length at first maturity (L_m) and asymptotic length (L_∞) for tropical marine IWP clupeid species and species-groups. The lower and upper hinges of each boxplot (in both dimensions) correspond to the first and third quartiles against the corresponding axis. The 'whiskers' extend to minimum and maximum values, up to 1.5 times the interquartile range from the first and third quartiles respectively; outliers beyond this range are shown as shaded circles. The point of intersection formed by each pair of whiskers corresponds to the median L_∞ and L_m value for each species-group. Boxplots are based on both separate and paired L_∞ and L_m observations, pooled for each species-group. Plotted symbols for individual species represent paired L_∞ and L_m observations, i.e. from the same study or population. Data sources are provided in Online Resource 3 (Table S3.1)

(*Decapterus* spp.) (Conand and Kulbicki 1988; Dalzell 1993). However, as highlighted in the descriptions below, some variation in life history characteristics is evident between genera or 'species-groups' within this 'Type 2' category.

Comparison of available estimates suggests that maximum length and age are generally similar within IWP clupeid species-groups and broadly different between species-groups. Auximetric plots comparing growth of individual species suggest high similarity between species of the same species-group, although only limited data is available for the Tropical Pilchards and Tropical Herrings (see Online Resource Fig. S2.3). This is further reflected in the similar growth performance index values (see Online Resource Fig. S2.1). The Tropical Pilchards are possibly an exception, with a somewhat higher median ϕ' value, indicating faster growth to reach their maximum size. However the available data are highly variable, suggesting possible discrepancies or biases in previous studies. Further comparison of life history characteristics within each species-group is provided below.

Round-bodied Sardinellas

Round-bodied Sardinellas commonly reach lengths up to 24 cm TL (Whitehead 1985), and live up to 3–4 years in Indian (*S. longiceps*, Devaraj et al. 1997; Rohit et al. 2018) and Indonesian waters (*S. lemuru*, Merta 1995; Pet et al. 1997). A possible life span of 6–7 years for *S. lemuru* has been reported in higher latitude Western Australia (28°S) based on otolith ring counts. This is consistent with general trends of slower growth rates and longer life spans in cooler waters, although annual deposition of rings was unable to be validated (Gaughan and Mitchell 2000). The average maximum longevity (T_{max}) calculated from growth parameters is 3.0 years for both *S. longiceps* and *S. lemuru* (Table 1). Most estimated L_∞ values for *S. longiceps* range from 19–27 cm TL and from 18–27 cm TL for *S. lemuru*. Estimated *K* values mainly range from 0.4–2.1 year^{-1} and 0.5–1.4 year^{-1}

Table 1 Summary of growth and reproductive parameters for selected tropical marine clupeids in the Indo-West Pacific, from genera *Amblygaster*, *Herklotsichthys* and *Sardinella*

SpG	Species	Maximum length (cm)		Common length (cm)		Summary of growth parameters									Reported lifespans (years)	Reproductive parameters				
						n	L_∞ (cm TL)		*K* (year^{-1})		ϕ'		T_{max} (years)			L_m (cm TL)			L_m/L_∞	
		SL	TL	SL	TL		Mean	SE	Mean	SE	Mean	SE	Mean	SE		*n*	Mean	SE	*n*	Mean
TP	*A. clupeoides*	21.0	25.4	15	18.1	*1*	24.5	-	1.82	-	3.04	-	1.4	-	-	*2*	19.3	1.2	*1*	0.84
TP	*A. sirm*	27.0	32.5	20	24.1	*30*	25.1	0.4	1.35	0.15	2.85	0.05	3.2	0.5	1.2–8	*8*	18.8	0.9	*2*	0.68
TH	*E. thoracata*	10.0	11.8	8	9.5	*4*	11.5	0.3	1.91	0.09	2.40	0.04	1.3	0.1	1	*2*	7.5	0.5	*1*	0.67
TH	*H. quadrimaculatus*	25.0 [b]	30.3 [b]	10	12.1	*11*	14.0	0.8	3.05	0.60	2.69	0.04	1.1	0.3	1–1.5	*5*	10.4	0.5	*3*	0.72
FBS	*S. albella*	14.0	16.9	10	12.0	*9*	15.8	1.0	1.40	0.10	2.52	0.05	2.0	0.2	-	*2*	11.1	0.9	-	-
FBS	*S. fimbriata*	13.0	16.2	11	13.7	*6*	21.2	1.2	0.99	0.12	2.62	0.07	3.1	0.5	-	*2*	13.9	0.7	*2*	0.66
FBS	*S. pacifica* [a]	10.5 [b]	13.1 [b]	-	-	*13*	20.4	0.8	1.02	0.06	2.61	0.04	2.9	0.2	-	*1*	15.5	-	*1*	0.78
FBS	*S. gibbosa*	23.8	29.6	15	18.7	*18*	19.1	0.6	1.45	0.21	2.63	0.05	2.8	0.5	1–7	*8*	13.8	0.5	*5*	0.68
FBS	*S. jussieu*	16.5	20.8	10	12.6	*2*	21.5	3.3	0.51	0.14	2.35	0.26	6.2	1.8	-	-	-	-	-	-
FBS	*S. melanura*	20.3	24.7	10	12.2	*1*	27.4 [b]	-	0.70	-	2.72	-	4.1	-	-	-	-	-	-	-
FBS	*S. sindensis*	17.0	20.6	14	17.0	*5*	19.8	0.6	1.09	0.14	2.61	0.07	2.9	0.6	-	-	-	-	-	-
FBS	*S. zunasi*	14.3	18.0	10	12.6	*2*	16.3	0.6	0.56	0.06	2.17	0.02	5.2	0.6	-	-	-	-	-	-
RBS	*S. lemuru*	23.0	28.0	20	24.4	*24*	21.7	0.5	1.00	0.04	2.66	0.02	3.0	0.2	3–4; 6–7	*3*	16.6	0.7	*3*	0.80
RBS	*S. longiceps*	23.0	26.6	20	23.1	*33*	22.0	0.4	1.26	0.16	2.71	0.03	3.0	0.3	3–4	*3*	15.3	0.5	*2*	0.67

Species-group (SpG) refers to Tropical Pilchards (TP), Tropical Herrings (TH), Flat-bodied Sardinellas (FBS) and Round-bodied Sardinellas (RBS). Maximum lengths were obtained from FishBase (Froese and Pauly 2021); all lengths were originally described in standard length (SL) except for *S. gibbosa*, *S. zunasi* and *S. aurita* which were in total length (TL). Common lengths were obtained from Whitehead 1985; all lengths were originally described in SL. Length conversions were carried out using species-specific length–length tables available from FishBase. Summary growth parameters were calculated from available studies (*n*) sourced from FishBase and other published sources that had estimated von Bertalanffy growth function parameters, asymptotic length (L_∞) and *K*. All data and source details are provided in Online Resource 2. The growth performance index (ϕ') was calculated for each record following Pauly and Munro (1984) as $\phi' = \log_{10} K + 2\log_{10} L_\infty$. Maximum longevity ($T_{max}$) was estimated following Taylor (1958) as $T_{max} = t_0 + 3/K$, where t0 was estimated from $\log(-t_0) = -0.3922 - 0.2752 \log_{10} L_\infty - 1.038 \log_{10} K$ following Pauly (1979) (both cited in Froese and Pauly 2000). The mean and standard error (SE) of each summary statistic are provided. Reported lifespans indicate the range reported in the literature (sources as referenced in the main text). Summary reproductive parameters were calculated from available published studies (*n*) that had estimated length at first maturity (L_m). The mean L_m to L_∞ ratio was averaged from studies (*n*) that provided estimates for both L_m and L_∞ (i.e. paired records)

[a] *S. pacifica* includes records reported as *S. fimbriata* from the Philippines, to reflect the recent re-description of this species in the Philippines (Hata and Motomura 2019b)

[b] Indicates potentially questionable records based on other data presented for that species

respectively (Online Resource Table S2.2). Two lower L_∞ (< 16.5 cm TL) and higher *K* (> 2.7) estimates for *S. longiceps* from Yemen and Sri Lanka in a study by Dayaratne and Gjøsaeter (1986) are probably less reliable given the small length range of fish sampled (11.8–16.2 cm TL) using gill nets. Excluding these records, ϕ' values for *S. longiceps* range from 2.33 to 2.98, and from 2.41 to 2.84 for *S. lemuru* (both average of 2.7; Table 1).

Round-bodied Sardinellas first reach maturity around 14.7–16.3 cm TL, although 18 cm TL has been reported for both species; latitudinal trends are not apparent (Online Resource Table S3.1). Reported age at first maturity varies from 4–6 months (Naguit 2016) to 2 years of age for *S. lemuru* (Gaughan and Mitchell 2000; Pet et al. 1997); and from 6–7 months (Rohit et al. 2018) to 1–2 years (Devaraj et al. 1997; Jayaprakash and Pillai 2000 and references therein) for *S. longiceps*. Variation in estimated length and age at first maturity may be partly explained by differences in developmental stage used to categorise fish as 'mature' (see Online Resource Table S3.1) and possibly due to the spatial and temporal distribution of sampling (Lowerre-Barbieri et al. 2011). However research on temperate sardines has also shown that both length and age at maturity can change in response to population size due to impact of food availability per capita on growth rates (Ganias et al. 2014 and references therein). Comparable detailed studies are not available for these tropical species, however higher growth rates observed for *S. longiceps* in Indian waters in recent years are suggested to be due to decreased population size (Rohit et al. 2018 and references therein).

The reported spawning duration for Round-bodied Sardinellas also varies across studies, from 2-months to year-round (Table 2). While some of this variation is likely real due to differences in local temperature regimes or other environmental factors (e.g. between higher latitude Western Australia and lower latitude locations), variation between studies at the same location is probably due (at least in part) to the spatial distribution of sampling (Lowerre-Barbieri et al. 2011). Given samples have usually been collected via fisheries activities, expansion of fishing grounds over time (and therefore fish sampling area) may explain some differences between studies. For instance, early studies on *S. longiceps* in Indian waters reported a spawning season from May to October at a time when fisheries were restricted to within 20 km of the coast (5–25 m depth) (Jayaprakash and Pillai 2000; Nair 1973). More recent studies, carried out since fishing grounds have expanded to offshore waters up to 100 m deep, found evidence of year-round spawning at some locations (Rohit et al. 2018). Early fishery-independent plankton surveys also reported the presence of *S. longiceps* larvae throughout the year (NORAD/IMR 1976) therefore this is unlikely to reflect a shift in species biology or climate.

Flat-bodied Sardinellas

Flat-bodied Sardinellas vary in maximum length, commonly reaching sizes from 12 to 19 cm TL (Whitehead 1985). Reported life spans vary for individual species—e.g. *S. gibbosa* from 1–2 years (Bennet et al. 1986; Cappo 1995a; Devaraj et al. 1997), 3 years (Ghosh et al. 2013) and up to an estimated 7 years (Froese and Pauly 2021; Sanders et al. 1984). However this longer life span was based on the assumption that fish may reach this age without fisheries exploitation; the maximum age 'observed' in this study was around 4 years (Sanders et al. 1984). Average maximum longevity ($T_{\max}$) calculated from growth parameters for *S. gibbosa* is 2.8 years. Across the Flat-bodied Sardinellas, average $T_{\max}$ estimates range from 2.0 years (*S. albella*) to 6.2 years (*S. jussieu*), although the latter is based on only two studies (Table 1). The median L_{∞} estimate for most species falls between 19.4 and 21.5 cm TL, although there is considerable range reported for some species—e.g. estimates for *S. fimbriata* in the Philippines (now redescribed as *S. pacifica*) range from 14–24.8 cm TL. Median estimates for *S. albella* and *S. zunasi* are shorter at 13.8 and 16.3 cm TL respectively, while the only observation for *S. melanura* is longer (27.4 cm TL) perhaps overestimated when converting from standard length (22.5 cm SL) or possibly an error in the original length type reported. Median *K* estimates for most species range from 1.0 to 1.3 year^{-1}. Lower values are reported for *S. jussieu*, *S. zunasi* and *S. melanura* (0.5–0.7 year^{-1}), although these are based on limited observations (n = 1 or 2). Again there is considerable range in *K* estimates within individual species—e.g. most estimates for *S. gibbosa* range from 0.32 to 2.2 year^{-1} (Online Resource Fig. S2.1). Two studies reporting higher *K* values (3.5 year^{-1}) and correspondingly low L_{∞} values (14.1 cm TL) are probably less reliable due to limited sampling (maximum length was 13.2 cm TL in one study, Dayaratne and Gjøsaeter 1986). Mean ϕ' values for *S. gibbosa*, *S. sindensis*, *S. fimbriata* and *S. pacifica* are around 2.6, while mean estimates are lower for *S. albella* (2.5), *S. jussieu* (2.3) and *S. zunasi* (2.2).

Flat-bodied Sardinellas *S. gibbosa* and *S. fimbriata* reach first maturity at lengths averaging 13.8–15.5 cm TL; other species mature at slightly smaller sizes (Table 1 and Online Resource Table S3.1). Estimated age at first maturity varies in different studies—e.g. for *S. fimbriata*, from 9 months (Bennet et al. 1992) to 12 months (Bennet et al. 1986; Dayaratne and Gjøsaeter 1986; Okera 1974) to 2 years (Pet et al. 1997 and references therein). Spawning aged 6 months at shorter lengths (8.5–10.3 cm) has been reported for *S. albella* and *S. gibbosa* in north-east Australia (Cappo 1995b) however calculation methods are not specified and this may refer to the smallest size and youngest age of spawning fish (rather than 50% of sample). Reported spawning durations for Flat-bodied Sardinellas range from 2 months to year-round, varying by location and species, and between studies at some locations (Table 2). For example, in northern Australia, *S. gibbosa* has an extended spawning season over early spring and summer, while *S. brachysoma* and *S. albella* have a shorter spawning duration (4 and 5 months respectively, also from early spring) (Cappo 1995b).

Table 2 Spawning seasons reported for tropical marine clupeids in the Indo-West Pacific

Species	Location	Latitude	J	F	M	A	M	J	J	A	S	O	N	D	Ref. & notes
Round-bodied Sardinellas															
S. longiceps	Oman	24°N		+	+						+	+			[1] [b]
S. longiceps	India (SW)	8-12°N					+	X	X	X	+	+			[2] [c]
S. longiceps	India (SW)	8-12°N	+	+	+	+	+	X	X	X	+	+	+	+	[3] [c]
S. longiceps	India (SW)	10-11°N					+	+	+	+	+				[4] [d]
S. longiceps	Sri Lanka (E)	7°N				+	+								[5] [e]
S. lemuru	China	22-23°N			X	X	X	+	+	+					[6]
S. lemuru	Philippines (Zamboanga N)	8°N	+	+									+	+	[7] [f]
S. lemuru	Philippines (Zamboanga S)	7°N	+	+				+	+	+	+		+	+	[7] [g]
S. lemuru	Indonesia (Madura Str.)	7°S											+	+	[8] [h]
S. lemuru	Indonesia (Bali Str.)	8°S	X	·							·	·	·	X	[6] [i]
S. lemuru	Indonesia (Bali Str.)	8°S						+	+						[9]
S. lemuru	Indonesia (Bali Str.)	8°S							+						[10]
S. lemuru	Indonesia (Bali Str.)	8°S						+							[11]
S. lemuru	Australia (W)	28°S	X	X	+									+	[12] [j]
Flat-bodied Sardinellas															
S. fimbriata	India (W)	14°N	+	+	+	+									[13]
S. fimbriata	India (SW)	11°N				+	+	+							[13]
S. fimbriata	India (SW)	8°N	+	+	+	+	X	X	+	X	+	X	X	+	[14]
S. fimbriata	India (SW)	8°N	+	+						+	+	+	+	+	[13]
S. fimbriata	India (E)	16-20°N	·	·	·	·	X	X	X	·	·	·	·	·	[15]
S. fimbriata	India (E)	17°N							X	+					[16]
S. fimbriata	India (E)	17°N	+						X	X	X	X			[17]
S. fimbriata	India (SE)	8°N										+	+		[14]
S. gibbosa	India (W)	14°N	+	+	+	+					+	+	+	+	[16]
S. gibbosa	India (SW)	8-12°N	+	+	+	+	+								[14]
S. gibbosa	India (SW)	8°N					+	+			+	+			[16]
S. gibbosa	India (SW)	8°N	+	+					+	+	+	+	+	+	[13]
S. gibbosa	India (E)	20° N	·	·	X	X	·	·	·	·	·	·	·	·	[15]
S. gibbosa	India (E)	17°N			X	X									[18] [k]
S. gibbosa	India (E)	17°N	+	+	+	+									[16]
S. gibbosa	India (E)	17°N		+	+	+	+								[14]
S. gibbosa	India (E)	16-17°N	·	X	X	·	·	·	·	·	·	·	·	·	[15]
S. gibbosa	India (E)	13°N	+	+	+	+								+	[16]
S. gibbosa	India (SE)	8-9°N		+	+	+	+	+	+	+					[13, 14]
S. gibbosa	India (SE)	8°N	·	·	·	·	·	·	·	·	·	·	·	·	[16] [l]
S. gibbosa	Sri Lanka (W)	7°N					+	+	+	·	·			+	[5, 19] [m]
S. albella	India (SW)	8-12°N	+	+	X	X	X				+	+	+	+	[14]
S. albella	India (SE)	8-9°N		+	X	X	+	+	+						[13, 14]
S. albella	Sri Lanka (W)	7°N		X	X	X						+	+	+	[5, 19]
S. albella	Tanzania	6°S	+	+	+						X	X	+	X	[20]
S. gibbosa	Tanzania	6°S	+	+	+						X	X	+	X	[20]
S. albella	Tanzania	6°S					+	+	X	X					[21]
S. gibbosa	Tanzania	6°S				+	+	X	X	+					[21]
S. fimbriata [a]	Indonesia (Madura Str.)	7°S	+											+	[8] [h]
S. albella	Australia (NE)	9°S								+	+	+	+	+	[22]
S. brachysoma	Australia (NE)	9°S								+	+	+	+		[22]
S. gibbosa	Australia (NE)	9°S	+	+						+	X	X	+	+	[22, 23] [n]
S. marquesensis	Marquesas Islands	9°S	+	+	+	+	+	+	+	+	+	+	+	+	[24]
Tropical Pilchards															
A. sirm	India (E)	8°N		+	X	X	X	X	+						[13]
A. sirm	India (E)	8°N		+	+		+	+					+	+	[14]
A. sirm	India (W)	8°N	+	+										+	[25]

Table 2 continued

Species	Location	Latitude	J	F	M	A	M	J	J	A	S	O	N	D	Ref. & notes
A. sirm	Sri Lanka (W)	7°N				X	X	X							[5]
A. sirm	Sri Lanka (W)	7°N				+	+			+	X				[26] [o]
A. sirm	Kiribati	0°					+	X	+	X	X	X			[27]
A. sirm	Indonesia (Java Sea)	4-6°S		+	+	+	+	+							[28]
A. sirm	Australia (NE)	9°S	+	+	+					+	X	X	+	+	[22, 23] [n]
A. sirm	New Caledonia	21°S										+	X	X	[29, 30] [p]
A. clupeoides	New Caledonia	21°S										+	X	X	[29]
Tropical Herrings															
H. quadrimaculatus	Japan	26°N			+	X	X	X	+	+					[31] [q]
H. quadrimaculatus	Hawaii	21°N	·	·	+	+	X	X	X	+	+	+	·	·	[32] [r]
H. quadrimaculatus	Kiribati	0°	+	+	+	+	+	X	+	+	+	+	+	+	[27] [s]
H. punctatus	Seychelles	4°S	+	+	+	+	+	+	+	+	+	+	+	+	[33, 34] [t]
H. castelnaui	Australia (NE)	9°S								+	+	+			[35]
H. castelnaui	Australia (NE)	9°S								+	+				[22, 35]
H. koningsbergeri	Australia (NE)	9°S								+	+	+			[22]
H. lippa	Australia (NE)	9°S								+	+	+	+		[22]
H. quadrimaculatus	Fiji	17°S	·	·	·	·	·	·	·	·	·	X	X	X	[36]
H. quadrimaculatus	New Caledonia	21°S	·	·	·	·	·	·	·	·	+	+	X	X	[29] [u]
E. thoracata	India (SW)	9°N	X	+								+	+	X	[37]
E. thoracata	Australia (NE)	9°S								+	+				[22]

'J' to 'D' correspond to months of the year, from January to December. Reported spawning activity is indicated by '+'. Where stated in the cited reference, peak spawning activity is indicated by 'X', and possible spawning activity by ' · '. Rows are ordered by latitude within each species-group

[a] Species distribution has been revised or questioned (Hata and Motomura 2019b) since cited document was published. References: [1] Zaki et al. (2012); [2] Jayaprakash and Pillai (2000); [3] Rohit et al. (2018); [4] Kripa et al. (2018); [5] Dayaratne and Gjøsaeter (1986); [6] Whitehead (1985); [7] Naguit (2016); [8] Pet et al. (1997); [9] Dwiponggo (1974); [10] Merta, 1992 cited in Merta (1995); [11] Buchary (2010); [12] Gaughan and Mitchell (2000); [13] Bennet et al. (1986); [14] Devaraj et al. (1997); [15] Ghosh et al. (2013); [16] Bennet et al. (1992); [17] Luther (2001); [18] Sekharan et al. (1969); [19] Dayaratne (1997); [20] Okera (1974); [21] Losse, unpubl. cited in Okera (1974); [22] Cappo (1995b); [23] Cappo (1995a); [24] Nakamura and Wilson (1970); [25] Lazarus (1990); [26] Jayasuriya (1989); [27] Milton et al. (1994b); [28] Atmaja et al. (1995); [29] Conand (1988); [30] Conand (1991); [31] Oka and Miyamoto (2015); [32] Williams and Clarke (1983); [33] de Moussac and Poupon (1986); [34] Hallier (1990); [35] Robertson and Duke (1990); [36] Lewis, 1983 cited in Rawlinson (1993); [37] Abdussamad et al. (2018)

Notes on spawning season from cited reference(s): [b]Sea surface temperature different during the two spawning events. [c]Peak coincides with SW monsoon. [d]Duration and timing varies between years. [e]Coincides with onset of SW monsoon. [f]Coincides with NE monsoon. [g]Coincides with NE & SW monsoon. [h]Coincides with onset of wet NW monsoon. [i]Assumed spawning period [but evidence?]. [j]Coincides with warmer sea surface temperatures. Peak spawning period likely variable. [k]Observations of eggs. [l]Spawns periodically. [m]Coincides with onset of SW & NE monsoons. [n]Peak spawning coincides with spring. [o]Coincides with start & end of SW monsoon. [p]Occurs prior to hot rainy season. [q]Photo period suggested as spawning cue. [r]Peak spawning coincides with summer period. [s]Increase in water temperature suggested as spawning cue. [t]More active spawning some months. [u]Peak coincides with increasing water temperature.

[a] Species distribution has been revised or questioned (Hata and Motomura 2019b) since cited document was published

[b] References: [1] Zaki et al. (2012); [2] Jayaprakash and Pillai (2000); [3] Rohit et al. (2018); [4] Kripa et al. (2018); [5] Dayaratne and Gjøsaeter (1986); [6] Whitehead (1985); [7] Naguit (2016); [8] Pet et al. (1997); [9] Dwiponggo (1974); [10] Merta, 1992 cited in Merta (1995); [11] Buchary (2010); [12] Gaughan and Mitchell (2000); [13] Bennet et al. (1986); [14] Devaraj et al. (1997); [15] Ghosh et al. (2013); [16] Bennet et al. (1992); [17] Luther (2001); [18] Sekharan et al. (1969); [19] Dayaratne (1997); [20] Okera (1974); [21] Losse, unpubl. cited in Okera (1974); [22] Cappo (1995b); [23] Cappo (1995a); [24] Nakamura and Wilson (1970); [25] Lazarus (1990); [26] Jayasuriya (1989); [27] Milton et al. (1994b); [28] Atmaja et al. (1995); [29] Conand (1988); [30] Conand (1991); [31] Oka and Miyamoto (2015); [32] Williams and Clarke (1983); [33] de Moussac and Poupon (1986); [34] Hallier (1990); [35] Robertson and Duke (1990); [36] Lewis, 1983 cited in Rawlinson (1993); [37] Abdussamad et al. (2018)

Tropical Pilchards

Tropical Pilchards commonly reach up to 24 cm TL (Whitehead 1985), although recently described *A. indiana* is larger (up to 29.3 cm SL in paratypes described, Mary et al. 2017). Reported life spans range widely. For the most commonly reported species, *A. sirm*, estimates range from 1.2–2 years (across latitudes 0° to 21°S Cappo 1995b; Conand 1991; Milton and Blaber 1993; Milton et al. 1994b), 2–4 years in Indian waters (8°N, Bennet et al. 1986; Devaraj et al. 1997) to an estimated 8 years (28°N, Sanders and Morgan 1989), although this longer life span was also assumed rather than observed. Almost all available growth parameters are for *A. sirm*. Estimated L_∞ values for *A. sirm* range from 21.7 to 31.3 cm TL (median 24.9 cm TL); the single observation for *A. clupeoides* is similar (24.5 cm TL). K values for *A. sirm* range widely, generally from 0.2 to 2.7 year^{-1} (median 1.3 year^{-1}) and up to 3.7 year^{-1} in one study. Correspondingly, maximum longevity estimates calculated from these parameters also vary widely, from 6 months to 12.4 years (mean 3.2 years). Growth performance index ϕ' values range from 2.2 to 3.3 (mean 2.9). Estimates for *A. clupeoides*, available from a single study, fall within the range of values reported for *A. sirm* (Online Resource Fig. S2.1 and Table S2.2). While some of the observed variation in *A. sirm* parameters between studies and countries may reflect real differences in maximum size and growth rates between populations and locations (Milton et al. 1993), some variation can probably be attributed to inadequate sampling (e.g. using gillnets, Dayaratne and Gjøsaeter 1986) and/or differences in methods. Daily otolith increment formation has been only indirectly validated in *A. sirm* based on back-calculated birthdates and adult spawning periods (Dayaratne and Gjøsaeter 1986; Milton et al. 1993). However, while studies using otolith-based methods have typically resulted in lower L_∞ values and a higher range of K values than those resulting from length-frequency methods, mean values are not significantly different (Online Resource Fig. S2.4).

Length and estimated age at first maturity also range widely (*A. sirm,* Fig. 3), without any obvious latitudinal trend (Milton et al. 1994b), from around 16–21.9 cm TL, aged 7 months (Milton and Blaber 1993), 10–12 months (Conand 1991), to over 1 year (Bennet et al. 1986). A detailed study in Kiribati found *A. sirm* reached sexual maturity quickly (smallest fish with ripe oocytes was 11 cm SL, aged 150 days), but first spawning (50% fish with 85% running-ripe oocytes) did not occur until 18 cm SL, aged 330 days (Milton et al. 1994b). This could explain some differences between studies. *A. sirm* spawns over an extended period (3–8 months; Table 2), but probably not year-round even near the equator (Milton et al. 1994b).

Tropical Herrings

Tropical Herrings are smaller than species in the other three species-groups. *Herklotsichthys* spp. commonly reach lengths from 8 to 16 cm TL (Whitehead 1985). The largest maximum size reported for *H. quadrimaculatus* (25 cm SL, Froese and Pauly 2021) appears inconsistent with other observations and may be a case of misidentification. Tropical Herrings are consistently reported to have life spans around 1–1.5 years (Cappo 1995a; Milton et al. 1993; Oka and Miyamoto 2015). *Escualosa* spp. commonly reach lengths from 8 to 10 cm TL, and have an estimated life span of around 1 year (Abdussamad et al. 2018 and references therein; Whitehead 1985). Growth parameters are currently only available for *H. quadrimaculatus* and *E. thoracata* (Table 1 and Online Resource Table S2.2). Mean estimated L_∞ values for *H. quadrimaculatus* and *E. thoracata* are 14.0 and 11.5 cm TL respectively. Mean K for *E. thoracata* is 1.9 year^{-1}, and average $T_{\max}$ calculated from these parameters is 1.3 years. K values for *H. quadrimaculatus*, however, range considerably: from 1.0 to 3.6 year^{-1} in most studies (Online Resource Fig. S2.1). Two higher K values (5.7 and 7.5) from the Solomon Islands were probably due to inadequate sampling (Milton et al. 1993). Maximum longevity estimates also range widely: from 0.5 to 2.8 years, with an average of 1.3 years (excluding the two Solomon Islands records). Growth performance index ϕ' mean values are slightly higher for *H. quadrimaculatus* (2.7) compared to *E. thoracata* (2.4).

Tropical Herrings mature at a small size and young age (Fig. 3). For the widely distributed *H. quadrimaculatus*, length and age at first maturity appear to decrease with latitude, from 8.5 cm TL at 4–5 months in equatorial Kiribati (Milton et al. 1994b) to 11 cm TL at less than 12 months in higher latitude

New Caledonia (21°S, Conand 1988). The spawning duration of *H. quadrimaculatus* also varies with latitude (Table 2), from year-round activity in Kiribati, to a restricted spring and summer spawning season in higher latitude Japan (Oka and Miyamoto 2015). Other *Herklotsichthys* species may spawn for shorter periods—e.g. *H. caustelnaui* is reported to spawn over a 2–3 month period (Cappo 1995b; Robertson and Duke 1990). *E. thoracata* matures around 8 cm TL and spawns over a 5 month period in Indian waters (Abdussamad et al. 2018); in northern Australia, it starts to mature at 6 cm (approx. 6 months old) and spawns over 2 months (Cappo 1995b).

Trophic biology

Tropical clupeids, like temperate species and other clupeoids, consume low trophic level prey items such as zooplankton, small nekton, phytoplankton and detritus. They can feed both by visually selecting food particles from the water column as well as filter-feeding through gill rakers (Dalzell 1993; Garrido and van der Lingen 2014). The size and types of prey consumed reflects available food, which varies geographically and seasonally, as well as prey selection mechanisms such as feeding apparatus morphology and feeding mode, which may vary by species and life stage (Garrido and van der Lingen 2014). The number and density of gill rakers vary widely between IWP species-groups. The number of gill rakers on the lower gill arch, used taxonomically to distinguish several genera and species, ranges from 26–43 in Tropical Pilchards, 28–58 in Tropical Herrings, 39–134 (but usually less than 90) in Flat-bodied Sardinellas, and from 77–188 and 150–250 + in Round-bodied Sardinellas *S. lemuru* and *S. longiceps* respectively. In Round-bodied Sardinellas and some Flat-bodied Sardinellas, gill rakers continue to develop during adult stages. However, in Tropical Pilchards, Tropical Herrings and most Flat-bodied Sardinellas, gill raker numbers show little increase with body size after early juvenile stage (Stern et al. 2018; Whitehead 1985).

Zooplankton such as copepods and small crustacea are the most important prey for juveniles and adults of most tropical species, including Tropical Herrings *H. quadrimaculatus* (Milton et al. 1994a; Williams and Clarke 1983), *H. castelnaui* (Egan et al. 2018b) and *E. thoracata* (Abdussamad et al. 2018)); Tropical Pilchard *A. sirm* (Whitehead 1985); Flat-bodied Sardinellas *S. gibbosa* (Bennet et al. 1992; Egan et al. 2018b; Mavuti et al. 2004), *S. albella* (Horinouchi et al. 2012) and *S. fimbriata* (Bennet et al. 1992); and one of the Round-bodied Sardinellas, *S. lemuru* (Gaughan and Mitchell 2000; Horinouchi et al. 2012; Merta 1995; Metillo et al. 2018). Many of these species also consume a variety of other food items, although this may vary by life stage. Some phytoplankton is eaten by juvenile *A. sirm* (Whitehead 1985) and small (< 5 cm) *S. fimbriata* (Appa Rao, 1981 cited in Bennet et al. 1992), and by larger sized (> 8 cm) *S. gibbosa* (Lazarus 1977) and *S. lemuru* adults (Metillo et al. 2018). Habitat location may also influence diets. Tropical Herring *H. quadrimaculatus* has been reported to consume some phytoplankton and algae in Sri Lanka (Deepananda et al. 2016) but elsewhere all life stages, including late stage larvae, were found to be exclusively zooplanktivorous (Kiribati, Milton et al. 1994a; Hawaii, Williams and Clarke 1983).

In contrast, Round-bodied Sardinella *S. longiceps* adults and larvae feed extensively on phytoplankton, particularly diatoms. Zooplankton is also consumed by adults, and may be dominant in the diet of juveniles (Jayaprakash and Pillai 2000; Kuthalingam 1960; Rohit et al. 2018 and references therein). This is similar to temperate species in upwelling regions, which as larvae are almost exclusively zooplanktivorous, but as juveniles and adults consume increasing quantities of phytoplankton as they develop finer filtration apparatus (Garrido and van der Lingen 2014 and references therein). Nevertheless, in temperate species, even when large quantities of phytoplankton are consumed, zooplankton can still provide the majority of dietary carbon (Garrido and van der Lingen 2014 and references therein). This may also be the case for tropical *S. longiceps*, however no comparable studies that assessed diet from the perspective of energy provision were identified.

Ontogenetic shifts in the type of prey consumed can be due to development of feeding apparatus (as mentioned above) as well as shifts in feeding mode and use of different habitats at different life stages. In temperate sardines, larvae are typically particulate-feeders, while adults can filter-feed using fully developed gill rakers. Adults may also switch feeding mode according to the characteristics of prey in the water column, particularly prey size, but also for some species, prey concentration, which can vary seasonally and by location (Garrido and van der Lingen 2014). Feeding mode studies on IWP clupeids are few and limited to adult fish but suggest strategies may vary between species-groups. The Tropical Herring *H. quadrimaculatus* is reported to be a highly selective particulate feeder that probably does not filter-feed under normal conditions (Milton et al. 1994a). Flat-bodied Sardinellas *S. marquesensis* and adult *S. albella* are both particulate and filter-feeders (Bennet et al. 1986; Nakamura and Wilson 1970), while Round-bodied Sardinella *S. longiceps* may predominantly filter-feed (Rohit et al. 2018). Size and diversity of prey consumed can also change with life history stage. A recent study showed that both small and large *S. gibbosa* consume small sized prey (< 500 um), but large fish also eat larger prey and hence a wider range of prey sizes (Egan et al. 2018b). Similar results were found in a qualitative assessment of diet in *H. quadrimaculatus* (Williams and Clarke 1983). Round-bodied Sardinella *S. lemuru* has been found to consume an increasing number of prey types with age (Metillo et al. 2018)**.**

There are few studies investigating patterns of feeding activity of IWP clupeids. While some species have been suggested to feed more intensely or predominantly at night, such as *S. fimbriata* (Bennet et al. 1986) and *H. quadrimaculatus* (Milton et al. 1994a; Williams and Clarke 1983), others are suggested to feed during the day, such as *A. sirm* (Rawlinson et al. 1992). Feeding activity can also vary seasonally with food availability. *H. quadrimaculatus* was found to feed in the daytime at some times of year, coinciding with high densities of certain prey (Milton et al. 1994a). Based on temperate studies, feeding behaviour may also be dependent on fish size, feeding mode and prey characteristics; for example, continuous day and night feeding is indicative of filter-feeding. Temperate sardines generally filter-feed in dense schools, but disperse to particulate feed, although this may also vary with water depth and prey availability (Garrido and van der Lingen 2014).

Habitat associations, migrations and movement

Tropical clupeids live in the water column of tropical and subtropical coastal waters, generally over the continental shelf and at depths from 0 to 200 m (Dalzell 1993; Whitehead 1985). Within this area, species occupy a range of habitats reflecting species-specific and life stage-specific physiological tolerances and requirements. Some tropical species have been described in relation to their distribution across the shelf, suggested to reflect differences in salinity tolerances or preferences (Potier and Nurhakim 1995). However this also depends on local bathymetry and hydrology. Where bathymetry is steep, the separation between inshore, neritic and open ocean habitats is less distinct and 'oceanic' species may occur closer to shore than in areas with wide gently-sloping shelves (Dalzell 1993). Small pelagic fish, like clupeids, are also highly mobile and can respond quickly to changing environmental conditions through horizontal or vertical migrations (Fréon et al. 2005). As a result, spatial distribution of species can change diurnally, seasonally and annually due to hydrological, climatic and interacting biotic factors such as food availability and population size. Such changes are also reflected in fishing activity, particularly in the seasonal nature of many clupeid fisheries in tropical, temperate and upwelling regions (Fréon et al. 2005; Giannoulaki et al. 2014; Hendiarti et al. 2005).

Species composition and the size of populations (and their associated fisheries) vary across the IWP region. Tropical clupeids, like their temperate counterparts, rely on plankton for food. The distribution and abundance of plankton depends on the availability of nutrients in the euphotic layer of the water column (Fréon et al. 2005). There are several types of processes that supply these nutrients, including: coastal and offshore upwelling, which brings cool, nutrient-rich water to the surface; and nutrient inputs from land sources delivered via terrestrial run-off and river flow (Caddy and Bakun 1994). These processes are driven by current and wind strength and direction as well as rainfall, which in many parts of the IWP are strongly seasonal and driven by large-scale atmospheric and oceanic circulation patterns. For instance, the monsoon climate systems that affect much of the region can result in seasonally reversing currents and winds, which along coastlines with certain orientation, can give rise to alternating upwelling and downwelling conditions with associated changes in nutrient availability, water temperature and dissolved oxygen concentrations. As a result, nutrient enrichment and subsequent primary production vary widely both spatially and temporally across the region (Bell et al.

2011; Groeneveld and Koranteng 2017; Hendiarti et al. 2004; Hood et al. 2017; Villanoy et al. 2011). However not all nutrient-enriched environments support a high abundance of small pelagic fish (Bakun et al. 1998). Habitats favourable for successful coastal pelagic fish reproduction (i.e. larval survival) and population growth tend to be characterised by not only *enrichment* processes (such as upwelling and mixing) that fuel food production, but also processes that promote *concentration* and *retention* of food particles, eggs and larvae – together referred to as an 'ocean triad' (Bakun 2010). Concentration processes include features such as ocean fronts where different density waters converge and accumulate food particles enabling larvae to feed expeditiously; while retention processes retain eggs and larvae within (or propel eggs and larvae towards) suitable conditions, thereby reducing the loss of eggs and larvae via passive drifts in ocean currents (Bakun 2010).

Round-bodied Sardinellas

Round-bodied Sardinellas in the IWP form large populations in areas characterised by productive monsoon-driven upwellings, where they tend to be the dominant clupeid caught—e.g. south-west coast of India (*S. longiceps*, Kripa et al. 2018), off Oman (*S. longiceps*, Piontkovski et al. 2014), the Bali Strait in Indonesia (*S. lemuru*, Merta et al. 2000; Hendiarti 2005) and off Zamboanga Peninsula in the Philippines (*S. lemuru*, Villanoy et al. 2011). Large populations of temperate clupeoids similarly occur in upwelling regions (Checkley et al. 2017). However some intense upwellings, such as the Somali Current in the Western Indian Ocean, do not appear to support such large populations. Strong mixing and offshore currents in this region are thought to counteract processes of concentration and retention, hence create unfavourable reproductive conditions (Bakun et al. 1998). Smaller Round-bodied Sardinella populations appear to occur in areas where nutrient enrichment is more localised and/or less consistent—e.g. Western Australia (*S. lemuru*, Gaughan and Mitchell 2000).

In all locations, the coastal habitats of Round-bodied Sardinellas are subject to wide seasonal variations in temperature, salinity, primary productivity and dissolved oxygen concentrations (Hendiarti et al. 2005; Kripa et al. 2018; Villanoy et al. 2011). Across their distributions, water temperatures typically range from 22–28 °C (*S. longiceps*, Rohit et al. 2018) and 19–30 °C (*S. lemuru*, Gaughan and Mitchell 2000). Round-bodied Sardinellas are migratory and move between nearshore and offshore habitats over the seasons and/or at different life stages. Details of habitat associations and seasonal movement of populations across the IWP region are summarised in Online Resource 4 (Table S4.1). A generalised pattern of movement—to coastal waters when food is abundant, spawning in coastal waters, then moving to deeper waters post-spawning—has been suggested for several *Sardinella* species, including *S. longiceps* in India and *S. lemuru* in the Bali Strait (Pet et al. 1997 and references therein); however this does not seem to be supported by clear evidence. Key parts of the life cycle, such as actual spawning grounds and larval habitat and movement, are not well understood at any location (Merta et al. 2000; Rohit et al. 2018). Juveniles are often observed nearshore (e.g. in India, the Philippines and Indonesia), although not in all locations (e.g. Western Australia); adult populations are suggested to generally occur in deeper waters further from shore (e.g. India, Indonesia and Western Australia) but are also found nearshore in some locations or occasions (see Table S4.1). Spawning has been assumed to take place both nearshore and in deeper water based on reports of eggs and larvae in both shallow nearshore waters (e.g. India, 12 m deep) and further offshore (15–50 km from shore; e.g. India, the Philippines and Western Australia). These differences between locations probably reflect the strong influence of local seasonal oceanographic conditions.

The timing (and possibly location) of peak Round-bodied Sardinella spawning in populations associated with regular seasonal upwelling (i.e. most major fishery locations) appears to coincide with these periods of cool and productive upwelling (Table 2 and Table S4.1)—e.g. *S. longiceps* off the south-west coast of India (Jayaprakash and Pillai 2000; Kripa et al. 2018; Nair 1973; Rohit et al. 2018) and *S. lemuru* off Zamboanga Peninsula in south-western Philippines (Naguit 2016; Villanoy et al. 2011) and in Indonesia's Bali Strait (Dwiponggo 1974; Merta 1995). However comparative studies in wind-driven upwelling systems worldwide have found no general relationship between the timing of clupeoid spawning and upwelling period, but rather with a moderate level (or an 'Optimal Environmental Window', Cury and Roy 1989) of wind and turbulence, 5–6 m/s (Roy et al.

1992; Shin et al. 1998), which results in an optimal level of mixing and enrichment, but is neither too weak nor too strong to negatively impact the availability or accessibility of food for newly hatched larvae (Bakun 2010 and references therein). In high latitude Western Australia (not subject to regular seasonal upwelling), *S. lemuru* spawns in summer, coinciding with warmest water temperatures (~ 23 °C, which is near minimum temperatures elsewhere in its distribution) and strongest wind speeds (8 m/s). These prevailing southerly winds, together with weaker southward flowing currents during this time, probably enable eggs and larvae to be transported northward (towards the equator) to warmer, more favourable habitat for larval survival and growth (Gaughan and Mitchell 2000).

Associations between seasonal variation in phytoplankton productivity (indicated by surface chlorophyll concentrations) and Round-bodied Sardinella fishery landings have also been investigated in several studies. Off south-west India, increased chlorophyll concentrations during monsoon-upwelling were found to be correlated with higher *S. longiceps* landings 2–3 months later (Menon et al. 2019). Similarly, in the Bali Strait, peak *S. lemuru* landings have been reported to occur in the months following the monsoon and upwelling period (Hendiarti et al. 2005; Merta et al. 2000); higher catch rates were found to be significantly correlated with a 3-month moving average of chlorophyll-a concentration (Sartimbul et al. 2010). In the Philippines, seasonal increases in primary productivity coincided with peak *S. lemuru* landings (Villanoy et al. 2011), although a later study found a negative correlation and suggested a lag before peak landings (Naguit 2016). These studies imply that peak landings occurring 2–3 months after peak food availability are associated with increases in individual fish biomass via trophic transfer of energy and possibly through spawning and capture of young juveniles; no lag (i.e. a direct correlation) suggests sardines are migrating into the fishery area, perhaps attracted to the higher food availability. While these studies have evidently identified seasonal associations in fisheries landings and chlorophyll concentration, statements about underlying mechanisms are generally less convincing—many ecosystem characteristics will exhibit a seasonal cycle, and after introducing the potential for lagged effects, almost any type of relationship can be hypothesised.

Flat-bodied Sardinellas

Flat-bodied Sardinellas occur in coastal habitats ranging from mangrove estuaries to shelf waters (see population summaries in Online Resource Table S4.1). Some Flat-bodied Sardinellas also occur in areas characterised by strong seasonal upwellings, however they are reportedly not caught in such high abundance as the Round-bodied Sardinellas (e.g. Bali Strait, Merta et al. 2000). However, in other coastal waters, Flat-bodied Sardinellas may dominate landings (e.g. east and north-east coast India, Luther 2001). Larger populations are probably still associated with areas of higher productivity. For instance, '*S. fimbriata*' in the Philippines (now *S. pacifica*) was reportedly, prior to possible overfishing, the most abundant species in certain bays where high primary productivity is fuelled by river discharge (Naguit 2016; Villanoy et al. 2011).

Both fisheries-based evidence and habitat studies indicate that occurrence in nearshore habitats and more generally in coastal waters (at various depths and distances from shore) tends to be seasonal and/or part of the life cycle (see Table S4.1) but also varies by species (e.g. Biswas et al. 2014). Salinity tolerance, for example, appears to vary by species (Cappo 1995a; Cappo 1995b). Seasonal movements and the location and timing of spawning are not well understood at most locations (Table S4.1) and are probably influenced by local oceanographic conditions and species' physiological tolerances. Off north-east Australia, progressively larger *S. gibbosa* juveniles were found further from shore, and had become mature adults by the time they reached offshore spawning grounds (40 km offshore); newly hatched larvae then returned to shore by active swimming and passive transport (Cappo 1995a; Williams and Cappo 1990). Similarly in India, juveniles of several Flat-bodied Sardinella species are found in shallow and sheltered coastal waters. Spawning is also thought to occur in coastal waters (*S. gibbosa*, 20 km from shore) (Sekharan et al. 1969), as well as further offshore (*S. fimbriata*, > 60 m water depth) (Bennet et al. 1986; Luther 2001). Spawning activity has been reported in every month at one location or other in Indian waters, but perhaps less commonly in the period of monsoon-associated upwelling, unlike the Round-bodied Sardinella *S. longiceps* (Table 2). Off north-east Australia, spawning of several Flat-bodied Sardinellas coincides with warmer waters over spring and summer (Cappo 1995b).

Tropical Pilchard

Tropical Pilchard *A. sirm* has been reported to occur in deeper, oceanic waters and further offshore than other tropical clupeids (Cappo 1995a; Potier and Sadhotomo 1995) but in some locations moves to inshore waters during parts of its life cycle (see Online Resource 4). Off north-east Australia, *A. sirm* larvae, young juveniles and mature adults were found mainly in clear, offshore waters (30–40 m deep, 40 km from shore), suggesting spawning also occurs offshore (Cappo 1995a). In Kiribati, an atoll environment, *A. sirm* is similarly suggested to spend most of its life cycle offshore, but enters inshore lagoons as mature adults, probably to spawn (Rawlinson et al. 1992). Elsewhere, reports of habitat use and seasonal movements vary (Table S4.1). For instance, off south-west India, mature adults, eggs, larvae and juveniles are observed in coastal fishing grounds (Lazarus 1990). The timing of spawning appears to coincide with warmer or warming temperatures: spring and summer in northern Australia and New Caledonia; and inter-monsoon period in the Java Sea, and pre-south-west monsoon in Indian and Sri Lankan waters (see Table 2), both associated with warmer water (Durand and Petit 1995; Rao et al. 2011). However spawning stimuli for *A. sirm* have not been investigated in detail and other factors such as circulation patterns, salinity, depth or finer scale processes may be influential. Spawning near the equator is also seasonal, but not with any clear association with water temperature, rainfall or shifts in wind pattern (Milton et al. 1994b). There is little information on habitat associations or movement for other *Amblygaster* species. *A. clupeoides* is suggested to be a coral-reef associated species (Conand and Kulbicki 1988) but has also reportedly been caught in purse seine nets off the east coast of Malaysia (Rahman 2017).

Tropical Herrings

Tropical Herrings generally occur in nearshore habitats, such as mangrove estuaries, sheltered bays and coastal waters (see Online Resource 4). In several locations adult and juvenile *H. quadrimaculatus* are reported to school in shallow waters during the day and then move or disperse into deeper water at night (Foale 1998; Milton et al. 1994a; Williams and Clarke 1983); in Hawaii, adults have been caught at night in waters 10 km offshore and > 100 m deep (Williams and Clarke 1983). Other species may have more specific habitat requirements. For example, in north-east Australia, *H. koningsbergeri* lives mainly in deeper, clearer bay waters (5–20 m deep) and around nearshore structures such as jetties, but rarely enters turbid estuarine habitat; while *H. castelnaui* is common in mangrove estuaries and sandy and rocky nearshore habitats (Cappo 1995b). *E. thoracata* adults and juveniles also occur nearshore in shallow turbid waters and mangrove estuaries (Cappo 1995b; Sreekanth et al. 2017).

There is some evidence of seasonal movements and/or life stage-specific habitat associations, at least for some *Herklotsichthys* species. In Sri Lanka, *H. quadrimaculatus* stilt fisheries are highly seasonal and commence when young fish arrive in nearshore waters at the onset of the south-west monsoon (Deepananda et al. 2016). In Kiribati, it has been hypothesised that *H. quadrimaculatus* juveniles enter lagoons and shallow coastal areas, then leave the lagoon once mature and spawn over the reef (Cross, 1978 cited in Rawlinson et al. 1992). Spawning has also been suggested to occur outside a bay area in Hawaii (Williams and Clarke 1983); and related species *H. punctuatus* is suggested to spawn away from nearshore fishing grounds (Marichamy 1971). In contrast, *H. castelnaui* in Australia and *Herklotsichthys* spp. in Palau are reported to aggregate in creeks to spawn (Johannes 1978; Robertson and Duke 1990). Near the equator, where *H. quadrimaculatus* spawns year-round, periods of greater activity are suggested to depend on fish condition and nutrition rather than environmental factors directly (Milton et al. 1994b). However at higher latitudes (e.g. New Caledonia, Fiji, Hawaii and Japan), peak spawning coincides with the warmer spring and summer months (Conand 1988; Williams and Clarke 1983); although in Japan, photo period is the suggested cue rather than temperature (Oka and Miyamoto 2015).

Interannual variability in fisheries landings

Tropical clupeid fisheries in the IWP are characterised by variable annual landings, particularly evident in the major Round-bodied Sardinella fisheries. While some change is clearly driven by changes in fishing effort, historic records of *S. longiceps* landings in India during the 1800s and early 1900s, prior to extensive fishery exploitation, show evidence of naturally fluctuating populations (Nair 1951). This is consistent with decades of research on temperate clupeoids, which has generally concluded that fluctuations in abundance are primarily driven by climate and/or environmental variability (bottom-up control) and intensified by causes of mortality (top down control), particularly fishing and natural predation, which can accelerate population decline, slow recovery and prolong periods of low abundance (Checkley et al. 2017; Fréon et al. 2005). Temperate studies have shown that spatial and/or temporal variation in environmental conditions, such as temperature, salinity, turbulence and/or food availability, can directly affect the survival of early life stages (eggs, larvae and juveniles) and can also have impacts on adults, potentially affecting reproductive development and future spawning success (Ganias et al. 2014; Llopiz et al. 2014). Due to their short life spans and rapid maturation, and therefore short generation time, any changes in recruitment success can rapidly translate to large changes in population size (Ganias et al. 2014). Extensive research on temperate clupeoids demonstrates the complexity of mechanisms driving fluctuations over annual and longer timescales, which combined with the interactions and influences of human activities, are still not well understood worldwide (Alheit and Peck 2019; Checkley et al. 2017).

Round-bodied Sardinella

Round-bodied Sardinella fisheries in the IWP are typically dominated by a single species, *S. longiceps* or *S. lemuru*, and are characterised by high interannual variation in landings and catch rates. There have been many studies on the potential drivers of these fluctuations, particularly in India and to a lesser extent in Indonesia and the Philippines. While environmental factors have long been considered important (e.g. Nair 1973), research is increasingly recognising that drivers of interannual variation are complex, interacting and may operate at all sardine life stages (e.g. Kripa et al. 2018), although this is reflected in recent studies to varying degrees. Location-based summaries of findings from previous studies are provided in Online Resource 5 (Table S5.1).

The monsoon-driven upwellings that characterise the major Round-bodied Sardinella fisheries vary in timing, intensity and duration between years due to variation in broad-scale atmospheric and oceanic patterns, in particular, the El Niño Southern Oscillation (ENSO) and Indian Ocean Dipole (IOD). These processes affect parts of the IWP region differently (Kong et al. 2019), as reflected by the differing responses of Round-bodied Sardinella fisheries. In Indonesia's Bali Strait, landings and catch rates of *S. lemuru* are an order of magnitude higher during El Niño years (Buchary et al. 2011; Ghofar et al. 2000; Purwanto 2011) and positive IOD events (Sartimbul et al. 2010). *S. lemuru* landings in the Philippines (Zamboanga Peninsula) are similarly significantly correlated with ENSO (Naguit 2016) with El Niño generally associated with higher landings (Villanoy et al. 2011). In both locations, El Niño periods (and positive IOD events in Indonesia) are associated with stronger upwelling, cool surface water and high primary productivity (Sartimbul et al. 2010; Villanoy et al. 2011). Conversely, La Niña in the Philippines tends to be associated with lower landings; higher rainfall during La Niña is thought to increase water column stratification, reducing upwelling and primary production (Villanoy et al. 2011). In Indonesia, periods of very low landings have coincided directly with warmer than average water, which the authors of the study suggested implies an immediate effect of temperature on landings, possibly due to *S. lemuru* moving (vertically or horizontally) out of the usual fishing grounds (Puspasari et al. 2019). ENSO is also a key factor driving interannual variation in *S. longiceps* landings in India, however El Niño periods are associated with lower landings and catch rates (Kripa et al. 2018; Rohit et al. 2018). Unlike Indonesia and the Philippines, El Niño periods off the south-west Indian coast are associated with warmer waters (Krishnakumar and Bhat 2008). During the 2014–15 El Niño, *S. longiceps* maturation was reportedly poor and some stock moved to deeper waters and adjacent areas. In contrast, growth and maturation were normal in the 2010–12 La Niña (Rohit et al. 2018). La Niña periods are associated with higher rainfall (Krishnakumar et al. 2008), which has been associated with higher maturation rates in India (Kripa et al. 2018). Numerous studies have investigated the relationships between *S. longiceps* landings, catch rates and to a lesser extent reproductive processes and recruitment to the fishery, and various environmental variables, including upwelling intensity (indicated by sea level and other indices), phytoplankton biomass (predominantly in terms of remotely-sensed chlorophyll-a concentrations), monsoon onset and intensity, water temperature, rainfall and others (see Table S5.1). However links between *S. longiceps*, specific environmental conditions or processes, and different phases of ENSO and/or IOD, are not yet well-established, reflecting (at least in part) the complexity and interactions between factors.

Given the mobile and migratory nature of Round-bodied Sardinellas, interannual variation in landings may also occur due to shifts in distribution, resulting in lower landings in one location and higher landings elsewhere. This may occur in response to changes in environmental conditions between years, as suggested to explain fluctuations in *S. lemuru* landings off Western Australia (Gaughan and Mitchell 2000). Long-term shifts in conditions, such as those caused by climate change, may also cause shifts in species distribution. Rising seawater temperature is suggested to have led to increasing *S. longiceps* landings further north (poleward) off the east Indian coast (Vivekanandan et al. 2009), although there may also be other contributing factors such as fishing pressure on predatory species (Funge-Smith et al. 2012). Interactions with other small pelagic fish, such as Indian mackerel *Rastrelliger kanagurta*, may also contribute to observed fluctuations, although inconsistent evidence of a direct inverse relationship (see Table S5.1) suggests interactions between the two species may be more complex, possibly mediated through species-specific responses to environmental conditions.

Over the past 50 + years, the major Round-bodied Sardinella fisheries in the IWP have also all experienced periods of dramatic growth in fishing effort, and have all been described as overexploited at various times (e.g. Dalzell 1988; Kripa et al. 2018; Merta et al. 2000). Declining landings have been partly attributed to overfishing of mature adults and juveniles in preceding years and expansion of fishing grounds to previously unexploited areas and/or depths (Kripa et al. 2018). Instances of steep declines have occurred when heavy fishing pressure has continued when environmental conditions have been unfavourable for spawning and recruitment (Rohit et al. 2018). It is also likely that overexploitation reduces the capacity of some populations to recover after periods of unfavourable conditions and low abundance (Ghofar and Mathews 1996).

Flat-bodied Sardinellas, Tropical Pilchards and Tropical Herrings

Fisheries landings of Flat-bodied Sardinellas, Tropical Pilchards and Tropical Herrings have also been reported to fluctuate between years across their distributions (see Online Resource 5), although peak volumes are typically far lower than those of Round-bodied Sardinellas (e.g. Manjusha et al. 2013; Willette et al. 2011). These species-groups generally form mixed species fisheries (Bennet et al. 1986; Whitehead 1985), and interannual changes in the relative importance of individual species are also commonly reported (e.g. Ghosh et al. 2013; Rawlinson et al. 1992 and references therein; Rawlinson and Sharma 1993).

Compared to Round-bodied Sardinellas, few studies have investigated drivers of fluctuations in landings of these other species-groups. Sources of nutrient enrichment (food availability) and water temperature are likely important factors, however research to date suggests these species-groups differ in their responses to environmental variation, implying different recruitment strengths (see Table S5.1). For example, off the south-west coast of India, combined Flat-bodied Sardinella and Tropical Pilchard landings (mixed species) in the post-monsoon season were significantly negatively correlated with upwelling intensity and chlorophyll-a in the preceding monsoon season, opposite to the response of Round-bodied Sardinella *S. longiceps* (Manjusha et al. 2013). Changes in the relative importance of Tropical Herring *H. quadrimaculatus* and Tropical Pilchard *A. sirm* in mixed species catches are also thought to be due to different responses to variation in environmental conditions (Milton et al. 1994b). However comparison with environmental variables has been limited to rainfall, which was found to be not directly associated with catch rates in Kiribati (both species, Ianelli 1988) nor in Sri Lanka (*A. sirm*, Karunasinghe and Wijeyaratne 1996). Populations with shorter spawning periods (e.g. *A. sirm* in some locations) may exhibit higher recruitment variability (Lowerre-Barbieri et al. 2011), however this has not been tested for IWP species. Detailed studies on Tropical Herring *H. quadrimaculatus* (Kiribati, year-round spawning) found that interannual fluctuations were probably not due to variable egg production but rather post-hatching survival, possibly linked to movement between habitats throughout the life cycle (Milton et al. 1994b). The strong influence of environmental conditions on larval survival in particular can result in variable monthly recruitment even in populations that spawn year-round (Dalzell 1993).

Declines in landings of these species-groups have been attributed to heavy fishing pressure, for instance Tropical Herring *E. thoracata* in India (Abdussamad et al. 2018); and overfishing of juveniles using small-mesh nets, for instance Flat-bodied Sardinellas *S. gibbosa* and *S. fimbriata* off east Indian coast (Luther 2001). However it can be difficult to determine whether a decline in an individual species is due to overfishing, a shift in fishing ground to an area where that species is less dominant, or poor recruitment of that species due to unfavourable environmental conditions—as discussed in relation to *H. quadrimaculatus* in Fiji (Rawlinson and Sharma 1993).

Discussion

Species-group framework

This review attempts to collate and synthesise existing biological and ecological information on tropical marine clupeids important for IWP fisheries. By discussing clupeid attributes in terms of broad species-groups, I sought to identify shared characteristics and overcome some of the issues associated with uncertain species-level identification. Tropical clupeids have been categorised in groups of species in previous reviews and reports. As noted earlier, small pelagic fishes used as tuna baitfish have been previously grouped by life history traits, with tropical sardines and herrings (*Sardinella* spp., *Amblygaster* spp. and *Herklotsichthys* spp.) categorised as 'Type 2' species (Conand and Kulbicki 1988; Dalzell 1993). However, as demonstrated in this review, there is considerable diversity in the life history characteristics and habitat associations within this 'Type 2' category. Another grouping commonly used in India (e.g. Luther 2001; Nair 1973) distinguishes between 'oil sardines' or Round-bodied Sardinella *S. longiceps*, and 'lesser sardines' which includes all other *Sardinella* spp. (i.e. Flat-bodied Sardinellas) as well as *Amblygaster* spp. (i.e. Tropical Pilchards), which were formerly also classified in the *Sardinella* genus. While this distinction may be useful at a subregional scale, it is probably less applicable across the whole tropical IWP region as it does not encompass all genera. It is also not consistent with local name groups used elsewhere—for instance, in parts of Indonesia where *Amblygaster* spp. and *S. lemuru* share a single common name (Potier and Nurhakim 1995).

The four main groups of tropical marine clupeid reviewed here—Round-bodied Sardinellas, *S.* (subg. *Sardinella*) spp.; Flat-bodied Sardinellas, *S.* (subg. *Clupeonia*) spp.; Tropical Pilchards, *Amblygaster* spp.; and Tropical Herrings, *Herklotsichthys* and *Escualosa* spp.—are based primarily on current taxonomic classification. The two Tropical Herring genera were grouped retrospectively as they share some characteristics, there was a general paucity of information on *Escualosa* spp. and phylogenetic analyses indicate these two genera are closely related (Egan et al. 2018a; Lavoué et al. 2014). Genetic evidence also suggests *A. sirm* is more closely related to both *Herklotsichthys* spp. and *Escualosa* spp., than *Sardinella* spp. (Egan et al. 2018a), providing additional justification for a separate 'Tropical Pilchards' group, rather than adopting one of the groupings described above. These four species-groups have provided a useful and relevant framework for collating, comparing and synthesising information across species. As summarised below, characteristics such as maximum size, life span, size at maturity and some habitat associations are generally similar between group members and are distinguishing features between groups. However differences within the same reported species highlight the importance of continued work to improve taxonomic identification.

1. 'Round-bodied Sardinellas' are relatively large (commonly up to around 24 cm TL) compared to most other tropical clupeids, and probably live the longest (generally 3–4 years, and up to 7 years at higher latitudes). These species form large populations (and productive fisheries) in parts of the IWP characterised by strong seasonal upwellings. While other clupeids may also occur in these areas, Round-bodied Sardinellas tend to be

dominant suggesting they may be better adapted to utilising the seasonal peaks of productivity. Closely related *S. lemuru* and *S. longiceps* are distinguished only by their distribution, head length, feeding apparatus and trophic biology (Stern et al. 2018). The higher number of gill rakers and larger filtering cavity in *S. longiceps* adults probably equates to finer filtration capacity and therefore more efficient capture of smaller prey such as phytoplankton (Garrido and van der Lingen 2014), which is dominant in adults' diets (Rohit et al. 2018). These differing characteristics could be phenotypic responses in a single widespread species to different environmental conditions or food availability (Stern et al. 2018), as exhibited by some temperate clupeids in different habitats (Costalago et al. 2015). Round-bodied Sardinellas mature at larger sizes than most other tropical sardines (average 15.3–16.6 cm TL) although estimated ages at first maturity range widely (4–6 months to 2 years). Spawning grounds, larval habitat and migration patterns do not seem well understood at any location, but are probably strongly determined by local seasonal oceanographic conditions. The pelagic eggs hatch within 24 h (Gaughan and Mitchell 2000; Nair 1959) and around 40 days are spent in larval stages before metamorphosis into juvenile form is complete (Kuthalingam 1960). All major Round-bodied Sardinella fisheries have been characterised by wide fluctuations in landings and catch rates between years, driven largely by interannual variation in oceanic and atmospheric conditions, but also impacted by heavy fishing pressure. ENSO has a strong influence on landings and catch rates. The response of Round-bodied Sardinellas reflects the local change in environmental conditions: in Bali Strait (Indonesia) and the Zamboanga Peninsula (Philippines), El Niño is associated with strong monsoon-driven upwelling, cool water and high primary production, and coincides with higher than usual *S. lemuru* landings; off the south-west coast of India, El Niño is associated with warmer waters and poor maturation, and coincides with lower than usual *S. longiceps* landings.

2. 'Flat-bodied Sardinellas' vary in maximum length (commonly from 12 to 19 cm TL) but are typically smaller than Round-bodied Sardinellas. Life span estimates are generally in the range of 2–4 years. They also mature at shorter lengths, on average around 69% of maximum length based on available data, and usually by 12 months of age (although 6 months to 2 years has been reported). Flat-bodied Sardinellas occur in shallow shelf waters (< 200 m deep) ranging from nearshore habitats such as mangrove estuaries and sandy bays, to waters further offshore, and can tolerate a range of salinity levels, although this appears to vary by species. While they may occur in upwelling areas, they are not usually as abundant as Round-bodied Sardinellas in landings. In other coastal habitats, however, Flat-bodied Sardinellas may be the dominant clupeid caught. Movement between habitats over the season and life cycle is not well understood at most locations. Occurrence in coastal waters (at various depths and distance from shore) is often seasonal. Juveniles are often reported in nearshore habitats, while adults may also be found in deeper waters where spawning may occur. The timing and duration of spawning activities vary widely by location, probably highly dependent on local seasonal hydrodynamic conditions. Flat-bodied Sardinellas often form mixed species fisheries, and both total landings (and catch rates) and the relative importance of individual species are reported to vary between years. Drivers of interannual variation have not been studied in detail, but responses to environmental variability may differ to Round-bodied Sardinellas. No studies were found to have considered whether differing responses of individual species result in less variable mixed species fisheries (a potential 'portfolio effect', as per Schindler et al. 2015).
3. 'Tropical Pilchards' are relatively large (commonly up to 24 cm TL), similar to Round-bodied Sardinellas. Reported life spans range widely (1.2–4 years for *A. sirm*) as do estimated size and age at first maturity (15–22 cm TL at 7–12 + months). *A. sirm* has been found to mature quickly but not spawn until older and larger (Milton et al. 1994b), which could explain some reported differences. Spawning is seasonal (even near the equator) and may coincide with warmer or warming temperatures, although this has not been investigated in detail. Throughout its range, *A. sirm* is generally reported to occur in

deeper, oceanic waters and further offshore than other tropical sardines, although occurrence near river mouths after rain has also been noted. Tropical Pilchards have far fewer gill rakers than both Round-bodied and Flat-bodied Sardinellas; and while similar in number to Tropical Herrings (Whitehead 1985), gill raker spacing is probably wider in the larger-bodied Tropical Pilchards. This may mean these species feed predominantly by visual particulate feeding (Garrido and van der Lingen 2014), which can be less effective in turbid waters (Hecht and Lingen 1992). Seasonal movement and habitat use at different life stages vary widely in studies on *A. sirm* across its distribution. While this may reflect different local hydrodynamic conditions, there could be cryptic species within the widespread *A. sirm*, or species-level misidentification and differences within the *Amblygaster* genus, contributing to these apparent differences. Drivers of interannual fluctuations in landings have not been investigated in detail, but based on available research, favourable conditions for Tropical Pilchard recruitment probably differ to those of Round-bodied Sardinella *S. longiceps* and Tropical Herring *H. quadrimaculatus*.

4. ‘Tropical Herrings’ vary in maximum length but are typically smaller in size (commonly 8 to 16 cm TL) and have shorter life spans (1–1.5 years). Lengths at first maturity are also smaller and appear to decrease at lower latitudes for widespread *H. quadrimaculatus* (8.5–11 cm TL). Tropical Herrings are associated with nearshore habitats, including mangrove estuaries, atoll lagoons and shallow bays, although some species also move further offshore at night. Seasonal or life cycle associated movement between habitats, spawning grounds and spawning season also vary by species. For example, *H. castelnaui* remains in nearshore habitats and spawns over a 2–3 month period in creeks, while *H. quadrimaculatus* occurs in a range of habitats and spawns year-round at low latitudes, presumably offshore. In this sense, *H. quadrimaculatus* shares some characteristics of the Flat-bodied Sardinellas, although may not range as far from shore. Around 45–60 days is spent in the larval stages before metamorphosis into juvenile form is complete (Thorrold and Williams 1989; Williams and Clarke 1983). Interannual fluctuations in *H. quadrimaculatus* landings are suggested to relate to post-hatching survival rates, as monthly egg production was found to be relatively constant, at least near the equator (Milton et al. 1994b); recruitment strengths probably differ to those of Tropical Pilchards.

Challenges and research priorities

Most research on tropical clupeid biology and ecology in the IWP has been concentrated on the Round-bodied Sardinellas from a few major fishery locations, while other species-groups have been studied sporadically across their distributions. There remain substantial gaps in knowledge across all species-groups and lack of consensus on some findings.

Basic life history traits

Despite numerous studies, there remains uncertainty regarding basic life history characteristics for many tropical clupeids due to the range in values reported. While some variation likely reflects real geographic differences and possibly between years, this is difficult to distinguish from methodological differences between studies (particularly when methods are inadequately described) and sampling issues. Incorrect species identification and/or existence of cryptic species may also account for some differences. Adequate spatial and temporal sampling in reproductive studies is critical for accurate estimates. However, achieving this is particularly challenging when species are migratory and/or spawning habitats are not well understood (Lowerre-Barbieri et al. 2011). Tropical clupeids are thought to spawn at night (Antony Raja 1969; Gaughan and Mitchell 2000; Milton et al. 1994b) and may form spawning aggregations at depth or away from the general population like some temperate species (Ganias 2014). Most tropical IWP clupeid reproductive studies to date have obtained specimens from fisheries landings, restricting sampling to fishing grounds. Better understanding of habitat use throughout the life cycle (discussed below) will inform whether fishing ground-based sampling for reproductive studies is adequate. In marine fishes, spawning seasonality and timing of peak activity can vary spatially with latitude and depth, annually due to changes in exogenous cues, as well as with size and age of spawners (Lowerre-Barbieri et al. 2011). However, without standardised methods, any attempts at understanding these aspects for tropical IWP clupeids across locations and years will remain inconclusive. A detailed review of life history methodology currently in use in tropical clupeid research and identification of best practice methods would be useful to guide and improve future research.

Habitat and movement throughout the life cycle

For most IWP clupeids, habitat associations and movement throughout the life cycle are still not well understood. Even for the most well-studied Round-bodied Sardinella populations, understanding of migration and movement is hampered by lack of knowledge on spawning grounds and early life stages. Only a few studies have taken a deliberate, spatial or habitat-based approach. While localised fisheries descriptions could potentially provide interesting insight into habitat associations and seasonal movement, many currently lack sufficient information to enable comparison across locations. Marine environments vary widely throughout the IWP, and even around single islands, in terms of coastal and benthic habitats, coastline topography, bathymetry and local hydrodynamics, rainfall and temperature regimes, and how these different factors interact to influence water temperature, salinity and nutrient concentrations (Bell et al. 2011; Hendiarti et al. 2004; Hood et al. 2017). Patterns of clupeid habitat use and movement are likely strongly influenced by these local conditions, as reflected in differences across locations within species-groups, and in the documented responses of Round-bodied Sardinellas to ENSO-associated changes in environmental conditions. The current literature also regularly uses terms such as 'nearshore', 'inshore', 'coastal' and 'offshore' as well as relative terms such as 'shallower' and 'deeper' without explicit definition of, for instance, depth or distance from shore, which can vary dramatically with local environmental and fishery context. Understanding site-specific conditions and context, and including clear and detailed descriptions in localised studies, are critical for building hypotheses for observed patterns and making comparisons across the region.

Population dynamics

Research on fluctuations in clupeid landings in the tropical IWP has focused on the major Round-bodied Sardinella fisheries. However relationships between landings (and catch rates) and various environmental variables remain largely unclear due to inconsistent findings between studies, which vary in data used and complexity of analyses. For example, some studies on the Indian *S. longiceps* fishery (south-west coast) directly compared average monthly environmental data with monthly landings or catch rates (e.g. Kripa et al. 2018; Krishnakumar and Bhat 2008), while others considered lag periods (e.g. Abdussamad et al. 2018; Menon et al. 2019). Some compared environmental data in certain months or seasons with annual landings (e.g. George et al. 2012; Krishnakumar et al. 2008; Longhurst and Wooster 1990; Xu and Boyce 2009) or seasonal landings (e.g. Manjusha et al. 2013). Most studies of annual landings used a calendar year (or did not specify otherwise), but 'fishing years' were also used (i.e. starting in July, Longhurst and Wooster 1990). Landings were generally considered a proxy for abundance; only a few studies compared catch rates (e.g. Kripa et al. 2018) or statistically de-trended the data (e.g. Xu and Boyce 2009). While each of these methods may be a valid option for certain investigations, some approaches seemed unsuited for investigating the purported questions or making the stated conclusions. A thorough critical review of past research, to evaluate methods used and re-interpret their respective findings with consideration of methodological differences and potential non-linear relationships, could assist to develop a clearer picture of how *S. longiceps* landings respond to variation in environmental conditions. Greater emphasis on larval recruitment and dynamics is also required (Kripa et al. 2019).

There has been a long history of research worldwide on fluctuations in fish abundance caused by variability in reproductive success (i.e. recruitment variability), founded on and expanded from early hypotheses on the 'Critical Period' for larval first-feeding and 'Aberrant Drift' of larvae via unfavourable currents (Hjort 1914, in Houde 2008). Recruitment variability in fish populations can result from numerous, interacting processes operating at multiple spatial and temporal scales, which affect survival of eggs, larvae and juveniles (such as food availability, growth, predation, temperature and hydrodynamics) as well as abundance and fecundity of adults (Houde 2008). Research on IWP clupeid population dynamics to date has mainly focussed on describing relationships between fisheries landings (or catch rates) and environmental variables. While this is a useful first step, future research needs to move beyond correlations and towards building an understanding of underlying processes and mechanisms. This could be approached by developing knowledge on species-specific habitat requirements or preferences (such as temperature, salinity, and prey abundance and composition) for optimal growth and survival at each life history stage (Peck et al. 2013); and/or by taking a comparative approach to explore generalised theories across the region (Bakun 2010). It may also assist to create conceptual diagrams (or other basic models) that attempt to consolidate research findings with explicit consideration of all life history stages. As highlighted in temperate clupeoid reviews, this mechanistic knowledge is particularly important for understanding and predicting the impacts of human-induced climate change (Bakun 2010; Checkley et al. 2017; Peck et al. 2013).

The use of fishery-dependent data creates additional complexity when interpreting trends over time and relationships with environmental variables. This is illustrated by the range of hypotheses proposed (with varying levels of supporting evidence and consideration of alternatives) to explain monthly, seasonal or annual changes in clupeid landings and catch rates in previous IWP studies—including, changes in abundance due to variable maturation, spawning and larval survival (Kripa et al. 2018; Longhurst and Wooster 1990; Menon et al. 2019; Xu and Boyce 2009); changes in (individual) sardine biomass due to seasonal peaks in food availability and growth, which vary in magnitude between years (Sartimbul et al. 2010); movement in and out of fishing grounds associated with seasonal fish migrations (Deepananda et al. 2016; Hendiarti et al. 2005; Lazarus 1990; Nair 1973) and atypical environmental conditions (Puspasari et al. 2019); interactions between environmental conditions (turbidity, adverse weather) and fishing gear (Rawlinson et al. 1992) and fisher behaviour (Hallier 1990); changes in fisher behaviour due to socio-economic factors (Ellway and Kearney 1981); and deliberate or unintentional reporting errors (Ellway and Kearney 1981). Issues with using fisheries landings and catch rate data have been documented and debated elsewhere (e.g. Maunder et al. 2006; Pauly et al. 2013). The use of this data in the IWP is inevitable—it is the main documented source of information available—and is not a problem in itself. However many previous studies have not clearly acknowledged the caveats of using such data, leading to some fairly narrow 'explanations' of observations without explicit consideration of alternatives or confounding factors. Future studies must acknowledge the inherent complexity in clupeid population dynamics (with and without use of fisheries data) and use any uncertainties in research findings to develop hypotheses and design future studies.

Fishery-independent surveys, critical reviews, local knowledge and comparative studies

Many tropical IWP clupeid fisheries lack research institutions with sufficient funding and capacity to carry out detailed, fishery-independent research programs. As we enter the United Nations Decade of Ocean Science for Sustainable Development (2021–2030), there should be greater opportunities for developing research partnerships, data sharing and improving the scientific capacity of such institutions in the IWP. Increased fishery-independent data collection focused on fisheries oceanography, such as ichthyoplankton surveys, could greatly improve understanding on spawning, habitat associations and movement throughout the life cycles of these fishes, with direct relevance to improving the sustainable management of these fisheries. There is also significant potential to build knowledge on these species via detailed comparative studies, documentation of local knowledge and regular critical review of research undertaken in the region. As demonstrated by this review, useful comparisons can be made across the IWP. The scope of this review has been deliberately broad, intended to cover a breadth of biological and ecological topics across the main groups of species important for IWP fisheries. As a result, the depth of review in each research area has been limited, and some topics have not been covered—for example, fecundity and egg production, genetic delineation of populations, predation or the important role tropical clupeids play in food webs. Future critical reviews focused on single research areas (or geographic locations or individual species-groups) would assist to standardise methods and terminology used, enable consolidation and comparison of findings, identify local research agenda, and help build and improve research within the region. Information reviewed here has been restricted to published, English-language studies and reports available online. Sharing local research findings from university and national government fishery programs, via online publication and existing regional collaboration platforms (e.g. FAO 2019b), is important for building knowledge on these important species. However maintaining (and strengthening) peer review processes is also important for improving the quality of published research. Fishers' local and traditional ecological knowledge has also provided valuable insights on IWP clupeids in some locations (e.g. Deepananda et al. 2016; Foale 1998; Johannes 1978; Roeger et al. 2016) and similar studies could be carried out elsewhere.

Useful comparisons could also be made with clupeids in other tropical regions—in particular Round-bodied Sardinella *S. aurita* (which now also includes formerly separate species *S. brasiliensis*) and Flat-bodied Sardinella *S. maderensis* in the tropical Atlantic Ocean, where substantial research efforts have been made (e.g. Diankha et al. 2018; Thiaw et al. 2017). However differences in life history characteristics, such as maximum size and age, need to be kept in mind. Theories and mechanistic concepts developed from research largely in temperate and upwelling systems (e.g. Bakun 2010; Houde 2008) could also be tested, particularly on the large Round-bodied Sardinella populations in IWP upwelling areas (as per some past studies, e.g. Longhurst and Wooster 1990). Comparisons with smaller populations of these species, and with Flat-bodied Sardinellas, may also provide insights on habitat requirements and population dynamics. Ideas and approaches used in temperate studies could also be investigated to see if appropriate for tropical species—for instance, classification of species-groups' habitats by new nitrogen source (as per Checkley et al. 2017). It is also important to note that direct comparison of observations, patterns, trends or measurements may not be informative across locations that differ widely in their coastal orientation, hydrology and climatic patterns. However comparative studies that test and develop generalised ecological constructs and theories across locations or species-groups, with consideration of their differing contexts, can lead to important insights (Bakun 2010).

Conclusion

The high diversity of marine clupeids in the tropical IWP, their challenging taxonomy due to close morphological similarities, coupled with data collection from dispersed, often small-scale and mixed species fisheries, creates difficulties for synthesising species-level research and fisheries statistics across the region. By collating and synthesising existing published literature for the four species-groups most important for marine IWP fisheries—the Round-bodied Sardinellas, Flat-bodied Sardinellas, Tropical Pilchards and Tropical Herrings—this review provides an overview of current biological and ecological knowledge of these species and identifies areas for improvement and focus in future studies. It can also serve as reference source for data-poor clupeid fisheries in the region, and for comparing or contextualising information gathered through local knowledge studies. Small pelagic fisheries worldwide have unique management challenges due to their population dynamics and importance to both fisheries and the broader ecosystem (Alheit and Peck 2019), and even broader social-ecological systems. Tropical clupeid fisheries in the IWP are critical to the livelihoods and health of millions of people across the region, and sustaining these important benefits through management based on good information is essential.

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