

ISSN 1198-6727



# Fisheries Centre Research Reports

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*2024 Volume #32 Number #1*

## **The fisheries biology and ecology of the anchovy genera *Stolephorus* and *Encrasicholina* in the Indo- West Central Pacific Region**

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**Institute for the Oceans and Fisheries,  
The University of British Columbia, Canada**

## The fisheries biology and ecology of the anchovy genera *Stolephorus* and *Encrasicholina* in the Indo-West Central Pacific Region<sup>1</sup>

by

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**Fisheries Centre Research Reports**

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<sup>1</sup> Cite as: Dalzell, P.J., and A.D. Lewis. 2023. The fisheries biology and ecology of anchovy genera *Stolephorus* and *Encrasicholina* in the Indo-West Central Pacific Region. Fisheries Centre Research Reports 32(1). Institute for the Oceans and Fisheries, University of British Columbia.

<sup>2</sup> Cover photo shows a Vietnamese purse seiner midway in the process of hauling a school of stolephorid anchovies

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## FOREWORD #1

In their humble and understated way, the stolephorid anchovies (*Encrasicholina* spp and *Stolephorus* spp) have had a profound influence on the food cultures and cuisines of Japan, East Asia, the southeast and south Asian countries and across the northern Indian Ocean. These anchovies were also highly prized as the high-quality live bait for tuna, as required for the development of Okinawan-style tuna pole-and-line fisheries in the tropical Indo-Pacific. On a much grander scale, these little fish fill a critical ecological role as a forage base for tunas, sharks, seabirds, and even baleen whales across equatorial regions that are low in nutrients compared to temperate or upwelling areas.

These anchovies are salted and fermented for human consumption to produce distinctive fish sauce products that define many local dishes throughout Asia and the countries that border the northern Indian Ocean. Asian cuisines would not be the same without the distinctive umami flavors that result. The stolephorid anchovies are also seen in the neat piles of sun-dried fish graded into many sizes that are available in local markets or exported to high-end markets as an essential condiment to any meal. With the decline in pole-and-line fisheries due to the emergence of highly efficient purse seine fleets, we now see entire villages that are devoted to sun drying stolephorid anchovies as opposed to keeping them alive for tuna fishing operations.

At one time, skipjack pole-and-line fisheries existed throughout the western Pacific. The most productive pole-and-line fisheries in Fiji, Palau, the Solomon Islands, Papua New Guinea, and Indonesia occurred around high islands that had the combination of nearshore marine habitats with rainfall and freshwater mixing that maintained year-around stolephorid anchovy populations.

Although the pole-and-line fisheries have contracted due to economic factors, it is notable that the abundance of stolephorid anchovies provided these developing countries with their first experience in industrial-scale fisheries on, or near coral reefs and lagoons. This allowed them to begin to tap the immense and lucrative tuna resources within their home waters.

One of the most impressive impacts these anchovies have on tuna fisheries was due to a single species, the ocean anchovy, *Encrasicholina punctifer*, formerly referred to as *Stolephorus buccaneeri*. This is the only stolephorid species that can complete its life cycle in the open ocean; indeed, their larvae are the most abundant fish larvae encountered in pelagic fish surveys. The central equatorial Pacific is often characterized as a nutrient poor, oligotrophic environment, within which is with the most productive tuna habitat on the planet. This 'thin soup' paradox can be explained by periodic equatorial upwelling that creates discrete areas of productivity resulting in a short but enriched food chain of phytoplankton, copepods, anchovies and tuna.

The rapid growth and maturity of the ocean anchovy creates areas dense with anchovy shoals on which tuna schools that also brings the tuna into reproductive condition. Large surface concentrations of boiling and foaming tuna schools then result, which large-scale tuna purse seine vessels can easily capture while the anchovies slip through the meshes of their seine. In this respect, the ocean anchovy may be seen as a keystone species in the West-Central Pacific Warm Pool ecosystem, providing a vital link between primary production, zooplankton, tuna and seabirds.

This linkage of the food chain is accomplished in the open ocean and is rarely seen except by offshore fishers or deep-sea cargo vessels; it is a classic case of 'out of sight, out of mind.' However, fisheries

scientists are strongly urged to document the impact of global climate change and warming waters on the abundance and distribution of the stolephorid anchovies and, in particular, *E. punctifer*, and associated impacts to tuna stocks and their fisheries.

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## **FOREWORD #2**

This report is the work of two researchers with a near life-long interest in the fish and fisheries of the Indo-Pacific, and particularly in the biology and fisheries of stolephorid anchovies.

These tiny fish are unimportant to most ‘Westerners,’ and indeed they are widely underestimated in the global fisheries statistics published by the Food and Agriculture Organization of the United Nations (FAO), which are based on annual submission by their member countries.

In the real world, however, especially in Southeast Asia, stolephorid anchovies are part of the daily diet of hundreds of millions of people, where, besides being consumed as a dry snack, they contribute to the bulk of the ‘fish sauce,’ i.e., the *nuoc mam* of Vietnam, *nam pla* of Thailand, *patis* of the Philippines, etc., which makes otherwise bland food both savory and nutritionally complete.

Thus, not counting the stolephorid anchovies because they are small fish caught mainly by small-scale fisheries is a big mistake.

The *Sea Around Us* has worked relentlessly, by performing ‘catch reconstructions,’ to correct this big mistake – at least in part. These catch reconstructions always cover the years from 1950 to the near present, and it will be challenging to turn the catch estimates presented in this report – which usually pertain to a distinct year, or a period of a few years – into the time series required in a multi-year database. However, reporting millions of tonnes of stolephorid anchovies as part of an unidentified pile of ‘miscellaneous’ or ‘other fish’ is profoundly misleading. Thus, the forthcoming release(s) of the *Sea Around Us* database and website ([www.searoundus.org](http://www.searoundus.org)) will, thank to this report, document more stolephorid anchovies catches than ever before, along with their fisheries (including earlier bait fisheries).

The parts of this report which deal with the identity of the various species of stolephorid anchovies will be found difficult for most readers; this, however, is not the authors’ fault: the taxonomy of stolephorid anchovies is in flux, and even specialists are confused. Some of the name changes that are endorsed in this report, and the corresponding biological information – even if dated in some cases will, however, find it way into FishBase ([www.fishbase.org](http://www.fishbase.org)), where it may find users beyond the readership of this report.

Finally, I wish to congratulate Mr. Paul Dalzell, for completing an opus of such magnitude, and still giving credit to his departed co-author, and thank Ms. Elaine Chu for her assistance in giving this report the shape that was required.

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## ABSTRACT

Two Indo-Pacific anchovy genera (*Encrasicholina* and *Stolephorus*) are reviewed with respect to their fisheries, contribution to food security and as important baitfish for tropical pole-and-line fisheries. In the Pacific Islands, the use of stolephorid anchovies has been largely limited to live bait for pole-and-line tuna fisheries. Their inclusion in official catch statistics, however, is spotty at best, and this contribution is meant to partly compensate for this, by providing catch data which will be included in the database and website of the *Sea Around Us* ([www.seaaroundus.org](http://www.seaaroundus.org)). In contrast, stolephorid anchovies form the basis of food cultures from Southeast Asia to the coast of East Africa. They are consumed in varying degrees by 30-50% of the global population, and are eaten fresh, dried and fermented into fish sauce and paste. The majority of the stolephorid anchovies landed are *Encrasicholina heteroloba*, *E. pseudoheteroloba*, *E. punctifer*, *Stolephorus indicus*, and *S. commersonii*. The biology and population dynamics of stolephorids are reviewed based on studies conducted across their geographic range. The members of the two genera are short-lived (1-2 years), fast growing species with high natural mortality rates, for example, as caused by seabirds. Fishing obviously impacts stolephorid anchovy populations, but the dynamics of their populations are also strongly influenced by oceanic and climate effects. A principal driver in coastal lagoons is allochthonous freshwater input that in turn influences plankton production, especially of copepods, with stolephorid spawning tied to periods of zooplankton blooms. Another major influence is from monsoon-driven upwelling of deeper waters that fertilize the upper surface layers. The ocean or buccaneer anchovy, *E. punctifer* in the Western and Central Pacific Ocean can be found in all stages of life history on the high seas, where they are an important forage for a range of species such as tunas and seabirds. In this they differ from all other stolephorid anchovies, which complete their life cycles in coastal waters.

## INTRODUCTION

Stolephorid anchovies (*Encrasicholina* and *Stolephorus*) are typically found in depths between 5 and 30 m in the tropical and -tropical coastal zones of the Indian and the West-Central Pacific Ocean (Hoedt 1994; Dalzell 1983b; The distribution and of anchovies in PNG waters. Res-Rep 83-03. Fisheries Research and Surveys Branch. Department of Primary Industry, Porty Moresby, Papua New Guinea, 24p). The stolephorid anchovies are amphidromous fish migrating between fresh/brackish and saltwater, but most likely following zooplankton aggregations and not for spawning (Saffrudin and Zainuddin 2018). They are widely distributed across a variety of coastal habitats and may be found in high salinity waters (33-34 psu) surrounding coral reefs and in coastal areas influenced by river outflow.

Like many fish genera in the tropics and sub-tropics, the stolephorid anchovies have many members and a sometimes-confusing taxonomy with new species regularly being added to the grouping and older species reassigned. These anchovies (Family: Engraulidae) are economically and culturally important throughout East Asia, Southeast Asia, South Asia, West Asia, and Africa. They are consumed fresh, dried, and fermented to produce fish sauces and pastes (Lopetcharat *et al.* 2001; Narzary *et al.* 2021). In Southeast Asia, the catches of stolephorid are such that they support major industries for fish sauce production (Figure 1; Table 1), i.e., *patis* in the Philippines, *nuoc mam* in Vietnam, *nam pla* in Thailand, or *ngan bya yay* in Myanmar (see Pauly 1996; Ruddle and Ishige 2010).

In addition to being used for making fish sauce, stolephorid anchovies are sold dried, fresh, and frozen. With respect to dried stolephorid anchovies, freshly caught fish are usually processed on board after being caught by methods such as purse seines or lift nets operated in shallow waters from a wooden platform mounted on stilts, the *kelongs* of Indonesia, Malaysia, and the Philippines. The anchovies are first boiled in about 10% brine solution, then removed from the brine solution and allowed to drain. The cooked anchovies are then brought to shore where they are spread on straw mats on the ground and sun-dried (Imran and Yamao 2014).

Further east, in the Pacific Islands, the stolephorids have been important as live bait in support of Okinawan-style tuna fisheries. What is especially noteworthy about these bait fisheries is that they are probably the only widespread industrial-scale fisheries operating within the coral reefs and lagoons of the Pacific Islands (Dalzell and Lewis 1989).



**Figure 1.** A selection of fish sauces made from fermented stolephorid anchovies. (Source: [ourdailybrine.com/fish-sauce-taste-test/](https://ourdailybrine.com/fish-sauce-taste-test/))



**Table 1.** Fish sauces and pastes based on fermentation of anchovies or a mix of anchovies, other fish and crustaceans.

Country	Local name of product
Philippines	Patis
Vietnam	Nuoc mam, teuk trei
Laos	Padaek
Thailand	Nam Pla
Myanmar	Ngan bya Yay, ngapi
Bangladesh	Chepa shuṭki
Sri Lanka	Colombo cure
Cambodia	Prahok, teok trei
India	Chepa Shuṭki, Shidal
Pakistan	Colombo cure
China	Yeesu, yu lu, xing tang,
Korea	Aekjeot
Japan	Shottsuru, ikanago ishiri, ishiru, shotssuru
Malaysia	Budu
Iran and Saudi Arabia	Mahyawa
Egypt	Fesikh
Maldives	Rihaakuru
Sudan	Mindeshi

Note: No fermented fish products were found for Kuwait, Yemen, South Africa, Eritrea, Somalia, Kenya or Tanzania.

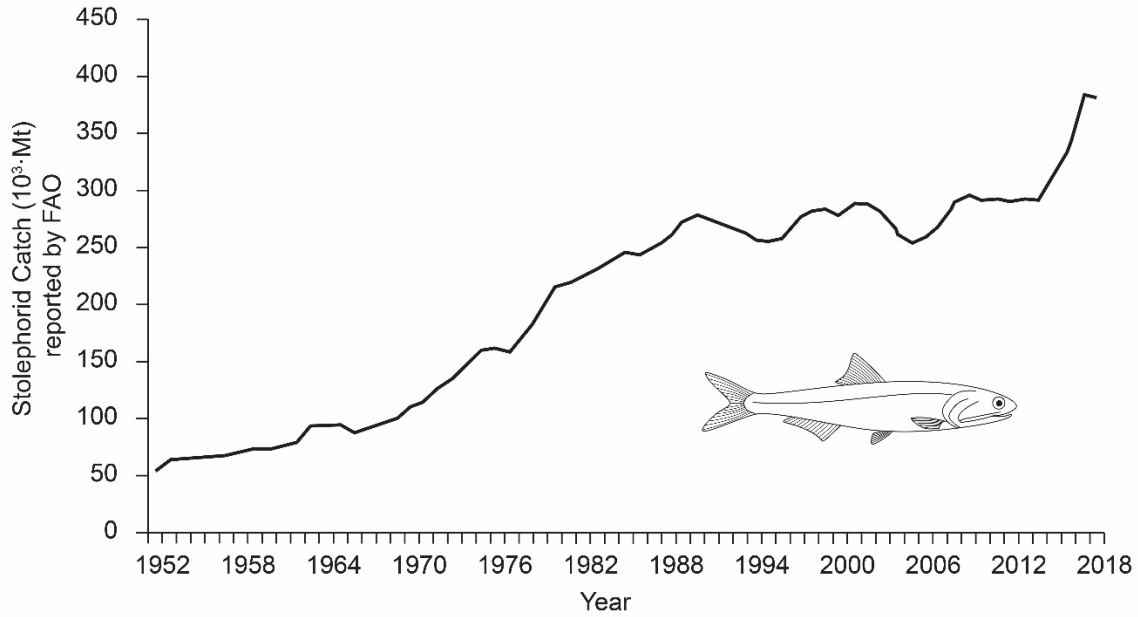
16 million t of anchoveta (*Engraulis ringens*) caught by Peru in 1970 (Castillo and Mendo 1983; Mendo and Wosnitza-Mendo 2016), a figure currently reduced to 4-6 million t per year.

Stolephorid anchovies contribute to human nutrition in countries with about 50% of the global population, or about 30% excluding China (Table 2). While fresh stolephorid anchovy consumption deep in the interior of China is unlikely, dried anchovy and fish sauce may be distributed to all parts of the country, without refrigeration. Yet, for all their importance, stolephorid anchovies are understudied and underdocumented.

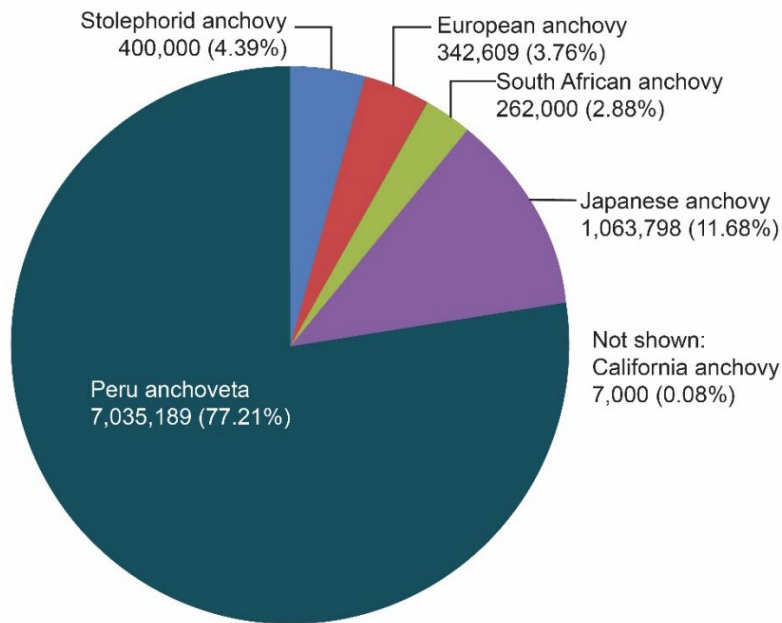
This contribution seeks to offer some redress for a series of mixed anchovy fisheries that extend across most of the Indo-Pacific faunal continuum, by documenting the fishing methods, catches, post-harvest industries, and the biology and ecology of these anchovies. Also, it presents catch data that will be included in the fisheries catch database of the *Sea Around Us* ([www.seaaroundus.org](http://www.seaaroundus.org)).

Prior to the advent of the pole-and-line tuna fisheries in the Pacific Islands, these fish populations were largely untouched by the local people living on the margins of what became bait grounds, and who typically fished for other small pelagics such as the scad (*Selar crumenophthalmus*), goldspot herring (*Herklotsichthys quadrimaculatus*), and small scombrids/chub mackerels (*Rastrelliger* spp.) (Dalzell *et al.* 1996).

Though included in some detail in earlier FAO Fisheries Yearbook and in FAO online statistics (see [www.fao.org/fishery/en/fishstat](http://www.fao.org/fishery/en/fishstat)), the stolephorid anchovies are overlooked by FAO in terms of global anchovy catches, which amount to almost 400,000 t annually (Figure 2). By comparison, historic Californian anchovy (*Engraulis mordax*) annual catches were ~500-600,000 t annually and the European anchovy (*Engraulis encrasicolus*) annual catch is 342,000 t (Figure 3). Globally, the highest catch ever of anchovies is the



**Figure 2.** Global landings of stolephorid anchovies for the years 1952 to 2018, as generated by combining the national landings reported by the member countries of FAO (see [www.fao.org/fishery/statistics-query/en/capture](http://www.fao.org/fishery/statistics-query/en/capture)). Note that this figure underestimates catches (see text).



**Figure 3.** Landings (tonnes) of major engraulid and stolephorid anchovy fisheries in 2018, excluding California landings of Northern anchovy (*Engraulis mordax*) of about 7,000 t (Source: [www.fao.org](http://www.fao.org)).

**Table 2.** Population size, percentage growth rate and generational doubling time of the population of countries and territories in the Indo-Pacific (data from [www.ceicdata.com/en](http://www.ceicdata.com/en) and [www.worldometers.info/](http://www.worldometers.info/))

Country/ Territory	Population (N)***	Growth rate (%)	Principal uses of stolephorid anchovies
Philippines	103,000,000	1.35	Food and fermentation
Papua New Guinea	8,947,024	2.55	Historically used for a now defunct pole-and-line fishery
Vietnam	96,483,981	2.13	Food and fermentation
Thailand	66,558,935	1.17	Food and fermentation
Myanmar	54,410,000	1.61	Food and fermentation
Bangladesh	165,550,000	1.46	Food
Sri Lanka	21,670,000	1.59	Food
Cambodia	16,718,971	1.92	Food and fermentation
Laos	7,013,000	2.13	Laotians ferment fish to make a fish sauce (Padaek), but not with stolephorid anchovies
India	1,341,000,000	1.93	Food and fermentation
Oman	4,490,000	4.49	Food
Pakistan	212,000,000	2.54	Chicken feed
New Caledonia	285,498	1.92	Generally not consumed
China (Hong Kong)	7,496,981	1.69	Food and fermentation
Indonesia	264,616,000	1.99	Food and fermentation and Live Bait
Yemen	29,160,000	2.30	Food
Malaysia	32,521,000	2.69	Food and fermentation
Iraq	40,222,493	2.78	No anchovy fishery
Kuwait	4,270,571	2.27	Fixed stake net trap catches <i>Thryssa vitirostris</i>
Iran	83,000,000	2.00	Food and fermentation
Egypt	98,902,000	2.38	Egyptians ferment mullet to make <i>fesikh</i>
Sudan	37,289,406	2.51	Sudanese ferment freshwater fish to make <i>mindeshi</i>
Djibouti	988,000	1.48	No record of fish fermentation and no stolephorid catch
Eritrea	3,546,421	1.41	No record of fish fermentation and no stolephorid catch
Somalia	15,893,222	2.85	Limited amount of fish fermentation and no use of stolephorid anchovies
Kenya	47,564,000	3.07	Limited amount of fish fermentation and no use of stolephorid anchovies
Tanzania	59,734,218	2.99	Large stolephorid anchovy catch but dried and not fermented
Mozambique	31,255,435	2.50	Food
Natal, South Africa	3,158,313	2.72	Not utilized
Solomon Islands	700,000	2.55	Tuna baitfish
Fiji	896,445	1.41	Food and baitfish

\*\*\*China 2021 population = 1.4 billion, with a coastal population = 0.85 billion based on information from Worldometer

The scope of this contribution is to review the fisheries for stolephorid anchovies across their range, from Africa and the West Asia to their easternmost occurrence in French Polynesia.

The FAO estimates of annual stolephorid anchovy landings in the Fisheries Yearbook ([www.fao.org/fishery/static/Yearbook/YB2019\\_USBcard/root/capture/b35.pdf](http://www.fao.org/fishery/static/Yearbook/YB2019_USBcard/root/capture/b35.pdf), accessed January 11 2022) range from 345,000 t to 439,000 t in the years 2015 to 2019, with a mean of about 376,000 t (Figure 1). This is a gross underestimate, as will be shown later when we summarize stolephorid anchovy catches by the national groupings listed in the preceding paragraph.

We will examine the the taxonomy and systematics of the stolephorids, which are presently in a state of flux with several extant species being renamed and several new species being described from fresh material and museum specimens (see [www.fishbase.org](http://www.fishbase.org)). The biology and ecology aspects of this paper address habitat use, early life history, reproduction and spawning, age, growth and mortality, and stock-recruitment relationships. Information on standing stock biomass and fishery impacts thereon is dated, but may nevertheless be useful to obtain a sense of scale and seasonal abundance. The role of stolephorid anchovies in the trophic dynamics of coastal and open ocean are described qualitatively, i.e., there are no attempts to develop quantitative food web models (Pauly *et al.* 2000), or a trophic-level-based ecosystem models of the type described by Gascuel *et al.* (2011). Neither do we address the effects of climate change, heavy metal accumulation in tissues, pharmaceutical accumulations, and the recently emerging issue of microplastic ingestion. While stolephorid anchovies are marketed fresh, dry and post-fermentation, this contribution does not explore the economics and market linkages for these industries and enterprises.

Associated with many of the same habitats and species assemblages of stolephorids are the anchovies belonging to the genus *Thryssa* (Whitehead *et al.* 1988), apart from the open ocean. We will not be considering species of this genus unless there is a direct connection with stolephorid anchovies.

The critical role of freshwater inflow on the ecology of stolephorid anchovies along coastal margins and its influence on feeding and reproduction of these anchovies is discussed. Natural fluctuations in allochthonous freshwater inflow to coastal ecosystems and the role in biomass, migration and spawning is demonstrated. Anthropogenic influences on stolephorid anchovies from construction, medical waste pollution, plastics and heavy metals are reviewed.

We also review the cultural importance of stolephorid anchovies, and in particular, the fermented fish products based on these fishes (Ruddle and Ishige 2010). The products of stolephorid anchovy fermentation by country are shown in Table 1. Fermented fish products made from stolephorid anchovies appear to be absent from the East African countries that border the Red Sea and Indian Ocean. However, this does not mean that fish fermentation does not occur in East Africa. Indeed, Sheikha *et al.* (2014) provide a comprehensive review of African fermented fish products, including the risks associated with their consumption.

## **Taxonomy, Systematics and Distribution in the Indo-Pacific Region**

The following account of stolephorid anchovy systematics is freely adapted from Whitehead *et al.* (1988), Marramà and Carnevale (2016), Lavoué *et al.* (2017), Ronquillo and Dalzell (1989), and other papers referenced in Table 3. Most clupeiforms are small marine fishes, under 30 cm in length, although some species may exceed 50 cm (Whitehead *et al.* 1988; Bloom *et al.* 2018). The Indo-Pacific faunal region in which the stolephorid anchovies are found, extends from the East coast of Africa and the Red Sea to the Hawaiian Islands and Easter Island (Randall 1998). Several authors such as Springer (1982) have attempted to describe the longitudinal shore fish distribution in this region based on Manila as a species “hot spot,” and enumerated the number of species at distances east and west from Manila, tied to the plate tectonics of the region.

However, several authors have questioned this hypothesis, noting that a number of different geographical and historic factors have played a role in the pattern of present-day clupeoid distribution (Mittelbach *et al.* 2007; Egan *et al.* 2018, 2022). Global clupeoid distribution appears to follow two general patterns of species richness, along longitudinal and latitudinal gradients (Egan *et al.* 2018, 2022; Lavoué *et al.* 2013).

Lavoué *et al.* (2013) suggest that the probable region of origin and diversification of the Clupeoidei during the Cretaceous period was the tropical precursor to the present Indo-West Pacific. Further, Egan *et al.* (2022) concluded that the results of their study supported the “time for speciation hypothesis,” which proposes that climate niche conservatism and fluctuations in the extent of temperate climates limited the time for clupeoid species to accumulate in temperate climates, partially explaining why clupeoid species richness is higher in the tropics.

Anchovies are widely distributed in the world, with most species living in marine tropical environments, and few species secondarily adapted to marine temperate environments and freshwater tropical environments. Anchovies likely originated in the proto-Indo West Pacific region when this region was connected to the Atlantic Ocean through the Tethys Sea (Lavoué *et al.* 2017). The anchovy genus *Encrasicholina* is an important coastal marine resource of the tropical Indo-West Pacific (IWP) region for which insufficient comparative data are available to evaluate the sustainability of current exploitation levels. *Encrasicholina* currently comprises eleven valid species that are morphologically similar. Only three species, *Encrasicholina punctifer* (the ocean or buccaneer anchovy); *E. intermedia* and *E. gloria* in the Indian Ocean) *E. heteroloba* (previously *E. devisi*), and *E. pseudoheteroloba*, occur in the Northwest Pacific subregion of the north-eastern part of the IWP region. These species are otherwise broadly distributed and abundant in the IWP region, making them the most important species for local fisheries and research accounts. Similarly, there are currently about 40 species in the genus *Stolephorus*, and it was previously believed that *Stolephorus indicus* and *S. commersonii* were the most widely distributed species; indeed, these two species had been the focus of more research than other members of the genus. *Stolephorus indicus* has now been divided into seven species, i.e., *S. balinensis* (SE Asia), *S. belaeius* (east Africa), *S. commersonii* (Mauritius), *S. horizon* (Fiji and Tonga), *S. indicus* (Arabian Sea to Andaman Sea), *S. meteorum* (Red Sea), and *S. scitulus* (French Polynesia) (Hata *et al.* 2019).

The *Stolephorus commersonii* of Whitehead *et al.* (1988) includes at least four species, *S. mercurius* (India to Ryukyu Archipelago), *S. rex* (India to Philippines), and *S. zephyrus* (East Africa), and described in Hata *et al.* (2021) and *S. grandis* (newly described by Hata and Motomura (2021b), and found from New Guinea to Australia). *S. commersonii*, now part of the *S. indicus* group, is an endemic restricted to Mauritius

Lavoué *et al.* (2017) used mitochondrial gene sequencing to reconstruct the phylogeny of these three species of *Encrasicholina* within the Engraulidae. The phylogenetic results showed that the genus *Encrasicholina* is monophyletic, and it is the sister group to the more-diverse “New World anchovy” clade. The mitogenome-based dating results indicated that the crown group *Encrasicholina* originated about 34 million years ago (near the transition from the Eocene to the Oligocene), and each species of *Encrasicholina* has been reproductively isolated from the others for more than 20 million years, despite their morphological similarities. In contrast, preliminary population genetic analyses across the Northwest Pacific region using four mitogenomic sequences revealed very low levels of genetic differentiation within *Encrasicholina punctifer*. These molecular results combined with recent taxonomic revisions are important for designing further studies on the population structure and phylogeography of these anchovies.

Unlike other shore fish such as surgeonfish, clupeoids have rapid growth and transformation, thus making them poor candidates for invasive settlement. By contrast surgeonfish (Acanthuridae) have 3-4 months oceanic larval stage, as a consequence of which species such as *Acanthurus xanthopterus* and *A.*

*trioestegus* have been able to cross into the Eastern Pacific Ocean and become part of the reef fish fauna of the Gulf of California (Trujillo-Millán *et al.* 2006).

**Table 3.** Species authorities of the genera *Encrasicholina* and *Stolephorus* based on Whitehead *et al.* 1988.

\* Indicates species by that name in Whitehead *et al.* 1988. \*\* Indicates Lessepien migration through Suez Canal from the Indian Ocean to the Mediterranean<sup>3</sup>

Species	Original Description	Distribution	Status in Whitehead	Comments
<b>ENCRASICHOLINA</b>				
<i>Encrasicholina auster</i>	Hata and Motomura (2017a)	Fiji	Not included (or included in <i>E. pseudoheteroloba</i> , by inference).	--
<i>E. gloria</i>	Hata and Motomura (2016a)	Persian Gulf, Red Sea and the Eastern Mediterranean**	Included in <i>E. punctifer</i> Fowler, by inference	--
<i>E. heteroloba</i> *	Rüppell (1837) as <i>Engraulis heteroloba</i> ((2017b)	Aden to southern Japan, Caroline Islands, and Samoa	Included as <i>E. devisi</i> (Whitley). The <i>E. heteroloba</i> of Whitehead <i>et al.</i> (1988) was <i>E. pseudoheteroloba</i> (Hardenberg).	<i>Amentum devisi</i> Whitley 1940, later recognized as <i>Stolephorus devisi</i> and then as <i>Encrasicholina devisi</i> , is a synonym. See Hata and Motomura (2016b)
<i>E. integra</i>	Hata and Motomura (2020b)	New Guinea	Not included	Similar to <i>E. oligobranchus</i> Wongratana (1983)
<i>E. intermedia</i>	Hata and Motomura (2016a)	India and East Africa to South Africa	Included in <i>E. punctifer</i> Fowler by inference	--
<i>E. macrocephala</i>	Hata and Motomura (2015)	Red Sea, Arabian Sea, and Somalia	Not included	Similar to <i>S. heteroloba</i> and <i>S. pseudoheteroloba</i>
<i>E. oligobranchus</i> *	Wongratana (1983) as <i>Stolephorus oligobranchus</i>	Taiwan, the Philippines, Indonesia and Tonga	Included as <i>E. oligobranchus</i> (Wongratana)	--
<i>E. pseudoheteroloba</i>	Hardenberg (1933a) as <i>Stolephorus pseudoheterolobus</i>	Africa to the Ryukyu Islands, New Caledonia, Tonga, and Samoa.	Misidentified as <i>E. heteroloba</i> (Rüppell).	--
<i>E. punctifer</i> *	Fowler (1938)	Indonesia and the Pacific from Southern Japan and Australia to Hawai'i and French Polynesia in clear coastal and oceanic environments.	Included as <i>E. punctifer</i> Fowler (but only their Pacific Ocean populations).	<i>Stolephorus buccaneeri</i> Strasburg is a synonym. The western Indian Ocean populations included in <i>E. punctifer</i> by Whitehead <i>et al.</i> (1988) are now recognized as <i>E. intermedia</i> and the Red Sea and Persian Gulf populations as <i>E. gloria</i> . <i>Stolephorus zollingeri</i> (Bleeker), a synonym of <i>Engraulis japonicus</i> Temminck and Schlegel, was used for this species in some older publications.
<i>E. purpurea</i> *	Fowler (1900) as <i>Stolephorus purpureus</i>	Hawai'i	Included as <i>E. purpurea</i> (Fowler)	Endemic
<i>E. sigma</i>	Hata and Motomura (2020a)	Sulawesi, Indonesia	Not included.	Similar to <i>E. pseudoheteroloba</i> (Hardenberg 1934)

<sup>3</sup> See Por (1978)

Species	Original Description	Distribution	Status in Whitehead	Comments
<b>STOLEPHORUS</b>				
<i>Stolephorus acinaces</i>	Hata <i>et al.</i> (2020b)	Northern coast of Borneo, Malaysia	Not included.	Similar to <i>Stolephorus andhraensis</i> Babu Rao
<i>Stolephorus advenus</i> *	Wongratana (1987)	Northern Australia	Included as <i>S. advenus</i> Wongratana	--
<i>S. andhraensis</i> *	Babu Rao (1966)	Eastern Indian Ocean, western Pacific: east coast of India east to Singapore and Thailand; Gulf of Papua, north and northeast coast of Australia	Included as <i>S. andhraensis</i> Babu Rao	--
<i>Stolephorus apiensis</i> *	Jordan and Seale (1906) as <i>Anchovia apiensis</i>	Fiji, Samoa, Papua New Guinea, Japan	Included as <i>Stolephorus apiensis</i> (Jordan and Seale)	--
<i>S. babarani</i>	Hata <i>et al.</i> (2020a)	Panay, Philippines	Included in <i>Stolephorus waitei</i> Jordan and Seale, according to Hata and Motomura (2021a)	--
<i>S. baganensis</i>	Delsman (1931)	Eastern Indian Ocean from Myanmar to Sarawak, Malaysia	Included as <i>S. baganensis</i> Hardenberg	--
<i>S. balinensis</i>	Bleeker (1848) as <i>Engraulis balinensis</i>	Western Pacific from southern Japan to New Caledonia	Included as a synonym of <i>S. indicus</i> (van Hasselt)	<i>Stolephorus indicus nanus</i> Hardenberg, <i>Engraulis russellii</i> Bleeker, and <i>Engraulis samaminan</i> Thiollière are synonyms.
<i>S. bataviensis</i>	Hardenberg (1933a) as <i>S. insularis bataviensis</i>	Western Pacific: Taiwan to Indonesia	Included as a synonym of <i>Stolephorus waitei</i> Jordan and Seale	--
<i>S. baweanensis</i>	Hardenberg (1933b) as <i>S. insularis baweanensis</i>	India to northern Vietnam, Indonesia, and southern China	Included as a synonym of <i>S. insularis</i> Hardenberg and also included in part in <i>S. waitei</i> Jordan and Seale	--
<i>S. belarius</i>	Hata <i>et al.</i> (2021)	eastern coast of Africa and Madagascar	Included as part of <i>S. indicus</i>	Similar to <i>S. commersonnii</i> Lacepède and <i>S. indicus</i> (van Hasselt 1823).
<i>S. bengalensis</i>	Dutt and Babu Rao (1959) as <i>Anchoviella baganensis bengalensis</i>	Northern Indian Ocean	Included as a synonym of <i>S. baganensis</i>	Hata <i>et al.</i> (2019) resurrected this taxon as a full species.
<i>S. brachycephalus</i> *	Wongratana (1983)	Australia and Papua New Guinea	Included as <i>S. brachycephalus</i> Wongratana	--
<i>S. carpenteriae</i> *	de Vis (1883) as <i>Engraulis carpenteriae</i>	Papua New Guinea to northern Australia	Included as <i>S. carpenteriae</i> (de Vis)	<i>Stolephorus tysoni</i> Wongratana is synonym
<i>S. celsior</i>	Hata and Motomura (2021a)	Luzon, Philippines	Not included	Similar to <i>S. waitei</i> Jordan and Seale (1926), and perhaps included in that species by Whitehead <i>et al.</i> (1988).
<i>S. chinensis</i>	Günther (1880) as <i>Engraulis chinensis</i>	Chinese coast	Included as <i>S. chinensis</i> (Günther)	--Also see Lowe and Neal (2013)
<i>S. commersonnii</i>	Lacepède (1803)	Mauritius	Included as part of <i>S. indicus</i>	<i>Stolephorus extensus</i> Jordan and Seale (1926) is a synonym.
<i>S. concursus</i>	Hata and Motomura (2021a)	Tonga and Fiji	Not included.	Similar to <i>S. waitei</i> Jordan and Seale (1926), and perhaps included in that species by Whitehead <i>et al.</i> (1988)

Species	Original Description	Distribution	Status in Whitehead	Comments
<i>S. continentalis</i>	Hata and Motomura (2018b)	Currently known only from Hong Kong and northern Vietnam	Included in <i>S. chinensis</i> (Günther) according to Hata and Motomura (2018b)	--
<i>S. continentalis</i>	Hata and Motomura (2018b)	Currently known only from Hong Kong and northern Vietnam	Included in <i>S. chinensis</i> (Günther) according to Hata and Motomura (2018b)	--
<i>S. diabolus</i>	Hata <i>et al.</i> (2022b)	Western coast of Malay Peninsula to Singapore	Included as part of <i>S. insularis</i>	--
<i>S. eclipsis</i>	Hata <i>et al.</i> (2022b)	Bintan Island, Riau Archipelago, Indonesia	Included as part of <i>S. insularis</i>	--
<i>S. eldorado</i>	Hata <i>et al.</i> (2022b)	Taiwan to Indonesia	Included as part of <i>S. insularis</i>	--
<i>S. grandis</i>	Hata and Motomura (2021b)	New Guinea and northern coast of Australia	Not included	Similar to <i>Stolephorus mercurius</i> Hata, Lavoué and Motomura, <i>Stolephorus multibranchus</i> Wongratana, and <i>Stolephorus rex</i> Jordan and Seale.
<i>S. holodon</i>	Boulenger (1900) as <i>Engraulis holodon</i>	Mozambique to Port Elizabeth	Included as <i>S. holodon</i> (Boulenger)	--
<i>S. horizon</i>	Hata and Motomura (2023)	Fiji and Tonga	Included as part of <i>S. indicus</i>	--
<i>S. hindustanensis</i>	Hata and Motomura (2022)	West coast of India	Not included	<i>Stolephorus hindustanensis</i> Hata and Motomura 2022, sp. nova
<i>S. indicus</i>	van Hasselt (1823) as <i>Engraulis indicus</i>	Northern Indian Ocean (from Arabian Sea to western coast of Malay Peninsula) The Mediterranean record of <i>S. indicus</i> by Fricke <i>et al.</i> (2012) is a misidentification of an <i>Encrasicholina</i> sp. (probably <i>E. gloria</i> )	Included as <i>S. indicus</i> (van Hasselt)	<i>Elops (Engraulis) albus</i> Swainson is a synonym.
<i>S. insignis</i>	Hata and Motomura (2018a)	Currently known from northern Taiwan, the Philippines and Moluccas, Indonesia	Not included	Similar to <i>S. apiensis</i>
<i>S. leopardus</i>	Hata and Motomura (2021a)	North Sumatra		--
<i>S. mercurius</i>	Hata <i>et al.</i> (2021)	Japan to Singapore, India and Sri Lanka	Included as part of <i>S. commersonnii</i> Lacepède	--
<i>S. meteorum</i>	Hata <i>et al.</i> (2023)	Red Sea	Included as part of <i>S. indicus</i> (van Hasselt)	--
<i>S. multibranchus</i>	Wongratana (1987)	Pohnpei and Kosrae	Included as <i>S. multibranchus</i> Wongratana	--
<i>S. nelson*</i>	Wongratana (1987)	Northwestern Australia and Irian Jaya	Included as <i>S. 15elson</i> Wongratana	--
<i>S. oceanicus</i>	Hardenberg (1933b)	Gulf of Thailand and western Indonesia to Vietnam	Included in <i>S. chinensis</i> (Günther)	--
<i>S. pacificus*</i>	Baldwin (1984)	Guam, Kosrae	Included as <i>S. pacificus</i> Baldwin	--
<i>S. rex</i>	Jordan and Seale (1926)	India to Philippines	Included as s synonym of <i>S. commersonnii</i> Lacepède	--
<i>S. ronquilloi*</i>	Wongratana (1983)	Philippines	Included as <i>S. ronquilloi</i> Wongratana	--



Species	Original Description	Distribution	Status in Whitehead	Comments
<i>S. scitulus</i>	Fowler (1911) as <i>Anchoa scitula</i>	French Polynesia	Included as a synonym of <i>S. indicus</i>	<i>S. insularum</i> Jordan and Seale (not to be confused with <i>Stolephorus insularis</i> Delsman) is a synonym of <i>S. scitulus</i> according to Hata et al. (2021)
<i>S. shantungensis</i>	Li (1978) as <i>Anchoviella shantungensis</i>	China	Not included	This species has not been mentioned in recent reviews of the genus and its status needs more research.
<i>S. tamilensis</i>	Gangan <i>et al.</i> (2020) ahageerdar and Jaiswar (2020)	Tamil Nadu State, India	Not included	--
<i>S. taurus</i>	Hata <i>et al.</i> (2022c)	Northern Bay of Bengal	Included as <i>S. dubiosus</i> Wongratana (in part)	--
<i>S. teguhi</i>	Kimura <i>et al.</i> (2009) Hata and Motomura (2021d).	North Sulawesi, Indonesia and Luzon and Jolo, Philippines	Not included	Similar to <i>S. pacificus</i>
<i>S. tri</i> *	Bleeker (1852) as <i>Engraulis tri</i>	Gulf of Thailand to western Indonesia	Included as <i>S. insularis</i> Delsman (in part), <i>S. baganensis</i> Delsman (in part), and <i>S. tri</i> (Bleeker).	<i>Stolephorus insularis</i> Delsman (not to be confused with <i>S. insularum</i> Jordan and Seale), <i>S. baganensis macrops</i> Hardenberg, and <i>S. baganensis megalops</i> Delsman are synonyms of <i>S. tri</i> , according to Hata et al. (2019).
<i>S. waitei</i> *	Jordan and Seale (1926)	Queensland, Australia	Included as <i>Stolephorus</i> sp. A	--
<i>S. zephyrus</i>	Hata et al. (2021)	Eastern coast of Africa and Madagascar	Included in <i>S. commersonii</i> Lacepède	--
<i>S. lotus</i>	Hata and Motomura (2022)	Northern Australia	<i>S. andhraensis</i>	--

Members of the genus *Encrasicholina* are mostly clear water species and tend to midwater schooling in open water, while species of the genus *Stolephorus* tend towards more muddy estuarine environments, schooling closer to the seabed, and have more deciduous scales (Smith 1977; Whitehead *et al.* 1988). This makes most *Stolephorus* species less attractive as tuna bait due to higher captive mortality from scale loss (see Smith 1993 for review of scale loss and mortality).

There is moderate evidence that the tropical genus *Encrasicholina* is extending northwards in the north-western Pacific, probably through the effects of global warming (Cheung *et al.* 2009; Hata *et al.* 2012). The reported northernmost record of *Encrasicholina* spp. was believed to be Taiwan. However, *E. punctifer*, recorded as *Stolephorus zollingeri*, was observed in Sagami Bay, Kanagawa Prefecture on Honshu (Hayashi and Nisiyama 1980). The northernmost record of *Stolephorus* is *S. balinensis* (as *S. indicus*) from Wakayama Prefecture, in southern Honshu (Ikeda and Nakabo 2015).

Whitehead *et al.* (1988) documented five species of *Encrasicholina* and a dozen species of the genus *Stolephorus*. In the interim, six more species of *Encrasicholina* and 34 species of *Stolephorus* have been described, bringing the total to 57. The full list of stolephorid anchovies and their authorities is given in Table 3, along with other relevant papers. The genus *Encrasicholina* currently comprises eleven valid species that are morphologically very similar. Two species, *Encrasicholina heteroloba* (formerly *Stolephorus devisi*), and *E. pseudoheteroloba* (formerly *Stolephorus heterolobus*), are broadly distributed and abundant in the coastal waters of the Indo-West Pacific region. The buccaneer or ocean anchovy, *Encrasicholina punctifer* (formerly *Stolephorus buccaneeri*), is endemic to the Pacific, including the open ocean. Like many of the tropical clupeoids, these species have a number of synonyms and descriptions dating back 200 years or more (see Whitehead *et al.* 1988). Table 4 summarizes the current names for *E. heteroloba* and *E. pseudoheteroloba*, and the most widely used synonyms and authority.

**Table 4.** Summary of current nomenclature for *E. heteroloba* and *E. pseudoheteroloba*.

<b>Current species name</b>	
<i>Encrasicholina heteroloba</i>	<i>Encrasicholina pseudoheteroloba</i>
<b>Widely used synonyms and authorities</b>	
<i>E. heteroloba</i> was regarded as a senior synonym of <i>E. devisi</i> (Whitley 1940)	<i>E. pseudoheteroloba</i> (Hardenberg 1933a and b) previously regarded as a junior synonym of <i>E. heteroloba</i> , is in fact a valid species

Fisheries scientists conducting studies on the stolephorid anchovies have struggled with determining the species composition of catches. This creates uncertainty when interpreting the results of studies comparing results across geographic distributions. It was thought, for example, that *E. punctifer* was spread across the entire Indo-Pacific. However, Hata and Motomura (2016a) concluded that *E. punctifer* extends only across the Western and Central Pacific (possibly into the Eastern Pacific (Hida 1973)). What was previously thought to be *E. punctifer* in the Indian Ocean comprises *Encrasicholina intermedia*, extending across the Indian Ocean, from East Africa to the Indian sub-continent, and *E. gloria*, confined to the Arabian Gulf and the Red Sea (Hata and Motomura 2016a). *Encrasicholina punctifer*, *E. intermedia* and *E. gloria* are readily distinguishable from *E. heteroloba* (formerly *E. devisi*) and *E. pseudoheteroloba* (formerly *E. heteroloba*)

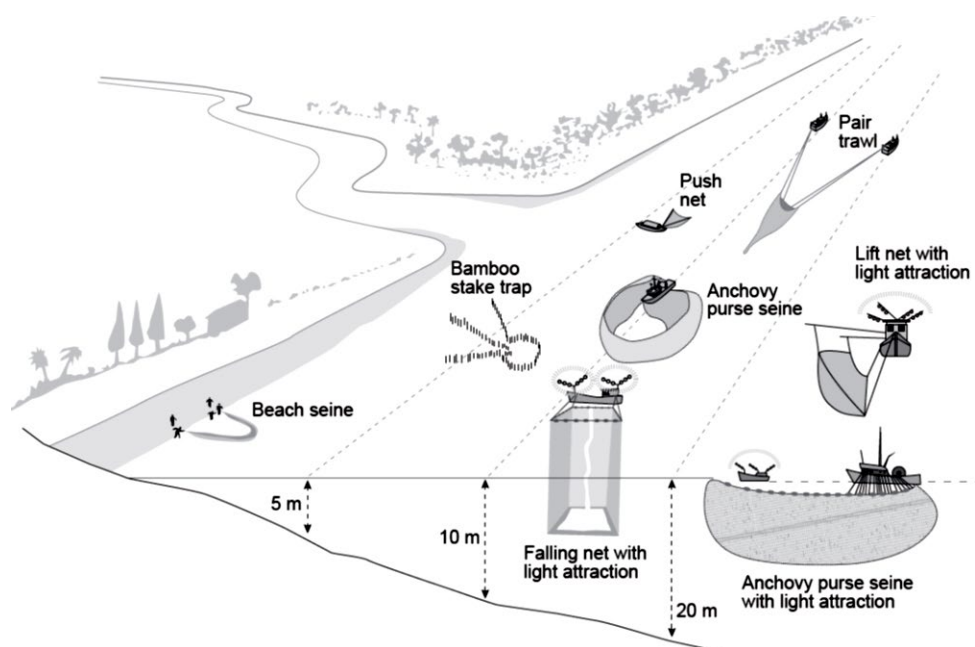
It was hoped that the FAO Species Catalogue by Whitehead *et al.* (1988), which is based primarily on the work of Wongratana (1980), would resolve the confusion surrounding the *E. heteroloba* and *E.*

*pseudoheteroloba* (listed as *E. heteroloba* and *E. devisi*). However, the descriptions of these species were still unclear in the Whitehead *et al.* (1988) accounts, despite genetic evidence that *E. heteroloba* and *E. pseudoheteroloba* are separate species (Daly and Richardson 1980).

Given the fluid state of stolephorid taxonomy, we have provided the old names according to Whitehead *et al.* (1988), if only for the sake of clarity. The genus and species names used in the various fishery and biological studies cited herein, are given in parentheses (in addition to the revised species name) in order to avoid exacerbating an already complex account of stolephorid anchovy nomenclature. However, readers are strongly advised to consult Table 3, where the nomenclatural changes are summarised.

### Fisheries for stolephorid anchovies

A review of fishing gears employed in Southeast Asia, is given in SEAFDEC (2017a). Fisheries that target stolephorid anchovies or which form a major fraction of the incidental catch extend from the Southeast African coast to the islands of the Western and Central Pacific Ocean. This includes the Middle East and Red Sea, the shores of the Arabian Peninsula, the Persian Gulf and Sea of Oman, South Asia, Southeast Asia, north to Taiwan, Japan and the South China coast, Philippines, northern Australia and east to the Pacific Islands, including Hawai'i.



**Figure 4.** Anchovy fisheries by type of fishing and by depth zone in Thailand. This graph captures almost all of the methods of catching stolephorid anchovies in other countries exploiting anchovy resources. Source: Supongpan *et al.* (2000).

The fisheries for stolephorids described in this paper all use variations of net fishing, including passive net methods, those that use light attraction, trawls and surround seines with and without light. The vessels, gears and catch disposition are worthy of a detailed review in themselves. However, in the interests of brevity, we have summarised the salient features of these fisheries, by country, in the Tables 5-11. Moreover, a useful guide to the fishing gears used across much of the Indo-Pacific is shown in Figure 4. This graphic is from Thailand and embraces most, if not, all the stolephorid fishing gears, and the typical depths at which they are deployed.

All the fishing methods shown in Figure 4 use nets to catch stolephorid anchovies and other clupeoid species. Within the immediate coastal zone manual or passive gears such as beach seines, bamboo stake traps and push nets are used. Stake traps concentrate the target species, which are removed with hand-held dip nets. Further offshore, stolephorid anchovies are caught in trawl fisheries targeting demersal species, but with a trawl mouth opening high enough to catch small pelagic species like stolephorid anchovies. Various permutations of nets and light attraction are employed to catch stolephorid anchovies in the 10-20 m depths. These include purse seine fishing with and without light attraction, stick-held lift nets and drop or falling nets that both employ light attraction.

## OVERVIEW – Pacific Island Region

Pacific Island countries (PICs) have no established tradition of anchovy consumption, fresh or preserved, unlike the rich tradition of South and South East Asian countries. Native Hawaiians fished seasonally for *nehu* (*Encrasicholina purpurea*). However, this fishery was supplanted by the live bait fishery for the *aku* (skipjack) boat pole-and-line fishery after it began operating in the early 1900s. The only known example of a PIC anchovy fishery, in Fiji, involves harvest and consumption by mostly Indo-Fijians who apply the names *nuttlee* or *nataly*, from the Hindi *nethili* (A.D. Lewis, personal observation).

Anchovies provided the major contribution to live bait tuna fisheries in several PICs where large pole-and-line tuna fisheries have existed in the past, for example Papua New Guinea, Solomon Islands, Palau, and Fiji. These were the only examples of industrial scale fisheries operating in coral reef lagoons. A few of these survive, albeit in much reduced form. For example, in the Solomon Islands, and the PIC commercial anchovy catch, was never greater than 5,000 t in any given year and is now negligible. Taken almost entirely with lift nets (Okinawan-style *bouké ami* net), anchovies were highly regarded as live bait, with the three *Encrasicholina* species (*heteroloba*, *devisi* and *punctifer*) the dominant and preferred species in the catch. All three species are widely distributed, notably *S. punctifer* with its partially oceanic habitat, though generally absent from atolls.

Most of the other species catch at the Ysabel Passage bait-ground was composed mainly of Clupeidae (41.8%), Apogonidae (15.5%), Caesionidae (13.7%), Atherinidae (8.9%), and Carangidae (6.4%). Similarly, 89% of other species at the Cape Lambert bait-ground comprised Caesionidae (65.2%), Clupeidae (13.6%), and Scombridae (10.2%).

Table 5b is based on baitfish surveys throughout the PICs, and records the presence of stolephorids in 19 PICs or component islands. Further, nine of the countries in Table 5b lack suitable anchovy baitfish habitat, particularly atolls. *E. heteroloba* seems to exhibit the strongest link to high islands and larger land masses, with *E. devisi* possibly more of an island colonizer species in some cases.

## KEY REFERENCES:

### Geography:

Population size ([www.ceicdata.com/en](http://www.ceicdata.com/en)), EEZ area, shelf area ([www.liquisearch.com/exclusive\\_economic\\_zone/rankings\\_by\\_area](http://www.liquisearch.com/exclusive_economic_zone/rankings_by_area)), and land area.

### By country:

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<b>Papua New Guinea</b>	Dalzell (1983a and b, 1984a and b, 1990), Kailola and Wilson (1978), Kearney <i>et al.</i> (1971), Lewis and Allain (2021) Lewis <i>et al.</i> (1974), Milton <i>et al.</i> (1990 a and b), SSAP (1984a)
<b>Solomon Islands</b>	Dalzell and Lewis (1989), Lewis (2019), Nichols and Rawlinson (1990), Rawlinson and Nichols (1990); Argue and Kearney (1982)
<b>Palau</b>	Lewis and Heri (2019), Muller (1976), SSAP (1984b), <a href="http://www.palau.emb-japan.go.jp/itpr_en/11_000001_00470.html">www.palau.emb-japan.go.jp/itpr_en/11_000001_00470.html</a> (accessed November 27, 2022)
<b>Hawai'i</b>	Beckley (1904), Boggs and Ito (1993), Schug (2001), Somerton (1990), Uchida (1977), Wetherall (1977)
<b>Fiji</b>	Ellway and Kearney (1981), Lewis <i>et al.</i> (1983), Iwakiri and Ram (1988), Sharma (1988)
<b>New Caledonia</b>	Conand (1988), SSAP (1985)

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**Table 5a.** Summary of current and historical fisheries catching stolephorid anchovies in the Pacific Islands

PACIFIC ISLANDS						
Country (EEZ and shelf; km <sup>2</sup> )	Land area, population	Stolephorid fishery and main gear used	Annual catch (estimated)	Main species	Utilization	MSY/ biomass estimates
<b>Papua New Guinea</b> (2,410,000; 191,256)	462,243 km <sup>2</sup> 8.935 million	Tuna live bait (1970- 1985), trawl bycatch (minor, mostly non- stolephorid spp) Lift net ( <i>bouké ami</i> ), live bait	Max at 49,000 t tuna catch (1978) 2,000 - 3,000 t comprising anchovy live bait	<i>E. heteroloba</i> <i>E. devisi</i> <i>E. punctifer</i> <i>Spratelloides</i> (3 spp.)	Tuna live bait, minor subsistence	MSY and biomass estimates available for Ysabel Pass, Cape Lambert; local management actions
<b>Solomon Is.</b> (1,612,000; 36,282)	27,556 km <sup>2</sup> 700,000	Tuna live bait (1973- present) taken by lift net ( <i>bouké ami</i> )	Max bait catch 2,400 t (1986), now ~ 100 t	<i>E. heteroloba</i> <i>E. devisi</i> , <i>Spratelloides</i> (2 spp.)	Tuna live bait, minor subsistence	MSY Munda 560 t live bait; Local management actions, no apparent depletion
<b>Palau</b> (603,978; 2,837)	459 km <sup>2</sup> 18,200	Tuna live bait (1964- 1982) new vessel acquired in 2022 Lift net ( <i>bouké ami</i> )	Max bait catch 1978 750 t (~ 9,700 t tuna)	<i>E. heteroloba</i> <i>E. devisi</i> (90%)	Tuna live bait, minor subsistence	MSY 160 t (1976), part of fishery only
<b>Hawai'i</b> (1,580,000; n/a)	28,310 km <sup>2</sup> ~ 1.5 million	In the past, traditional nehu fishery (seasonal), then tuna live bait (now defunct) day surround net, night float boom lift net	Max 1977 @ 20 sites, 18 vessels, now 2; average catch 1960-72 108 t	<i>E. purpurea</i> ( <i>nehu</i> ) (97%)	Tuna live bait	No estimates of MSY and biomass but daily EPM est. Site closures eg Pearl Hbr
<b>Fiji</b> 1,283,000; 47,705)	18,274 km <sup>2</sup> 900,000	Seasonal shore fishery; beach seine, push nets; tuna livebait (1976 - 1991), lift net ( <i>bouké</i> <i>ami</i> )	140 t (1981), 14 p/l vessels; 10% anchovy, so ~14 t	<i>E. heteroloba</i> <i>E. devisi</i> , <i>E. punctifer</i> <i>Stoleph. 2</i> spp.	Now defunct una live bait Minor subsistence	No estimates of MSY/ biomass Was self- regulating, now declining
<b>New Caledonia</b> 1,422,540/ n.a)	18,576 km <sup>2</sup> 273,000	No commercial fishery Tuna livebait survey (1981-1983); lift net ( <i>bouké ami</i> )	< 10 t (anchovy 62% of catch)	<i>E. heteroloba</i> <i>E. devisi</i> , <i>E. punctifer</i> <i>Stoleph. 2</i> spp.	Tuna live bait	No commercial fishery established

**Table 5b.** Synopses of other Pacific Islands not covered in detail in this section, noting presence of *Encrasicholina* spp. suitable as baitfish and other *Stolephorus* species. (Source: Secretariat of the Pacific Community's Skipjack Survey and Assessment Program)

<b>Archipelago/Island</b>	<b>Stolephorid anchovies suitable for baitfishing</b>	<b>Other stolephorid anchovies</b>
Vanuatu	<i>E. devisi</i>	<i>S. indicus</i>
Tonga	<i>E. devisi</i>	--
American Samoa	<i>E. devisi</i>	<i>S. indicus</i>
Nauru	None	None
Wallis and Futuna	<i>E. devisi</i>	--
Samoa	<i>E. devisi</i>	<i>S. indicus</i>
Yap FSM	<i>E. heteroloba</i>	<i>S. indicus</i>
Chuuk FSM	<i>E. devisi</i> and <i>E. heteroloba</i>	--
Pohnpei FSM	<i>E. devisi</i> and <i>E. heteroloba</i>	<i>S. indicus</i>
Kosrae FSM	<i>E. devisi</i> and <i>E. heteroloba</i>	<i>S. indicus</i> and <i>S. bataviensis</i>
Marshall Islands	None	None
Pitcairn	None	None
New Zealand	None	None
Tuvalu	None	None
French Polynesia	<i>E. punctifer</i>	<i>S. indicus</i>
Kiribati	None	None
Cook Islands	None	None
Norfolk Island	None	None
Tokelau	None	None



## OVERVIEW – East Asia and Australia

Large continental land masses – East Asia and Australia – lie on the western margins of the Pacific Ocean in both hemispheres. Very large populations in East Asia (over 1,500 million people) create strong demand for anchovy products. In these areas, the distribution of stolephorids is largely constrained between the tropics, not extending north of 33° N (southern Japan) and south of 27° S (Shark Bay, Moreton Bay, Australia). Stolephorids are stragglers at these extremes, and fisheries for them are inconsequential, as they are replaced by *Engraulis* species – *Engraulis japonicus* which supports large fisheries in East Asia and *Engraulis australis*, which supports minor fisheries in southern Australia and New Zealand. In Taiwan, the anchovy fisheries show latitudinal overlap, with *Engraulis japonicus* predominant in the north, and *Encrasicholina* spp. in the south (Hsieh *et al.* 2009). There may be poleward shifts north in stolephorid populations in East Asia as climate change impacts increase.

The stolephorid species array is most diverse in these continental areas between the tropics, with the usual three *Encrasicholina* species plus rarer less well-known ones, and up to 20 *Stolephorus* species. Other engraulid genera, particularly *Thryssa*, *Setipinna*, and *Coilia*, tend to dominate anchovy trawl bycatch in turbid inshore and estuarine waters.

Two countries (Japan and Taiwan) have important fisheries for larval anchovy (*sirasu*) which require careful management (Hsieh *et al.* 2009). Japan also has a live bait fishery which supplies offshore and long-range pole-and-line vessels with robust *Engraulis japonicus* from holding pens (Oda *et al.* 2018). Adults are taken mostly by purse seine and surround nets, and utilized fresh, dried and salted (JFA 2013).

### KEY REFERENCES:

#### Geography:

Population size ([www.ceicdata.com/en](http://www.ceicdata.com/en)), EEZ area, shelf area ([www.liquisearch.com/exclusive\\_economic\\_zone/rankings\\_by\\_area](http://www.liquisearch.com/exclusive_economic_zone/rankings_by_area)), and land area.

#### By country:

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Hong Kong	FAO (2023); Hong Kong Fish Net (2022; Microsoft Word - 0359722_HKOLNG EIA_10_Fisheries_Rev 3.DOCX ( <a href="http://epd.gov.hk">epd.gov.hk</a> ))
Taiwan	Chiu <i>et al.</i> (1997), Hsieh <i>et al.</i> (2009), Lee <i>et al.</i> (2021), Young <i>et al.</i> (1994)
China	Zhang (2015), 'Fishing industry in China' (Wikipedia 2022)
Japan	OECD (2021), FAO (2020), Hata <i>et al.</i> (2012), Hata and Motomura (2018c), Hayasi (1966)
Australia	Engraulidae - Fishes of Australia.net.au; accessed November 27, 2022, Blackburn (1966), Australian anchovy ( <i>Engraulis australis</i> ) ( <a href="http://nsw.gov.au">nsw.gov.au</a> )

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**Table 6.** Summary of the fisheries catching stolephorid anchovies in East Asia and Australia.

EAST ASIA – AUSTRALIA						
Country (EEZ, shelf; km <sup>2</sup> )	Land area, population	Stolephorid fishery and main gears used	Annual catch (estimate)	Main anchovy species	Utilization	MSY/ biomass estimates
<b>Hong Kong</b> (n/a; 1,645)	1,110 km <sup>2</sup> 7.5 million	Engraulidae top 10 production by family, but most non-stolephorid spp. Trawl, gillnet, purse seine	stolephorid production since 2000 < 20 t pa	<i>E. heteroloba</i> <i>E. punctifer</i> <i>Stoleph.</i> 4 spp. <i>Engr.</i> <i>japonicus</i>	Fresh, dried salted, fish paste; large amounts imported	No estimates of MSY, biomass available, production decreasing, with habitat alteration; trawl ban 2012, effort limitation
<b>Taiwan</b> (83,231; 43,016)	32,260 km <sup>2</sup> 23.8 million	<i>Engr. japonicus</i> north, <i>E. heteroloba</i> , <i>punctifer</i> south; trawl, purse seine (adults), trawl, fyke nets (larvae)	~ 250,000 t total (1999); larvae 1,100 t (2012)	<i>E. heteroloba</i> <i>E. punctifer</i> <i>Stoleph.</i> 4 spp. <i>Engr.</i> <i>japonicus</i>	Larval speciality product; adults boil-dried, salted	Larval fishery managed; adult management not known.
<b>China*</b> (879,666; 832,340)	9,326,410 km <sup>2</sup> 1,400 million	No info on stolephorid catch, but probably small; <i>Engr. japonicus</i> fishery large Trawl, gillnet, purse seine	~ 650,000 t, mostly <i>Engr. japonicus</i>	<i>E. heteroloba</i> <i>E. punctifer</i> <i>Stoleph</i> 4 spp. <i>Engr.</i> <i>japonicus</i>	Fresh, dried, salted fermented; fish meal, fish oil; significant imports	Complex management system (input, output controls etc); no specific anchovy measures
<b>Japan*</b> (4,479,388; 454,976)	364,485 km <sup>2</sup> 125 million	Fishery for adults and larvae ( <i>sirasu</i> ); mostly <i>Engraulis japonicus</i> ; Tuna live bait (holding pens); purse seine, lift net, surround net	Fluctuates with Japan sardine; large average catch ~ 150,000 t of <i>Engraulis japonicus</i>	<i>E. heteroloba</i> <i>E. punctifer</i> <i>Stoleph</i> 2 spp. <i>Engr.</i> <i>japonicus</i>	Fresh, boil-dried, salted; fish paste; fish stock; significant imports	Management of adult anchovies not known; Management measures for <i>sirasu</i> fishery
<b>Australia #</b> (8,505,358; 2,194,008)	7,682,300 km <sup>2</sup> 25.8 million	No commercial stolephorid fishery, only <i>Engr. australis</i> in Bass Strait Purse seine, midwater trawl	<i>E. australis</i> 3,500 t 2020-21; stolephorid catch ~ zero	<i>E. heteroloba</i> , <i>punctifer</i> , <i>devisi</i> <i>Stoleph.</i> 8 spp. <i>Engr. australis</i>	Fish paste, frozen bait (local), dried, fish sauce, paste (import)	Management of small pelagic fishery (SPF), of which anchovy minor part

## OVERVIEW – Southeast Asia

A diverse group of seven equatorial countries, mostly large, with a total population exceeding 600 million. Indonesia is the world's largest archipelagic state, and all countries have extensive Exclusive Economic Zones (EEZs) -except Cambodia and Singapore - totalling almost 10 million km<sup>2</sup>; most also have extensive shelf areas. Also, given its location at the centre of the Indo-Malayan archipelago, the greatest anchovy species richness occurs in Southeast Asia (Whitehead *et al.* 1988; Lavoué *et al.* 2017; Egan *et al.* 2022)

*Encrasicholina* anchovies dominate clear water catches, with smaller amounts of *Stolephorus* spp., whereas turbid water/delta catches are dominated by other non-stolephorid genera such as *Setipinna*, *Thryssa* and *Coilia*. Most fisheries supply food to the large populations, and anchovies are often a major component of the small pelagics catch. Indonesia alone has a large live-bait fishery supplying an extensive tuna fleet. There is growing competition in some areas with food fisheries, and the establishment of an increasing numbers of Marine Protected Areas (MPAs) is restricting operations in a few regions.

Gears used in anchovy fisheries are mostly artisanal and small-scale. Industrial scale fisheries operate only in the largest states, for example, Thailand and Indonesia. A range of gears including purse seines, surround nets, gillnets, liftnets, shore-based gears (beach seines, traps, corrals, and set nets), and pelagic and demersal trawls are used.

Data on the anchovy catches in Southeast Asia are often incomplete, with disaggregated data by species rarely available for the trawl and set net catches. Nonetheless, the total estimated stolephorid catch for SE Asia is over 800,000 t with three of the world's largest stolephorid fisheries (Vietnam, Indonesia, and Thailand) included. With the addition of trawl catches, this figure is likely to exceed one million t. Catches in several countries include large amounts of juvenile/post larval stolephorids, species unknown.

Curing and fermenting stolephorid anchovies to produce fish sauce and fish paste reaches its zenith in SE Asia. These products are essential parts of the national food culture and the output of large-scale production.

Few biomass estimates and stock assessments/MSY estimates are available for SE Asian anchovy fisheries, and a few examples of overfishing are evident. However, management interventions on a local scale have generally been restricted to closed seasons, zonation for gear use and establishment of MPAs. As noted, data on which to base such assessments and interventions are often incomplete or poor.

**KEY REFERENCES:** Southeast Asia

**Geography:**

Population size ([www.ceicdata.com/en](http://www.ceicdata.com/en)), EEZ and shelf area ([www.liquisearch.com/exclusive\\_economic\\_zone/rankings\\_by\\_area](http://www.liquisearch.com/exclusive_economic_zone/rankings_by_area)), and land area.

**By country:**

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Indonesia	Retnowati and Satria (2013), Ariansyach (2017), CAE (2018), Sapari (2019), Widodo <i>et al.</i> (2016), Bailey <i>et al.</i> (1987), Lewis and Heri (2019, 2020)
Philippines	Dalzell and Ganaden (1987), Dalzell <i>et al.</i> (1987, 1990), Lamarca (2017), Viron (2019)
Thailand	Chaitiamvong (1999), FAO (2023), Suwannapoom (2019), Yenpoeng (2017), Yoosooksawat (1990),
Vietnam	Bat and Tran (2017), Ha and Thi (2010), Ho (2019), Hoang and Ha (2019), Nghia (2017), Nguyen (2015, 2017), Phan and Luc (1991), Van Nguyen (2019), Thanh (2019), Thuy and Flaaten (2013), Teh <i>et al.</i> (2014b)
Malaysia	Omar (2017), SEAFDEC (2017a)
Cambodia	Gillett (2004), Kamsan (2019), Panha (2019), SEAFDEC (2017b), Teh <i>et al.</i> (2014a)
Myanmar	Hassan and Latun (2016), Mar (2017), Sætersdal <i>et al.</i> (1999), Tint (2019), Whitehead <i>et al.</i> (1988)
Singapore	Corpus (2014), Kwek (2017), SEAFDEC (2017b), Woo (1967)

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**Table 7.** Summary of the fisheries catching stolephorid anchovies in Southeast Asia.

SOUTH EAST ASIA						
Country (EEZ, shelf; km <sup>2</sup> )	Land area, population	Stolephorid fishery, and main gears used	Annual catch (estimated)	Main anchovy species	Utilization	MSY/ estimated biomass
<b>Indonesia</b> (6,159,000; 2,039,381)	1,922,570 km <sup>2</sup> 265 million	Coastal artisanal and industrial/commercial small pelagics Lift nets (56%), gillnets, purse seine, surround nets, trawls, traps	210,000 t 2016, stolephorids ( <i>teri</i> ); data for other anchovy spp. n/a; catches since 2016 stable	<i>E. heteroloba</i> <i>E. punctifer</i> <i>E. devisi</i> <i>S. indicus/comm</i> Juvenile stolephorids	Fresh, dried, salted; less to fermentation (sauce, paste), tuna live bait	Local management, 11 Fishery Management Areas; increasing number of MPAs
<b>Philippines</b> (1,590,780; 277,921)	287, 900 km <sup>2</sup> 103 million	Coastal artisanal and industrial small pelagics Ring nets, fish corrals, lift net ( <i>basnig</i> )	51,553 t (2018), stolephorids ~18% small pelagics catch, <i>E. heteroloba</i> dominant	<i>E. heteroloba</i> , <i>punctifer</i> , <i>devisi</i> <i>S. indicus</i> Juvenile stolephorids	Fish sauce Fresh, dried, salted	MSY 90,000 t for stolephorids; closed seasons
<b>Thailand</b> (299,397; 230,063)	514,000 km <sup>2</sup> 67 million	Coastal artisanal and industrial /commercial small pelagics; trawl bycatch, anchovy p/seine (day/night), lift net, falling net (light at night)	140,000 t (2018) but not including trawl bycatch	<i>E. heteroloba</i> <i>E. punctifer</i> <i>E. devisi</i> (80-90% of catch)	Fresh, canned boil/dried, fish sauce/paste, some fish meal	Potential biomass n/a, MSY n/a, no national level management
<b>Vietnam</b> (418,000 (undisputed) ; 365,198)	331,000 km <sup>2</sup> ~ 98 million	Commercial, industrial small pelagics fishery, two main fishing areas Purse seine, pelagic pair trawl and demersal trawl	~ 400,000 t? (Kien Giang 120,000 t+, Khanh Hoa 220,000 t) plus other provinces	<i>E. heteroloba</i> <i>E. punctifer</i> <i>E. devisi</i> <i>Stoleph. indicus commersonii, tri,</i>	Fish sauce ( <i>nuoc mam</i> ), dried, fresh, some fish meal	MSY 500,000 -600,000 t ; MSY Khanh Hoa 140-290 t Probable overfishing in SW (Kien Giang)
<b>Malaysia</b> (334,671; 323,412)	329,847 km <sup>2</sup> 33 million	Coastal artisanal and industrial commercial small pelagics Day and night purse seine, demersal trawl	18,000 t (2013), mostly West Malaysia; no trawl data	<i>E. heteroloba</i> <i>E. punctifer</i> <i>S. indicus</i> , <i>commersonii</i>	Fresh, dried, fried, fish sauce ( <i>budu</i> ), paste ( <i>belacan</i> )	Biomass, MSY n/a; zonation system by gear, sanctuaries inshore

Country (EEZ, shelf; km <sup>2</sup> )	Land area, population	Stolephorid fishery, and main gears used	Annual catch (estimated)	Main anchovy species	Utilization	MSY/ estimated biomass
<b>Cambodia</b> (55,600; 62,515)	181,035 km <sup>2</sup> 17 million	Artisanal coastal small pelagics, anchovy 70% Day surround nets, gill nets	~10,500 t (2015)	n/a -assumed <i>Encrasicholina</i> spp. ( <i>heteroloba punctifer</i> , <i>devisi</i> ), <i>Stoleph. Indicus</i>	Fresh, dried, salted, fish sauce	Open access, no TACs, some MPAs
<b>Myanmar</b> (486,000; 228,781)	676,600 km <sup>2</sup> 54 million	Coastal artisanal and commercial small pelagics; anchovy p/seine, trawl, set net	4,000 t (2013) by anchovy p/seine; no data for trawl, set net	<i>E. heteroloba</i> <i>E. punctifer</i> <i>E. devisi</i> , plus 7 <i>Stoleph.</i> spp.	Fresh/chilled, cured, some fish meal, some export	435,000 - 930,000 t small pelagics biomass, of which ~30% anchovy (~130,000-300,000 t)
<b>Singapore</b> (1,067; 1067)	709 km <sup>2</sup> 5.7 million	Coastal artisanal Bait platform (kelong)	Clupeoid fish 1,200 t (2014), anchovy average 31 t 2000-2014	<i>E. heteroloba</i> , <i>E. punctifer</i> , <i>E. devisi</i> <i>S. indicus</i> , <i>S. commersonii</i>	Most imported dried, salted, fish sauce	Catches declining with urbanization, reclamation; kelongs falling into disuse

## OVERVIEW – South Asia

Three large and heavily populated countries (India, Bangladesh, and Pakistan – total land area 4.3 million km<sup>2</sup>; total population 1.7 billion) occupy the Indian peninsula and its northern surroundings, with large artisanal and small-scale commercial fisheries targeting small pelagics in coastal waters. The total stolephorid catch is relatively small with much of the anchovy catch comprising other genera (*Coilia*, *Thryssa* and *Setipinna*) from the turbid waters of the large deltas (Indus/Sindh, Ganges/Sundarbans). Stolephorids, however, make up two thirds of the nominal Indian anchovy catch of 90,000 t and the resource is possibly underexploited. Movements of the large anchovy stocks off SW India are clearly aligned with the monsoon seasons.

Sri Lanka, off the SE tip of the Indian Peninsula (land area 66,000 km<sup>2</sup>; population 21.5 million), has a substantial catch of small pelagics in coastal waters. Anchovies make up 15-20% of this (~ 45,000 t total), with *Encrasicholina heteroloba* and *Stolephorus* spp. comprising the majority of catches by small mesh gillnets and beach seines.

In all four countries, anchovies are consumed fresh, dried, and salted, with less of the catch going to cured/fish sauce products than in SE Asian countries. Much of the small pelagics landings are diverted to fishmeal production in some countries, notably in Pakistan to support poultry production, but less so in other countries such as India.

In the three small atoll archipelagos to the west of the Peninsula, the Maldives, Lakshadweep (an Indian Union Territory), and Chagos (British Indian Ocean Territory or BIOT), little of the anchovy catch is utilized as live bait. No take occurs at all in Chagos, which is uninhabited (except for the Diego Suarez military base) and now mostly an MPA. The Andaman and Nicobar Islands (an Indian Union Territory, mostly small high islands), supported a small artisanal anchovy fishery in 1982, but the current status is unknown. The anchovy fauna is poorly known in most of these island/atoll groups. Live bait fishery management plans have been developed in Maldives and Lakshadweep.

## KEY REFERENCES: South Asia

### Geography:

General: Population size ([www.ceicdata.com/en](http://www.ceicdata.com/en)), EEZ, shelf area ([www.liquisearch.com/exclusive\\_economic\\_zone/rankings\\_by\\_area](http://www.liquisearch.com/exclusive_economic_zone/rankings_by_area)), and land area.

### By country:

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India	BoBP (2018a), Johannessen <i>et al.</i> (1981), Luther (1990), Whitehead <i>et al.</i> (1988), Pritchard <i>et al.</i> (1996)
Bangladesh	Barua <i>et al.</i> (2014), BoBP (2018b), Pritchard <i>et al.</i> (1996), Whitehead <i>et al.</i> (1988)
Pakistan	FAO (2003a), Groeneveld and Koranteng (2017), Nazir <i>et al.</i> (2016), Pritchard <i>et al.</i> (1996)
Sri Lanka	FAO (2006), FAO (2019), Gayathry (2020), Navarathne and Dissanyake (2016)
Maldives	Gillett <i>et al.</i> (2013), Hemmings <i>et al.</i> (2014), Jauharee (2015)
Lakshadweep	<a href="http://lakshadweep.gov.in/departments/fisheries">lakshadweep.gov.in/departments/fisheries</a> , Lakshadweep – Wikipedia, Koya <i>et al.</i> (2019)
Chagos (Biot)	British Indian Ocean Territory – Wikipedia, Dunne <i>et al.</i> (2014)
Andaman	The Andaman and Nicobar Islands Fisheries Department
Nicobar	Mustafa (1983), <a href="http://www.and.nic.in/fisheries/">www.and.nic.in/fisheries/</a>

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**Table 8.** Summary of the fisheries catching stolephorid anchovies in South Asia

<i>SOUTH ASIA</i>						
<b>COUNTRY (EEZ, shelf; km<sup>2</sup>)</b>	<b>Land area, population</b>	<b>Stolephorid fishery and main gears used</b>	<b>Annual catch (estimated)</b>	<b>Main anchovy species</b>	<b>Utilization</b>	<b>MSY/ biomass estimates</b>
<b>Bangladesh</b> (165,887; 66,400)	144,054 km <sup>2</sup> , 165 million	Artisanal coastal, small scale gillnets, trawls, set nets in delta areas	Stolephorid catch minimal; trawl/set net anchovy catch comprises <i>Coilia</i> , <i>Setipinna</i> , <i>Thryssa</i>	7 stolephorid spp. (3 <i>Encrasicholina</i> , 4 <i>Stoleph.</i> ) plus <i>Coilia</i> , <i>Thryssa</i> , <i>Setipinna</i>	Small pelagic utilization insignificant	Poor data, no estimates available
<b>India</b> (2,020,000; 402,996)	3,287,263 km <sup>2</sup> , 1,341 million	Artisanal coastal, small scale commercial; Gillnet, beach, shore and purse seine, trawl	Stolephorid ~ 60,000 t, total anchovy ~90,000 t (2017)	11 stolephorid spp. (4 <i>Encrasicholina</i> , 7 <i>Stolephorus</i> ) plus <i>Coilia</i> , <i>Thryssa</i> , <i>Setipinna</i>	Mostly human consumption, increasingly less to fishmeal	No MSY estimates known, 1,608,000 t biomass estimates South West, no estimates East coast/ Bay of Bengal
<b>Pakistan</b> (290,000; 50,270)	882,000 km <sup>2</sup> , 212 million	Artisanal coastal, small scale commercial; Demersal trawl, gillnets, surround nets, beach seine	~ 6,000 t total (2018); mostly Sindh coast and Indus delta; Baluchistan narrow shelf	11 anchovy spp. (incl 2 <i>Stoleph.</i> plus <i>Thryssa</i> (7), <i>Coilia</i> (2) but few data	Fresh, dried 30%; fish meal 50% (poultry); exports large	Small pelagics biomass ~ 600,000 t, most <i>S. indicus</i> ; assume underexploited, no management.
<b>Sri Lanka</b> (517,000; 27,800)	65,610 km <sup>2</sup> , 21.5 million	Coastal small pelagics, of which 15-20% anchovy; small mesh gillnets, beach seine	n/a, ~ 10-12 % coastal production, or ~ 45,000 t	<i>E. heteroloba</i> <i>S. indicus</i> <i>S. bataviensis</i>	Dried, fresh, fish sauce (Colombo cure)	n/a - no time series data available; probably some local overfishing
<b>Maldives</b> (923,000; 35,000)	300 km <sup>2</sup> , 391,000 (2021)	Live bait for tuna fishery Lift nets	Anchovy 7% of live bait; ~ 80 t (1994), less in recent years	<i>E. heteroloba</i>	Live bait	Livebait Fishery Management Plan
<b>Lakshadweep</b> (400,000; 20,000)	32 km <sup>2</sup> , 74,000 (2021)	Live bait for tuna fishery; Lift nets(sprat) surround nets (reef spp.)	Anchovy % negligible (no light use)	N/a – no anchovies listed	(live bait - stolephorids not recorded)	Livebait Fishery Management Plan
<b>Chagos (BIO Territory)</b> (639,631; 20,607)	56.13 km <sup>2</sup> , ~300 (Diego Suarez base)	Uninhabited, save military base on one atoll (DS) No commercial fishing	Zero catch	<i>E. heteroloba</i> , <i>punctifer</i> ; <i>Stoleph.</i> spp. (assumed)	No utilization	Most atolls (excl. Diego Garcia and 3 nm zone) now declared MPA
<b>Andaman/Nicobar</b> (600,000; 35,000)	8249 km <sup>2</sup> , 380,000	Coastal artisanal Shore seine, gillnet, cast net	293 t (1982), 7.6% of total fishery production	<i>S. commersonii</i> <i>Thryssa mystax</i> <i>Encrasicholina</i> spp.	Fresh, some dried	Anchovy potential yield 6,000 t

## **OVERVIEW – Western Indian Ocean Islands**

The islands of the Western Indian Ocean (WIO) are mostly small, high islands (for example Comoros, Reunion, etc), comparable in land area and elevation with those in the Western and Central Pacific. It might be argued that Madagascar is an analog of Papua New Guinea, and some of the same biomes exist, e.g., dryland savannah, grassy plains, and rainforest, the latter of which is extensive. Madagascar by contrast has undergone massive deforestation (Clark 2015). This has harmed agricultural prospects through soil erosion, loss of habitats for unique species, and an increase of carbon dioxide emissions (Clark 2015).

While there are some atolls in the WIO, they are currently uninhabited, unlike the many atolls of the Western and Central Pacific. The total population of the WIO islands is 31.3 million, with nearly 90% resident on Madagascar. Similar to the Pacific Islands there is little interest in harvesting stolephorid anchovies, unlike South Asia and SE Asia.

The only record of long-term exploitation of anchovies is for the Comoros Islands where catches in 2010 were 1,886 t and over the 50-year time series an average of 527 t and a median of 105 t (Le Manach *et al.* 2015b). There is no species composition given, but it is anticipated that much of the putative anchovy catch would be stolephorids such as *S. commersonii*, *S. indicus*, and *E. punctifer*, possibly mixed in with some *Engraulis capensis*. Such a time series could be used to generate a stock assessment of Comoros anchovies, but is not broken down by species, which would make such exercise problematic.

**KEY REFERENCES:** Western Indian Ocean Islands

**Geography:**

General: Population size ([www.ceicdata.com/en](http://www.ceicdata.com/en)), EEZ, shelf area ([www.liquisearch.com/exclusive\\_economic\\_zone/rankings\\_by\\_area](http://www.liquisearch.com/exclusive_economic_zone/rankings_by_area)), and land area.

**By country:**

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Madagascar	Stequert and Marsac (1989), Le Manach <i>et al.</i> (2011)
Comoros	Doherty <i>et al.</i> (2015a), Breuil and Grima (2014)
Reunion	Le Manach <i>et al.</i> (2015b)
Mayotte	Doherty <i>et al.</i> (2015b)
Mauritius	Boistol <i>et al.</i> (2011)
Seychelles	Stequert and Marsac (1989), Le Manach <i>et al.</i> (2015c), Breuil and Grima (2014)

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**Table 9.** Summary of the fisheries catching stolephorid anchovies in the Western Indian Ocean Islands

WESTERN INDIAN OCEAN ISLANDS						
Country (EEZ, shelf; km <sup>2</sup> )	Land area, population	Stolephorid fishery and main gears used	Annual catch (estimated)	Main species	Utilization	MSY/biomass (estimated)
<b>Madagascar</b> (225,2592; 101,505)	587,041 km <sup>2</sup> 28 million	No record of artisanal or subsistence anchovy fisheries. Brief (1973-75) pole & line fishery with <i>E. heteroloba</i> , <i>S. indicus</i> minor spp.		<i>S. indicus</i> <i>S. commersonii</i> <i>E. heterolobus</i> <i>E. punctifer</i> ??	Stolephorid anchovies included in live bait fishery	No biomass or MSY estimates for live bait fishery or for catch components. Baitfish fleet-wide yields averaged 485 kg/night, of which 70% was sardines
<b>Comoros</b> (163,752; 1,526)	1,861 km <sup>2</sup> 850,000	Coastal artisanal anchovy fishery 1,886 t (2010)	2010 anchovy catch = 1,886 t	<i>S. indicus</i> <i>S. commersonii</i> <i>E. punctifer</i> ?? <i>Engr. capensis</i>	Anchovy fishery documented in the Comoros	Despite annual catch data no estimates of MSY or biomass are available
<b>Reunion</b> (300,000; 66,592)	2,511 km <sup>2</sup> 868,846	No record of artisanal or industrial anchovy fisheries		<i>S. indicus</i> <i>S. commersonii</i> <i>E. punctifer</i> ??	No record of stolephorid anchovy use	No specific anchovy data and no biomass or MSY estimates
<b>Mayotte</b> (63,000; 248,300)	347 km <sup>2</sup> 256,518	No record of artisanal or industrial anchovy fisheries		<i>S. indicus</i> <i>S. commersonii</i> <i>E. punctifer</i> ??	No record of stolephorid anchovy use	No specific anchovy data and no biomass or MSY estimates
<b>Mauritius</b> (1,284,997; 29,061)	2,011 km <sup>2</sup> 1,264,866	No record of artisanal or industrial anchovy fisheries		<i>S. indicus</i> <i>S. commersonii</i> <i>E. punctifer</i> ??	No record of stolephorid anchovy use	No specific anchovy data and no biomass or MSY estimates
<b>Seychelles</b> (1,336,559; 39,063)	452 km <sup>2</sup> 90,000	No record of artisanal or industrial anchovy fisheries		<i>S. indicus</i> ? <i>S. commersonii</i> ? <i>E. punctifer</i> ??	No record of stolephorid anchovy use	No specific anchovy data and no biomass or MSY estimates

\* Where there is no anchovy fishery, the main species present in the Country/Territory are given

## OVERVIEW – Middle East and Red Sea

A relatively diverse group of States occupying the Arabian Desert margins and the desert lands around the Red Sea. Together, the 13 states account for about 330 million people living across the largely arid and desert regions of the Middle East. Iran has the greatest geographic diversity and the largest population, but even together with the other countries, its amounts to only about 0.04% of the global population.

The Importance of these countries economically comes from the vast deposits of oil and natural gas beneath their respective lands, territorial seas and EEZs. However, in the past and in some cases the present, national fishing fleets have either targeted stolephorid anchovies, or caught them as by-catch in other fisheries, primarily for small pelagics but also shrimp trawl fisheries.

This is the one part of the world where large catches of what was called *Encrasicholina punctifer* form a large proportion of the catch. Recent work by Hata and Motomura (2016a) suggests that *E. punctifer* is restricted to the Pacific Ocean, and is replaced in the Indian Ocean by *E. gloria* and *E. intermedia*. The latter species is possibly spread widely over the Indian Ocean, while *E. gloria* appears to be restricted to the Arabian Gulf and Red Sea. Distributional data are currently limited and more are needed.

Gears used in the anchovy fisheries are mostly artisanal and small-scale commercial enterprises, with some industrial scale purse seine fishing. The subsistence fisheries use broadly the same types of gear as the artisanal fisheries, and there is significant blurring between subsistence and artisanal catch.

Data on the anchovy catch in the Middle East and Red Sea are often incomplete, with disaggregated data by species rarely available for the catches. However, the total estimated stolephorid catch of 117,700 t is taken by slightly more than half of the countries in the Table 11.

The usually minor stolephorid catch is mostly consumed fresh and dried - fish fermentation is not common unlike South and South East Asia, but in Iran, a mix of clupeids and stolephorid anchovies is used for the production of the fish sauce (*mahyaveh*). An unknown fraction of the total is processed to make animal feed in some countries.

## KEY REFERENCES: Middle East and Red Sea

### Geography:

Population size ([www.ceicdata.com/en](http://www.ceicdata.com/en)), EEZ area, shelf area ([www.liquisearch.com/exclusive\\_economic\\_zone/rankings\\_by\\_area](http://www.liquisearch.com/exclusive_economic_zone/rankings_by_area)), and land area.

### By country

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Iran	Van Zailinge <i>et al.</i> (1993), FAO (2005a), Salarpouri <i>et al.</i> (2018)
Iraq	FAO (2004a)
Oman	FAO (2003b)
Kuwait	FAO (2003c)
Saudi Arabia	FAO (2003d)
Qatar	FAO (2003e), Al Abdulrazzak (2013)
United Arab Emirates	FAO (2004b)
Yemen	FAO (2022)
Jordan	FAO (2003f)
Israel	FAO (2007), Edelist <i>et al.</i> (2013)
Djibouti	Colléter (2015), Breuil and Grima (2014)
Egypt	FAO (2004c)
Sudan	Alamin Mohamed, Min. Anim. Resources, <i>pers. comm.</i> Dec 12, 2021
Eritrea	FAO (2005b)

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**Table 10** Summary of the fisheries catching stolephorid anchovies in the Middle East and Red Sea.

MIDDLE EAST AND RED SEA						
Country (EEZ, shelf; km <sup>2</sup> )	Land area, population	Stolephorid fishery and main gears used	Annual catch (estimated)	Main species*	Utilization	MSY and biomass estimates (t)
<b>Iran</b> (168,718; 196,000)	1,648,000 km <sup>2</sup> 83 million	Coastal artisanal and industrial small pelagics Purse and beach seine	37,000 t (2014)	<i>E. punctifer</i> <i>S. indicus</i>	Dried, salted Fish sauce (mahyaveh)	52,500 t (Arabian Gulf)
<b>Iraq</b> (771; 771)	437,367 km <sup>2</sup> 40.2 million	Coastal artisanal but minimal production – environ. change, war. Trawl, gillnet, trap, cast nets	Very small	<i>S. indicus</i>	NA	No specific anchovy data and no biomass or MSY estimates; coastline limited and severe environmental impacts on marshes
<b>Oman</b> (3,180; 59,071)	309,500 km <sup>2</sup> 4.9 million	Coastal artisanal Purse seine, gill net	13,000 t	<i>E. punctifer</i>	Dried	173,000 t (Arabian Gulf and Oman Sea)
<b>Kuwait</b> (11,026; 11,026)	17,818 km <sup>2</sup> 4,420,110	Coastal artisanal, plus industrial shrimp fishery; trawl, gillnet	Very small; trawl bycatch no data	<i>E. devisi</i> <i>E. punctifer</i> <i>S. indicus</i>	Fresh	Stolephorid anchovies present, but most of the fishery based on the clupeoids <i>Hilsa kelee</i> and <i>Tenuulosa ilisha</i>
<b>Saudi Arabia</b> (228,633; 107,249)	2,149,690 km <sup>2</sup> 34,218,169	Artisanal and industrial trawl; anchovies as demersal trawl discard (Red Sea): Traps, gillnet, stake net	Production Red Sea and Arabian Gulf; stolephorid catch n/a, probably minor	N.A.	Fresh High level of imports	No specific anchovy data and no biomass or MSY estimates
<b>Qatar</b> (31,590; 31,590)	11,581 km <sup>2</sup> 2,795,484	No stolephorid fishery Caught by artisanal encircling nets, gillnets	NA, minor	N.A.	Fresh	No specific anchovy data and no biomass or MSY estimates
<b>United Arab Emirates</b> (58,218; 57,474)	83,600 km <sup>2</sup> 9,970,529	Coastal artisanal Beach seines and round haul seines	Last UAE catch 300 t (2007), higher in past - 6,350 t 1999	N.A.		No specific anchovy data and no biomass or MSY estimates
<b>Yemen</b> (552,669; 59,071)	89,342 km <sup>2</sup> 9,531,712	Large stolephorid catch Yemeni artisanal fishery, Gulf of Aden; beach and purse seine	67,000 t (28 % of artisanal catch = 239,855 t in 2010)	<i>Stolephorus tri?</i>	Fresh fish consumption, rations for vessel crews	No specific anchovy data and no biomass or MSY estimates
<b>Jordan</b> (116; 59)	89,342 km <sup>2</sup> 11,042,719	N.A.	N.A.	N.A.	N.A.	No specific anchovy data and no biomass or MSY estimates
<b>Israel</b> (26,352; 3,745)	22,072 km <sup>2</sup> 9,481,820	N.A.	N.A.	N.A.	N.A.	No specific anchovy data and no biomass or MSY estimates

Country (EEZ, shelf; km <sup>2</sup> )	Land area, population	Stolephorid fishery and main gears used	Annual catch (estimated)	Main species*	Utilization	MSY and biomass estimates (t)
<b>Djibouti</b> (2,996,419; 19,403)	23,200 km <sup>2</sup> 921,804	Small pelagic catch in 2013 = 2,592 t, artisanal fishery from outboard powered skiffs	N.A.	N.A.	N.A.	No specific anchovy data and no biomass or MSY estimates; Catch estimate based on based on data in Breuil and Grima, (2014)
<b>EGYPT</b> (263,451; 61,591)	1,010,408 km <sup>2</sup> 102,674,145	Subsistence and industrial small pelagics Subsistence - gillnets, beach seines, cast nets; Industrial - purse seine	161 t	<i>E. punctifer</i> <i>Engr.</i> <i>encrasicolus</i>	Domestic consumption as fresh fish	No specific anchovy data and no biomass or MSY estimates
<b>SUDAN</b> (68,148; 19,827)	1,886,068 km <sup>2</sup> 44,909,353	Egyptian vessels fishing in Sudan waters; Purse seine, beach seine	Average annual catch of ≈ 230 t	<i>E. heteroloba</i> , <i>punctifer</i> , <i>Stoleph. indicus</i> , <i>Engr.</i> <i>encrasicolus</i>	Eaten fresh or mixed with fish sauce ( <i>feseekh</i> )	MSY for small pelagic fishery catch, which includes stolephorid anchovies catch estimated to be about 4,000 t (Alamin Mohamed, Ministry of Animal Resources, pers. com.)
<b>ERITREA</b> (77,728; 61,817)	117,600 km <sup>2</sup> 3.6-6.7 million	Coastal artisanal; beach seine for anchovies and sardines	Anchovies no more; reached 17,500 t, 1950s	<i>E. heteroloba</i> , <i>E. punctifer</i> , <i>Stoleph.indicus</i>	Fish meal	No specific anchovy data and no biomass or MSY estimates



## OVERVIEW – East Africa

The five countries of the East African coast on the Indian Ocean provide a range of socio-economic circumstances. The population of the four countries and the South African Province of Kwazulu-Natal amounts to 173 million people. The stolephorid catches of the clear waters of the coasts of Somalia to Tanzania are dominated by *Encrasicholina pseudoheteroloba*, *E. heteroloba*, and *E. punctifer*, with smaller amounts of *Stolephorus indicus*, *S. commersonii*, *S. bataviensis* plus *Thryssa vitirostris*, *T. setirostris* and *T. baelama*. The gears used to catch stolephorids from the East African Coast are mostly artisanal and small-scale. A range of gears including ringnets, beach seines, corrals, and set nets, and pelagic and demersal trawls are also used. Anchovy catches are consumed fresh and dried and dried and ground for fishmeal.

Data on the anchovy catch from East Africa with disaggregated data by species is rarely available for fisheries along the East African coasts. However, estimates of biomass, primarily from hydro-acoustic methods suggest that the stolephorid anchovy biomass may exceed 370,000 t. This is markedly influenced by upwelling driven by climate and prevailing oceanography.

MSY estimates were generated from the biomass estimates from earlier hydroacoustic surveys by the Norwegian research vessel, *R/V Dr Fridtjof Nansen* (Groeneveld and Koranteng 2017). The MSY estimates were generated using the simple model proposed by Gulland 1970, where  $MSY = 0.5 \cdot M \cdot B_0$ , with  $M$  the instantaneous natural mortality rate and  $B_0$  the unfished biomass. Re-examination of the MSYs generated for the stolephorid anchovies used natural mortality rates that were 50% lower than observed for stolephorid anchovy stocks elsewhere (see Table 15), potentially leading to underestimates of the MSYs from anchovy stocks from Somalia, Kenya, Tanzania and Mozambique.

## KEY REFERENCES: East Africa

### Geography:

Population size ([www.ceicdata.com/en](http://www.ceicdata.com/en)), EEZ, shelf area ([www.liquisearch.com/exclusive\\_economic\\_zone/rankings\\_by\\_area](http://www.liquisearch.com/exclusive_economic_zone/rankings_by_area)), and land area.

### By country:

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Somalia	Abdullahi (2001), Breuil <i>et al.</i> (2014), Chittick (1980), Cashion <i>et al.</i> (2018), Boldrocchi and Bettinetti (2019)
Kenya	Le Manach <i>et al.</i> (2015a), Jebri <i>et al.</i> (2020), Samoilys <i>et al.</i> (2011)
Tanzania	Jiddawi and Öhman (2002), Sekadende <i>et al.</i> (2020), Bodiguel and Breuil (2015), Baust <i>et al.</i> (2015)
Mozambique	Doherty <i>et al.</i> (2015c), Gislason and Sousa (1985), Jacquet <i>et al.</i> (2010)
Kwa-Zulu Natal (South Africa)	Beckley (1996), Horton and van der Lingen (2019), Baust <i>et al.</i> (2015)

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**Table 11.** Summary of the fisheries catching stolephorid anchovies in East Africa

<i>EAST AFRICA</i>						
Country (EEZ, shelf; km <sup>2</sup> )	Land area, population	Stolephorid fishery and main gears used	Annual catch (t)	Main species*	Utilization	MSY/ biomass (estimated)
<b>Somalia</b> (82,5052; 55,895)	15.89 million km <sup>2</sup> 16 million	Coastal artisanal. Stolephorid anchovies and <i>Engraulis japonica</i> . Small scale plank vessels, outboard and oar powered. Beach seines, cast nets, fish corrals	Poor recent catch data. Using biomass data (this table) and M of 5.9, catch of 37,700 t maybe achievable (Dalzell 1990)	<i>E. heteroloba</i> <i>S. bataviensis</i> <i>E. macrocephala</i> occasionally <i>E. punctifer</i>	Dried fish for fish meal export Somalis prefer meat to fish	1.3 million t biomass of small pelagics (1975), which comprised 13,000 t of stolephorids and 130,000 t of <i>E. japonicus</i>
<b>Kenya</b> (116,942; 11,073)	600,000 km <sup>2</sup> 55 million	Anchovy landings caught mainly by ring-nets from domestic wooden fishing vessels 12 - 19 m in length	454 t (2016), but not broken down by species.	<i>E. devisi</i> , <i>E. heteroloba</i> , <i>E. punctifer</i> , <i>Stoleph.indicus</i> , <i>S. commersonii</i> , <i>S. bataviensis</i> <i>Thryssa</i> (3 spp.)	Dried for local consumption	Pelagic biomass estimated to be 25,500 t, which includes <i>Thryssa vitirostris</i> and <i>S. commersonii</i> ; application of Cadima's formulation gives MSY = 75,000 t
<b>Tanzania</b> (241,888; 25,611)	950,000 km <sup>2</sup> 61million	Anchovy catch primarily ring-nets deployed from plank built vessels, 7-15 m in length but 90% < 11 m	Mainland catch estimates 49,000 - 92,000 t (2018-9), anchovies dominant Zanzibar fishery, anchovies 54% of ≈ 5,400 t catch	<i>E. devisi</i> , <i>E. punctifer</i> and <i>S. commersonii</i> catches dominate anchovy and small pelagic catch (51%), with <i>E. devisi</i> most abundant	Dried and fresh for local consumption.	Biomass of small pelagics estimated to be about 150,000 t with scope for expansion based on stolephorid catch and Cadima's formula of an anchovy MSY = 242,475 t
<b>Mozambique</b> (578 986; 94,212)	800,000 km <sup>2</sup> 30 million	Pelagic trawl	Average catch of anchovies 1998-2008 = 11,266 t	Anchovy catch primarily <i>E. punctifer</i> and <i>E. heteroloba</i> , smaller amounts of <i>S. indicus</i>	Dried and fresh for local consumption	Biomass estimates of stolephorids range from 30,000-310,000 t, and MSY of 310,000 t. Note extreme interannual variability and impact of rainfall on productivity.
<b>Kwa-Zulu Natal (South Africa)</b> (23,625*; 960*)	90,000 km <sup>2</sup> 11 million	Beach seine	Negligible anchovy catch in beach seine fishery	Main anchovies captured were <i>Thryssa vitirostris</i> and <i>T. setirostris</i>	Catch used primarily as bait for other fisheries	Data insufficient to generate total catch nor to estimate MSY

\* Rough estimates only based on one degree square EEZ information in Grantham *et al.* (2008) and 8 km shelf area given by Cawthra *et al.* (2012)

## Fisheries Statistics

Historically, there were no fisheries of any substance within the Pacific Islands area for stolephorid anchovies (Wright *et al.* 1983). The exception was the Hawai'i (*aku* boat) fishery which began in 1900 (Schug 2001) and persisted until the latter decade of the 20<sup>th</sup> Century (P. Dalzell, pers. obs.). The bait fisheries in the countries of the South Pacific, primarily Papua New Guinea (PNG) and the Solomon Islands, were the first intensive industrial fisheries within the coral reef environments of these countries. This is in distinct contrast to the fisheries from SE Asia to East Africa, where fishing for small pelagic fish has been conducted for centuries, if not millennia (O'Connor *et al.* 2011; Spoehr 1984; Morgan and Staples 2006).

Three species, *E. heteroloba*, *E. devisi*, and *E. punctifer* (see Table 3) dominated catches in most locations, especially where fishing was conducted in areas without major estuarine areas. Hawai'i is the exception with only the endemic *E. purpurea* being caught. Catches of stolephorids, where there are significant estuaries, especially on the SE Asian mainland and South Asia include species such as *S. indicus* and *S. commersonii* as well as the three species of *Encrasicholina* mentioned above. Moreover, other anchovy genera such as *Thryssa* and *Colia* are caught with stolephorids.

Stolephorid catches in the Western Indian Ocean Islands appear to be dominated by *S. indicus* and *S. commersonii*. However, this may be an artefact as there are no species composition data for these islands, meaning that the *Stolephorus* species in catches may be different in actuality and inclusion in the table is based on Whitehead *et al.* (1988). Every Southeast Asian country has distinctive postharvest utilization methods for anchovies. The true magnitude of annual stolephorid catches in South Asia, Southeast Asia, the Middle East, and East Africa may be as high as 1,000,000 t (Tables 5-11). This should be regarded as a minimum estimate, given that stolephorid anchovies could be aggregated with other clupeoids or other small pelagic fishes in national fisheries statistics.

Butcher (2004) and Morgan and Staples (2006) commented on the poor state of even basic statistics on landings, fishing methods and fishing effort in Southeast Asia. This lack of statistics from the past made the analysis by Butcher (2004) on the development of fisheries in the region very difficult, and often reliant on isolated, qualitative information. Initiatives such as the Experts Group Meeting on Stock Status and Geographical Distribution of Anchovy, Indo-Pacific Mackerel and Blue Swimming Crab (AIB) in the Gulf of Thailand (SEAFDEC 2017a), have been driven by the need for greater regional fishery data initiatives.

Despite such initiatives, there remain today virtually no stolephorid anchovy statistics that are collected on a regional basis. This is an important gap since many stolephorid stocks cross national boundaries and are fished by fleets from a number of nations. Moreover, there is no consistent regional approach to the type and methodology of fisheries statistics collection. Further, most national statistics are poor both in the extent of their coverage and precision. The basic data upon which to assess the impact of fishing on fish stocks and to make informed fisheries development and management, decisions was never collected in the past and this important gap in knowledge remains today, in spite of the information in this contribution being incorporated in the database and website of the *Sea Around Us*.

## Post-harvest production

The transformation of stolephorid anchovies into fermented fish sauce and dried product means that consumption of stolephorid anchovies is not limited to the coastal zones and immediate hinterlands.

Preserved stolephorid anchovy products may thus be distributed globally and contribute the food security of up 50% of the global population. Production fish sauce in 2020, for example, amounted to 377 million liter in Vietnam alone while the Asia-Pacific fish sauce market will grow at a compound annual growth rate of 3% over the next 5 years ([www.mordorintelligence.com/industry-reports/asia-pacific-fish-sauce-industry](http://www.mordorintelligence.com/industry-reports/asia-pacific-fish-sauce-industry); accessed on August 11, 2022)

The total volume of fish sauce produced in Southeast Asia is difficult to document due to the differences in national fisheries statistics. A simple ratio estimator using the Vietnamese catch (400,000 t) and fish sauce production in 2020 (377 million liter), would suggest that a total of almost 1 million t of fish sauce is produced in the region. This is a very rough estimate, but is useful in suggesting the scale of the magnitude of fish sauce manufacture from fermenting stolephorid anchovies.

Dried anchovy are another major stolephorid product. Obtaining production statistics are, needless to say, variable. In 2019, Vietnam dried anchovy exports amounted to 163,362 t and in India 348,967 t, based on a market intelligence site VOLZA Grow Global ([www.volza.com/exports-india/india-export-data-of-iran+dried+anchovy+export](http://www.volza.com/exports-india/india-export-data-of-iran+dried+anchovy+export); accessed July 11, 2022). Individual weights of dried stolephorid anchovies are  $\approx 4$  g (Shiriskar *et al.* 2010) and thus dividing through the exports expressed in grams gave a total of 530 million anchovies (Vietnam) and 87 billion anchovies (India), which is indicative of the scale of anchovy removals through fishing in South and Southeast Asia. Using data from Tables 6 and 7 for biomass (India) or MSY (Vietnam) and a 75% water loss (Shiriskar *et al.* 2010), the numbers of stolephorid anchovies represented by these numbers amounts to about 300 billion and 140 billion respectively.

While weight caught and processed is still of great importance, the representation of stolephorid anchovies catch or sustainable yields in numbers of fish, may provide a better reference point in terms of removals from and impacts to coastal ecosystems. This is of interest in wasp waist ecosystems (Rice 1995), where an intermediate trophic level, in this case stolephorid anchovies are expected to control the abundance of predators through a bottom-up interaction and the abundance of prey through top-down interactions.

### **Juvenile and adult distribution**

Stolephorid anchovies are widely distributed across the Indo-Pacific faunal continuum and beyond, with a single record of *Encrasicholina punctifer* in the Eastern Pacific Ocean (Hida 1973, as *Stolephorus buccaneeri*). Three species, *Encrasicholina gloria*, *Stolephorus indicus*, and *S. insularis* are Lessepsian migrants to the Mediterranean via the Suez Canal. The specimens of *E. punctifer* described in the Mediterranean may belong to the newly described species *Encrasicholina gloria*, which is recorded from the Arabian Gulf and Red Sea (Hata and Motomura 2016a). The Indian Ocean congener, *Encrasicholina intermedia*, separated from *E. punctifer* appears to present in southern India and the African East Coast (Hata and Motomura 2016a).

One of the commonest stolephorids *Encrasicholina heteroloba* is found inshore from East Africa to Fiji, and offshore in the shallow seas in Indonesia. This species is rarely recorded in coral atolls and some high islands which lack extensive shallow water, such as the Mariana Islands. However, this species is found in the Maldives, (consisting entirely of coral atolls (Hemmings *et al.* 2014) and also occurs around small high islands such as Pohnpei, Federated States of Micronesia, and Palau. Kearney *et al.* (1971) reported higher catches of *E. heteroloba* and *E. devisi* (cited as *S. heterolobus* and *S. devisi*) in areas of Papua New

Guinea with extensive freshwater input, and within a depth range of 12 to 25 m. Lee (1973) reported higher bait catches, including *E. heteroloba* (cited as *S. heterolobus*) in Fiji in areas with some freshwater flow.

Tham (1950) observed that stolephorid anchovies live primarily in waters ranging from 27.0 °C to 30.5 °C, and salinity range 17 psu to 32 psu which *E. heteroloba* has been reported is high productivity, as defined here as over 2 mg C per cubic meter of sea water, per hour, measured by the C<sup>14</sup> uptake method (Muller 1976).

*Stolephorus commersonii* is typical of the stolephorids found in coastal waters, and occasionally enters brackish water. It occurs in the Godavari estuary, India, from February to June in salinities of 19.6-32.0 psu, but is almost totally absent in the subsequent flood season. *S. commersonii* feeds on surface plankton, primarily copepods and prawn larvae (Tiews *et al.* 1971). Similarly, *Stolephorus indicus* is a schooling species occurring in coastal waters, and which appears to enter at least the estuarine parts of rivers and to tolerate brackish water. This species migrates out into deeper and more saline water to spawn in Manila Bay (Tiews *et al.* 1971).

Generalized additive models (GAMs) were used by Saffrudin *et al.* (2018) to reveal that selected environmental factors play an important role in the explanation of the distribution of stolephorid anchovies (species not given) in the Gulf of Bone in Sulawesi. Most of the anchovy schools were caught by large liftnets located in the coastal area.

The high anchovy concentrations corresponded well with Sea Surface Temperatures (SSTs) of 29.5–30.5°C, and Sea Surface Chlorophyll-a (SSC) ranging between 0.5 and 1.0 mg C·m<sup>-3</sup>. Anchovies migrating in the Gulf of Bone could have followed both SST and SSC optima during the southeast monsoon season, which they occupied in the warmer and highly productive waters. These preferred conditions may represent the optimal habitat of the anchovy in Bone Gulf during the southeast monsoon, returning inshore thereafter.

Streams and rivers are present in most of the areas inhabited by stolephorids except the Somali coast, the Gulf of Aden, and the Gulf of Oman. These three locales are influenced by upwelling during the southwest monsoon season (Wyrki *et al.* 1971). *E. heteroloba* occurs inshore in regions with narrow continental shelves and offshore in the shallow seas of Indonesia, which is consistent with the productivity explanation discussed by Muller (1976).

Local productivity ( $\geq 2$  mg C·m<sup>-3</sup>·h<sup>-1</sup>) also explains why *E. heteroloba* is found in high islands with lagoons, but generally not coral atolls and platform islands without lagoons. The high islands of Babelthuap (Palau) and Pohnpei (FSM) have sufficient land area to form rivers, which transport nutrients into the lagoons. Coral atolls, lacking enough land area to collect rainfall and form streams, must rely upon in situ recycling of nutrients (Suzuki and Kawahata 2003).

Chuuk is a State in the Federated States of Micronesia and is part of the Caroline Islands. Chuuk Lagoon has protective reef, 225 km (140 mi) around, and a land area of 93 km<sup>2</sup>. Tuna fishing interests have sought unsuccessfully for the past fifty years to find populations of *E. heteroloba* in Chuuk lagoon useful for live bait (Wilson 1971). Platform islands or pinnacles, such as Guam or Sonsorol, lack lagoons, or shallow embayments and their streams, if present, carry nutrients from the land to the sea where the nutrients are

quickly diluted and carried away down-current. Chuuk, although having a few high islands, has such an extensive surrounding lagoon that the terrestrial input is minor and has little to no impact on sea water productivity.

In contrast, *E. heteroloba* is found in the atolls of the Maldives (see Hemmings *et al.* 2014, Blaber and Copland 1990). Anderson *et al.* (2011) found that seasonally alternating currents are driven by monsoon winds that also alternate according to the season and bring clear oceanic water to the upstream sides of the Maldives atolls. As the currents pass over the Maldives ridge, nutrient-rich waters are lifted to the surface, promoting phytoplankton blooms on the downstream sides of the atolls. This manifestation of the island mass effect creates an abundance of zooplankton, which supports the presence of manta rays (Anderson *et al.* 2011) and other planktonic feeders such as *E. heteroloba* (Milton *et al.* 1990b; Egan *et al.* 2018).

Tham (1968) observed that *E. heteroloba* (cited as *Stolephorus pseudoheterolobus*), as well as the other species of *Stolephorus* found in Singapore Strait, are attracted by light, since fixed traps which do not use light to attract fish do not catch stolephorid anchovies in large quantities. The diet of the stolephorids consists almost entirely of planktonic organisms and may factor into the restriction of their abundance to coastal waters, since in the seas around Malaysia and Singapore, plankton is most abundant along the coastal area and is sparse in the open sea.

As noted earlier by Wetherall (1977), *E. purpurea* (cited as *Stolephorus purpureus*) CPUE was negatively correlated with stream discharge into Kaneohe Bay. Dalzell (1990) showed that *E. heteroloba* and *E. devisi* (cited as *Stolephorus heterolobus* and *S. devisi*) CPUE in the coastal waters of Papua New Guinea had dome shaped relationships with rainfall and salinity that could be fitted by a simple polynomial model of the form  $Y = a + bX + cX^2$ . Dalzell (1990) also showed that for the stenohaline buccaneer anchovy, *E. puncifer*, (cited as *Stolephorus buccaneeri*) CPUE had a negative relationship with increasing rainfall in coastal areas.

## BIOLOGY OF STOLEPHORID ANCHOVIES

The biology of most species of stolephorid anchovies remains little studied but three species of *Encrasicholina* (*E. heteroloba*, *E. pseudoheteroloba*, and *E. purpurea*), and two species of *Stolephorus* (*S. indicus* and *S. commersonii*) are thought to be representative of the species biology in the two genera. The life history and biology of the buccaneer or ocean anchovy, *E. punctifer*, occurring at coastal, offshore and high seas habitats is thus described separately from other species in the same genus.

### Schooling Behaviour

The association of fish into groups, known as schools or shoals is a behaviour exhibited by many fish species and has been the topic of many fisheries investigations (Cushing and Harden Jones 1968; Larsson 2012; Pavlov and Kasumyan 2000; Jhawar *et al.* 2020). Fishes, mostly with facultative schooling, tend to school in a homogeneous environment, whereas in a complex and visually heterogeneous environment, such fish prefer to keep independent from each other. Various reasons have been advanced for fish schooling including feeding, predator avoidance and reproduction.

Kasumyan and Pavlov (2018) have summarized the evolution of fish schooling of teleost or bony fishes. The authors state that “evolutionary pathway of formation of schooling might follow through several subsequent stages: from asociality to protoschools and then to true equipotential schools. Having been formed, the schooling behavior may disappear and be formed again independently in different groups of teleosts.”

Jhawar *et al.* (2020) showed that schooling (highly polarized and coherent motion) is *statistical noise* induced, arising from the intrinsic stochasticity associated with finite numbers of interacting fish. The fewer the fish, the greater the multiplicative noise and therefore the likelihood of alignment.

At a more empirical level, observations of *Stolephorus commersonii* schooling behaviour demonstrates the positive and negative aspects of school formation. This anchovy species features in the diet of many predators, including juvenile reef-associated sharks (Heupel and Hueter 2002). However, this small anchovy (max. length: 10 cm) is not typically predated by the bull shark, *Carcharhinus leucas*, whose adult specimens do not feed on small prey (Werry *et al.* 2012). However, adult bull sharks, ranging between 2-4 m have been observed preying, at sunset, on anchovy schools, near the Mtsamboro’ Pass north of Mayotte, in the southwestern Indian Ocean (Pinault and Wickel 2014).

This unusual foraging pattern may be triggered by the defensive behaviour in the anchovy toward mackerel tuna, *Euthynnus affinis*. In response to mackerel tuna predation, the anchovy gathered into a compact school formation. Within this school, individual anchovies were virtually indistinguishable and the mackerel tuna seemed incapable of targeting an individual fish.

When this compact school took on the appearance of a single prey, it triggered the attack of the bull sharks which were uninterested in isolated anchovies. Successive attacks by predators continued until the anchovy school disappeared into deeper water. The shark attacks initially broke up the cohesion of the school, permitting the mackerel tuna to hunt isolated anchovies, which immediately reorganized themselves into one or more smaller schools.

This regrouping had the effect of triggering further shark attacks. This suggests that in ecosystems with complex biomass structure such as a coral reef, the hunting patterns of different species may be mutually

beneficial. It is common to refer to the interactions among species of high trophic levels as intra-guild predation (eating a potential competitor of a different species) (Arim and Marquet 2004); however, the win-win outcome interaction between predators is rarely discussed.

Another aspect of anchovy schooling behaviour is the potential to influence the waters in which they swim. Castro *et al.* (2022) have shown that spawning aggregations of the European anchovy (*Engraulis encrasicolus*) can generate high levels of turbulent dissipation, comparable to storms. Castro *et al.* (2022) state that this behaviour highlights the potential of biophysical turbulence to drive enhanced vertical exchanges in upper ocean areas with a rich biota, in which biomixing could contribute to the supply of nutrients, and the ventilation of deoxygenated waters, therefore promoting phytoplankton growth and reducing low-oxygen stress for higher trophic levels. Whether analogous processes occur from stolephorid anchovies schooling, either naturally for spawning, or from light attraction for fisheries, is unknown, but may be a fruitful avenue of investigation.

### Early life history

Most species in the genus *Encrasicholina* have eggs with an internal oil globule and are found both inshore and seaward. In contrast, the species in the genus *Stolephorus* have eggs without an oil globule, and with a knob at the animal pole; they are found mostly inshore.

The exception in terms of habitats in genus *Encrasicholina* is *E. punctifer*, which can be found at all stages of development in the open ocean (Ozawa and Tsukahara 1973, as *Stolephorus buccaneeri*). The collected *E. punctifer* larvae did not show strong morphological differences among 6 samples taken in samples across the area of study. Ozawa and Tsukahara (1973) concluded that *E. punctifer* probably inhabits and completes its life history both in oceanic and neritic waters throughout the whole West Pacific region.

### Ecology of the Buccaneer anchovy (*Encrasicholina punctifer*)

The ecology of the ocean or buccaneer anchovy (*E. punctifer*) is discussed in detail here because several studies have identified it as a key forage species for fish, especially tunas, diving seabirds, sharks, whales, and dolphins (Hida 1973; Ozawa and Tsukahara 1973). *E. punctifer* seems to be a keystone species in the epipelagic food chain in West-Central Pacific with its rapid growth and sexual maturity (at 3-5 months) and high abundance driven by episodic blooms of phytoplankton and copepod prey (Lehodey 2010).

It was thought that the ocean anchovy is widely distributed across the entire Indo-Pacific region. However, Hata and Motomura (2016a) have shown that the newly described *Encrasicholina intermedia* and *E. gloria* have been wrongly attributed to *E. punctifer*. *Encrasicholina intermedia* is currently known from the southeast coast of South and East Africa and the southwest coast of India. *E. gloria* is known only from the Arabian Gulf, Red Sea and the eastern Mediterranean through Lessepsian migration. *E. punctifer*'s distribution, though still extensive and incompletely described, appears to exclude the Indian Ocean, apart from waters in western Indonesia.

Hida (1973) documented the presence of *E. punctifer* (cited as *Stolephorus buccaneeri*) by stomach content analysis of tropical tunas and other epipelagic species across a broad expanse of the Pacific. The species was found to be common in the offshore waters of the Mariana, Palau, Caroline, Marshall, Samoa and Fiji Islands, and also in the offshore region of the eastern Pacific Ocean near Clipperton Island. The



survey noted an abundance of post-larval samples taken far offshore suggesting the species to be capable of completing its life cycle in the oceanic environment.

This assumption was confirmed by research cruises of the *R/V Shunyo-maru* that conducted larval fish sampling between Japan, New Guinea and across the central western Pacific to Tahiti (Ozawa and Tsukahara 1973). Larvae of the ocean anchovy were abundant at all sampling stations, making up 45% or more of fish larvae sampled, leading the authors to conclude that *E. punctifer* inhabits, spawns and can complete its life history in oceanic environments throughout the central and western Pacific region, as well as in neritic areas.

Previous to the Hida (1973) study, *E. punctifer* was reported mostly from open ocean waters across the Indo-Pacific region. This is now considered an artefact stemming from where sampling was more commonly conducted. This species is also widespread in inshore catches in many countries, and often including reproductively active adults (Ozawa and Tsukahara 1973). In addition, five years of pelagic trawl surveys in the tropical oceanic western Pacific targeting skipjack larvae found all stages of ocean anchovy to be widespread and highly abundant in surface waters during the day and night (Ogura *et al.* 1999).

This is important from an ecological perspective, as it confirms that the ocean anchovy (*E. punctifer*) is the only member of the *Encrasicholina* and *Stolephorus* genera and, apparently in the family Engraulidae, capable of completing its life cycle in the open ocean. Notably, shoals of *E. punctifer* were observed being pursued and fed upon by yellowfin and skipjack tuna that when sampled had digestive tracts filled exclusively with ocean anchovy (Ozawa and Tsukahara 1973). The ocean anchovy may play an important ecological role as a forage fish in the Indo-Pacific region and serve as a vital link between primary production, zooplankton and larger predatory fishes, such as tuna (Ozawa and Tsukahara 1973).

More recently, the importance of the ocean anchovy to the ecology of the tropical western and central Pacific Ocean has been recognized in the work of Lehodey *et al.* (2020). This has been accomplished by the development of forage-based models to predict skipjack tuna distribution and abundance and a spatial ecosystem and population dynamics platform (SEAPODYM) to model tuna populations (Lehodey *et al.* 1998, 2010, 2020).

This research identified the ocean anchovy as a primary forage species for tropical tuna and a key component of a short food chain based on nutrient enrichment by equatorial upwelling, episodic phytoplankton blooms, zooplankton production and a fast growth and early maturing (3-5 months) forage fish that is targeted by tuna (Lehodey *et al.* 2010). Salarpour *et al.* (2007) conducted a detailed study of the diet of *E. punctifer* in Qeshm Island, the Persian Gulf. This study showed that *E. punctifer* is a planktonivore, consuming a broad board spectrum of food types, but crustaceans dominated the food with copepods and their eggs, nauplii and semidigested copepods constituting 54% of the diet. The next major food groups found in the diet of the fish were blue-green algae, diatoms, fish eggs and scales and dinoflagellates. Table 13 contains a detailed summary of the *E. punctifer* (now *E. gloria*, see Table 3) in the Persian Gulf.

Intense feeding activity of tropical tuna on surface concentrations of ocean anchovy have been noted across the western Pacific (Hampton and Bailey 1993; Orlov 1995). Tuna schools engaged in this activity are termed 'boilers' or 'foamers' by fishers due to the frothing white appearance of the water caused by the feeding tuna (Scott 1969).

Purse seining for tuna in the equatorial central and western Pacific is conducted either on tuna schools found in association with floating objects (natural logs, flotsam, rafts, and Fish Aggregation Devices of FAD) or on so called 'unassociated' schools. In reality, these unassociated tuna schools are frequently associated with and actively feeding on large concentrations of the ocean anchovy (Itano 2000). The baitfish keep the tuna on the surface and distracted long enough for the fishing vessels to surround and close the purse seine to capture the school. *E. punctifer* plays an important role in the vulnerability of tropical tunas to purse seine gear in the tropical western Pacific region.

In a histological study on the reproductive biology of yellowfin tuna in the central and western Pacific, Itano (2000) noted a positive relationship between intense feeding activity of yellowfin tuna on large surface concentrations of forage fish and high reproductive rates for yellowfin tuna. Sampling of ovaries and stomach contents from the same tuna confirmed they were feeding almost exclusively on the ocean anchovy (*E. punctifer*).

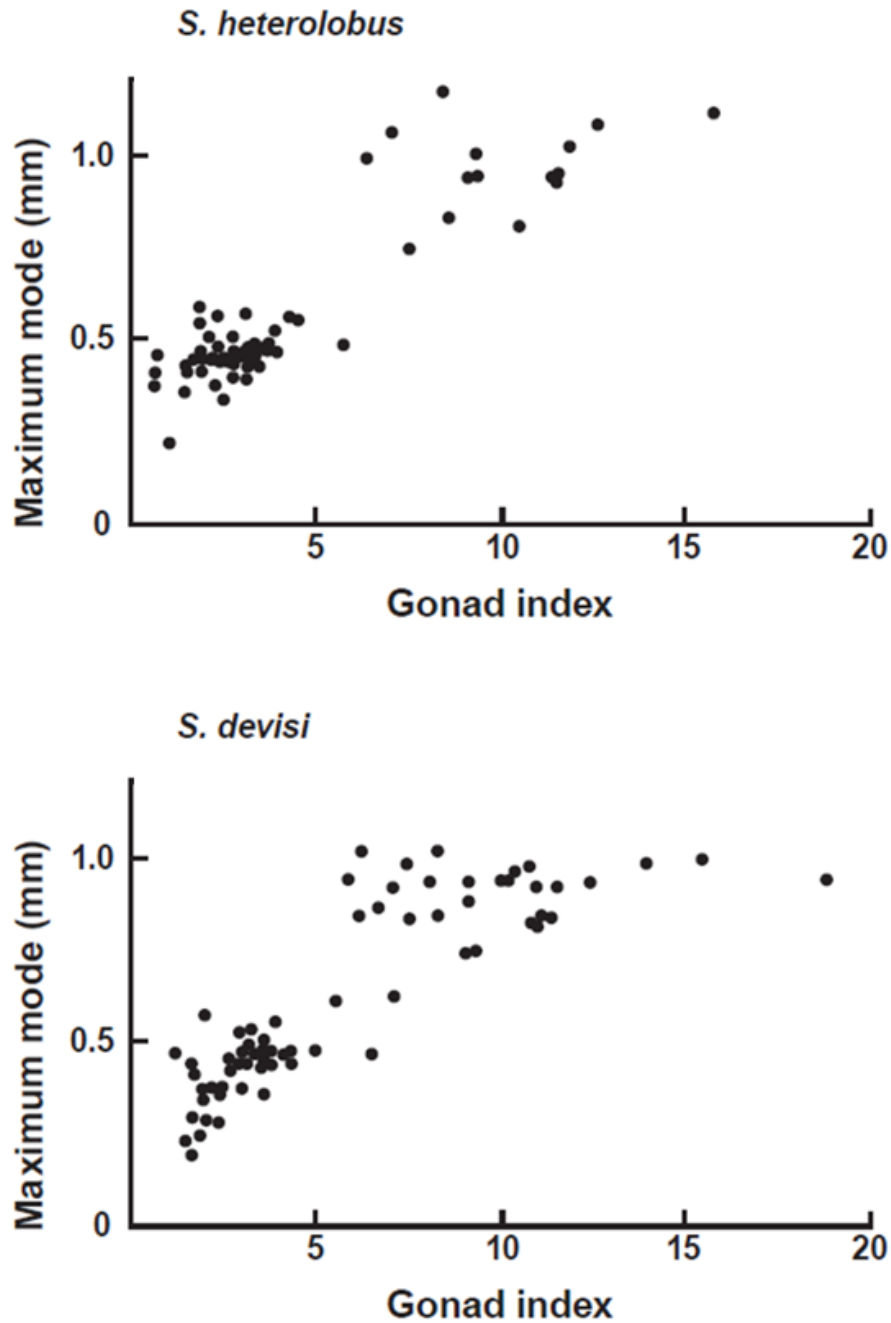
Histological analysis of ovary samples taken from tuna captured from these 'foaming' schools confirmed they were mature, reproductively active adults in active spawning condition. These findings were in sharp contrast to similar sized yellowfin sampled in the same study from deep-set longline gear that were often reproductively mature, but had regressed to a non-spawning stage. Itano (2000) suggested that discrete areas of elevated forage abundance that vary in time and space and between years could help to explain differences in proposed spawning areas and 'seasons' in this equatorial region (10 °N -10 °S, 120 °E – 150 °W) extending across 11,000 km and about 25 million km<sup>2</sup> of ocean.

The link between feeding on *E. punctifer* and spawning and also feeding on *E. punctifer* and vulnerability to purse seine gear are highly significant from an ecological and CPUE basis. In summary, *E. punctifer* is a very important baitfish species in the pelagic ecosystem. The congeners *E. gloria* and *E. intermedia* are likely just as important in the Indian Ocean.

### **Reproduction and spawning**

Table 12 summarizes the batch and absolute fecundities of stolephorid anchovies from various locations. Spawning periodicity and spawning seasons are discussed in the text. Maack and George (1999) studied *E. punctifer* in West Sumatra. They observed that encrasicholines are multiple spawners with asynchronous oocyte development. During one individual spawning season, oocyte development is a continuous process involving all stages of oocytes, clearly represented by a unimodal oocyte size-frequency distribution (OSFD).

Before spawning, a new batch of oocytes can be identified by its separation from the remaining oocytes, leaving a gap in the OSFD. Spawning can be confirmed by the presence of postovulatory follicles inside the ovary after ovulation. From a gonadosomatic index of 5.5 the ovaries contain hydrated oocytes, indicating a pre-spawning state. First maturity is reached at 57.5 mm and there is no relationship between fish condition and gonad weight. The necessary energy for the gonadal growth of the anchovies is not obtained from body fat, but most likely directly from its food. Dalzell (1987a) presented similar data for *E. heteroloba* and *E. devisi* in northern Papua New Guinea, where from a gonadosomatic index of about 5.0 (Figure 5), the ovaries contain hydrated oocytes, indicating a pre-spawning state.



**Figure 5.** Relationship between diameter of the most advanced mode of eggs in the ovary and gonad index for *S. heterolobus* (now *E. pseudoheteroloba*) and *S. devisi* (now *E. heteroloba*). Source: Dalzell (1987b)

In both instances, there is distinct separation of mature from maturing eggs. From these scatters, the minimum sizes at maturity of *E. heteroloba* and *E. devisi* in northern Papua New Guinea were 50 and 41 mm, respectively. Although histological methods have been used to describe the reproduction of stolephorid anchovies, it appears that there has been no application of these techniques to determine the mean size at first maturity ( $L_{50}$ ) or batch fecundities.

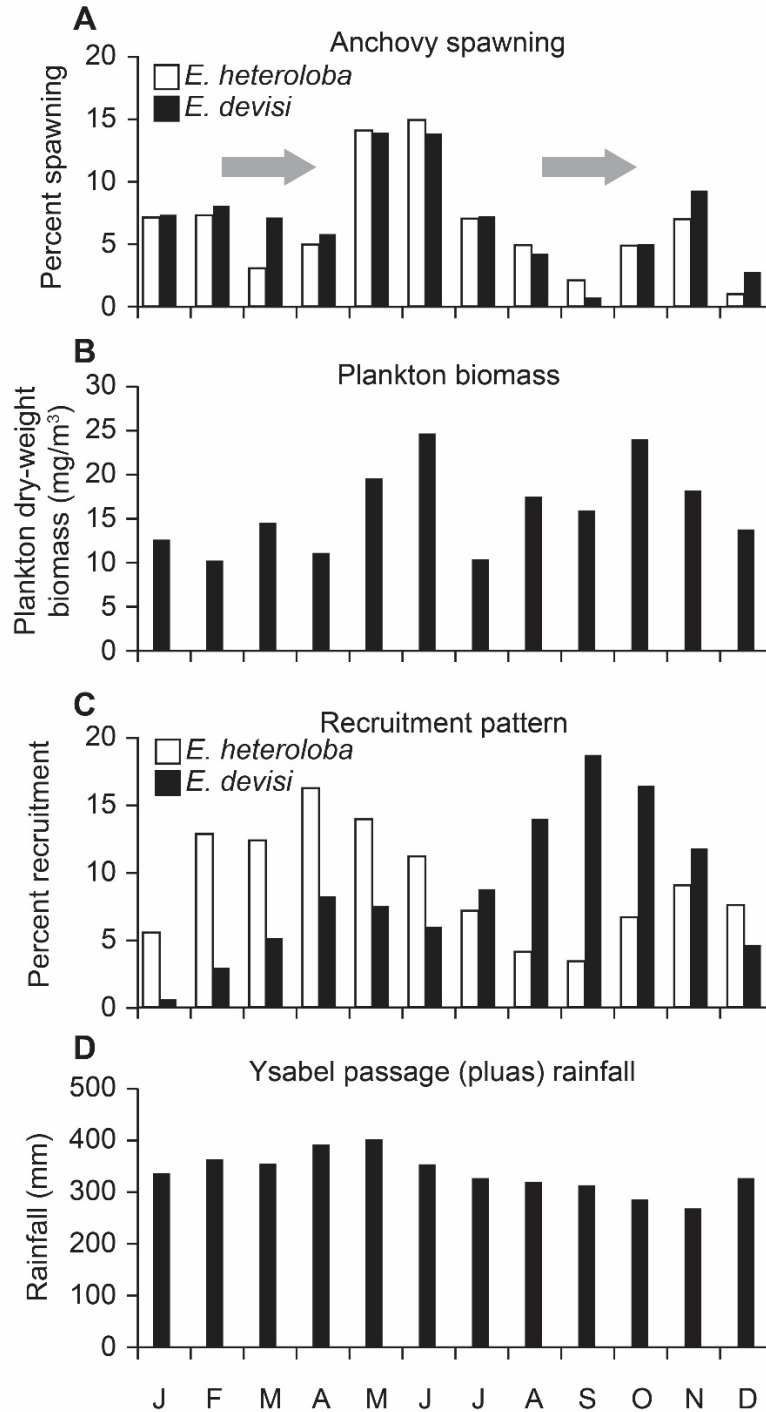
Dalzell (1987b) demonstrated that *E. heteroloba* and *E. devisi* had two peaks in spawning intensity; in May and June, and in October and November. These peaks coincide with the onset the Southeast Trade Winds in the middle of the year, and of the Northwest Monsoon towards the end of the year.

The timing of peak spawning coincides with peaks in total plankton abundance (Figure 6). Recruitment of successive cohorts also coincides with these spawning and plankton peaks, although the peak of recruitment in May/June is likely to be recruitment from the previous spawning in the Northwest Monsoon season. The fresh-water input to the Ysabel Passage is high all year round, but peaks in April/May and in December, and is likely to be the driving factor in the May/June spawning and plankton peaks, but less so for the October/November peaks, with a peak monthly rainfall in December (Figure 6).

The October/November spawning peak may be a response to upwelling or a decrease in stratification of Ysabel Passage waters as a result of the predominant Northwest Monsoon winds, driving plankton productivity in the latter half of the year. The recruitment patterns, generated from length frequency analysis show a separation of recruitment peaks between *E. heteroloba* (February to June) and *E. devisi* (August to November). These recruitment patterns may have evolved over time to minimize competition between recruits of these species.

The synchronicity of this biophysical system makes sense from an ecological perspective. However, the recruitment phase in particular, sometimes fails to match fishermen's expectations. In 1978 and 1979, *E. heteroloba* and *E. devisi* recruitment to the fishery occurred later than February/March, while the stock of adult *E. heteroloba* were reaching their maximum size and age, and declining in the fishery. The new recruits were too small to be effective as bait. Many juveniles slipped through the small 7 mm mesh of the *bouke-ami* net; those transferred to the bait wells were fragile and many died in the baitwells. In these circumstances, vessels tied up to the fleet mothership to wait until the new recruits grew and became large enough to be retained by the *bouke-ami* net and survive in the baitwells.

Wright (1990) observed that the percentage of *E. heteroloba* adults with mature gonads within monthly samples was positively correlated with the prevailing mean density of copepods off the northern coast of Indonesia at Jepara, on the north coast of Central Java. A comparison between prey abundance index and spawning frequency in months in which the incidence of females in samples was sufficient to estimate inter-spawning interval, which suggested that mean inter-spawning interval was inversely correlated with prey abundance. In summary to this section, anchovies benefit from enhanced productivity from equatorial or coastal upwelling or nutrient enrichment of coastal waters from rainfall and stream discharge. This enhanced productivity quickly converts to zooplankton such as copepods that are consumed by the anchovies. Enriched areas then fuel gonad development and reproduction (see Figure 6).



**Figure 6.** Anchovy spawning in the Ysabel Passage, Papua New Guinea and the influence of rainfall and plankton. Sources as follows, **A:** Mean of monthly percent spawning *E. heteroloba* (*E. pseudoheteroloba*), and *E. devisi* (*E. heteroloba*) in the Ysabel Passage, 1976-1985 (Dalzell 1983a). Solid arrow shows progression of anchovy recruitment from either mid-year spawning or last quarter spawning (from Dalzell 1993). Bars for January and February spawning are based on regression analysis of monthly percent spawning frequency versus rainfall. **B:** Mean of monthly plankton biomass in the Ysabel Passage (1980-1981) (Chapau 1983). **C:** Monthly recruitment pattern for *E. heteroloba* and *E. devisi* in the Ysabel Passage (based on ELEFAN, analysis of 1977 and 1978 length frequencies for this contribution). **D:** Mean monthly rainfall at the Ysabel Passage, 1978-1981 (Chapau 1983).

A cytological examination of the ovarian development revealed that *E. heteroloba* is a serial spawner (Wright 1990). This trait was associated with asynchronous spawning, both within the population, and the

different adult groups that comprised the spawning stock. The mean inter-spawning interval was estimated from the proportion of females with ovaries containing post-ovulatory follicles, and ranged between 2-14 days over the 21-month study period. Reproduction did not appear to involve the expenditure of somatic reserves, as neither relative condition nor biochemical composition varied significantly between pre- and post-spawned adults. Further, the high spawning frequency and egg batch biomass could only be explained by an energetic dependence on prevailing food availability. This reliance on prevailing prey availability was reflected in the significant correlations between prey density, and both the percentage and minimum length of sexually mature adults in monthly samples.

Milton *et al.* (1990a) included *E. heteroloba* in a study of the reproductive biology of tuna baitfish from Maldives and the Solomon Islands (*E. heteroloba*, *Spratelloides gracilis* and *S. delicatulus*). The reproductive biology of three major bait fish species was compared between Solomon Islands and Maldives. All species mature early and have a protracted spawning season in both countries. Fish in the Solomon Islands spawn throughout the year, with one or two more intense spawning periods. In the Maldives, *E. heteroloba* appeared to have a single spawning season within the atoll, and this may coincide with the May to December monsoon.

Length-weight relationships varied amongst sites within Solomon Islands, more than between countries. Milton *et al.* (1990a) showed that there were no differences in condition between baitfish populations from high islands and coral atolls. The sex ratio of *E. heteroloba* was biased towards males among small length classes. The proportion of females increased as length increased and large length classes were almost all females. This may explain the temporal pattern of sex ratios in this study and the bias towards males in most samples of *E. heteroloba*. Fecundity of baitfish from Solomon Islands and Maldives showed little intraspecific variation, except for *E. heteroloba* from Vona Vona, which had smaller eggs than fish from other sites, including the Maldives.

The necessary energy for gonad growth is not obtained from body fat, but most likely directly from food. The basic energy requirement is needed for swimming, body function, etc. and only a surplus of energy can be used for oocyte development. That means a change in prey density would have a direct influence on the fecundity of *Encrasicholina* species (Milton 1990a).

The high variability of the batch fecundity found for *E. punctifer* is similar to that of *E. heteroloba* (Dalzell, 1987b) and *E. purpurea* (Clarke, 1987). Clarke (1987) hypothesized that seasonal differences in fecundity could be explained by water temperature. The temperature in summer in the study area (Kaneohe Bay, Hawai'i) was 6-8°C higher than in winter. However, Clarke (1987) pointed out that there are no marked seasonal differences in macrozooplankton standing crop in Kaneohe Bay. Also, *nehu* feed almost exclusively at night and have a longer feeding period per diel cycle during the winter. Clarke speculated that the Kaneohe Bay water temperature is only about 5 °C and that the difference between summer maxima and winter minima may yet be possible that metabolic processes overall, and consequently both daily ration and reproductive output are slowed enough in winter to account for observed differences in volume of eggs and fecundity.

Wright (1989) suggested the availability of food as the main reason for regional and temporal differences of the batch fecundity in the genus *Encrasicholina*. Wright (1989) observed a spawning peak in *S. heterolobus*/*E. pseudoheteroloba* and *S. devisi*/*E. heteroloba* in Manila Bay during the south-west monsoon, while primary production was very high.

Clarke (1987) observed that one of the broader implications of these life history accounts is that, for tropical species, the time scale of sampling must be on the order of hours rather than weeks or days. The latter may be appropriate for investigation of species from higher latitudes, but would miss many events or stages in the reproductive cycle of Hawaiian nehu (*E. purpurea*). The likely incorrect conclusion of Leary *et al.* (1975) that *nehu* spawn only once per lifetime was in part based on the rarity of females with hydrated ova in their samples. This was almost certainly due to their not sampling during the short period between late afternoon and shortly after sunset when hydrated ova are found in the current night's spawners. Leary *et al.* (1975) stated that all females with hydrated ova were captured between 2100 and 2300 h, i.e., well after the peak of spawning even in summer.

This also has implications for the required sampling of baitfish catches every 10 days in Papua New Guinea, which might miss stolephorid anchovy spawning events between adjacent samples (Dalzell 1984b; Dalzell and Wankowski 1980). However, the prolonged periods of spawning were observed from the data, though this was due to luck rather than design. Nevertheless, sampling for tropical stolephorids needs to be conducted at a much shorter interval, perhaps 2-5 days, to have confidence in sampling to define important life history events.

**Table 12.** Batch and absolute fecundities of stolephorid anchovies from various locations in the Indo-Pacific. *Stolephorus heterolobus*, *S. devisi*, *S. buccaneeri* and *S. purpureus* are now *Encrasicholina pseudoheteroloba*, *E. heteroloba*, *E. punctifer* and *E. purpurea* respectively (See Table 3).

Species	Country/Territory	Relative fecundity (eggs/gram body weight)	Absolute fecundity (no. of eggs)	Source
<i>S. heterolobus</i>	Ysabel Pass PNG	592	374 to 2413	Dalzell (1990)
<i>S. heterolobus</i>	Palau	450	569 to 3020	Muller (1976)
<i>S. heterolobus</i>	Singapore	694	NA	Tham (1967)
<i>S. devisi</i>	Ysabel Pass PNG	1039	522 to 2513	Dalzell (1987a)
<i>S. punctifer</i>	Cape Lambert	875	781 to 6,237	Dalzell (1987a)
<i>S. waitei</i>	Ysabel Passage	224	943 to 1,516	Dalzell (1987a)
<i>S. purpureus</i>	Hawai'i	538	NA	Leary <i>et al.</i> (1975)
<i>S. heterolobus</i>	Munda SI	652	1,262	Milton <i>et al.</i> (1990a)
<i>S. heterolobus</i>	Vona Vona	901	1,850	Milton <i>et al.</i> (1990a)
<i>S. heterolobus</i>	Tulagi	695	1337	Milton <i>et al.</i> (1990a)
<i>S. heterolobus</i>	Maldives	653	2,243	Milton <i>et al.</i> (1990a)
<i>S. heterolobus</i>	New Caledonia	536	NA	Conand (1988)
<i>S. commersonii</i>	Tanzania	440 to 1449	47,029	Sululu <i>et al.</i> (2020)
<i>E. punctifer</i>	West Sumatra, Indonesia	985	-	Maack and George (1999)
<i>E. devisi</i>	Mangalore	523	1,700 to 6,790	Rao (1988a)
<i>E. devisi</i>	Tulagi	710	1423	Milton <i>et al.</i> (1990a)
<i>E. heteroloba</i>	Lizard Is Australia	912	1,925	Hoedt (1994)
<i>S. waitei</i>	Mangalore, India	-	3,580 to 24,180	Mohanty <i>et al.</i> (2005)
<i>E. punctifer</i>	West Sumatra	985	-	Maack (1997)
<i>E. devisi</i>	Bima Bay, Indonesia	1,578	1,698	Andamari <i>et al.</i> (2002)
<i>E. heteroloba</i>	Bima Bay, Indonesia	654	2,629	Andamari <i>et al.</i> (2002)
<i>E. punctifer</i>	Bima Bay, Indonesia	2,228	1,153	Andamari <i>et al.</i> (2002)
<i>S. commersonii</i>	Bima Bay, Indonesia	1,984	261	Andamari <i>et al.</i> (2002)
<i>S. indicus</i>	Bima Bay, Indonesia	186	1,573	Andamari <i>et al.</i> (2002)
<i>E. devisi</i>	Southern India	-	1,698 to 6,785	Luther <i>et al.</i> (1992)
<i>S. waitei</i>	Southern India	-	303 to 4,812	Luther <i>et al.</i> (1992)
<i>S. heterolobus</i>	Gulf of Thailand	-	2,000 to 4,000	Saikliang and Boonragsa (1997)
<i>S. indicus</i>	Thoothukudi Coast, India	-	970 to 6084	Patadiya <i>et al.</i> (2018)

In *Encrasicholina*, fecundity was positively correlated with water temperature and zooplankton density, whereas in *Spratelloides* it was correlated with the hepatosomatic index (Milton *et al.* 1995). These results strengthen the hypothesis that fecundity of *Encrasicholina* is directly related to food intake, while *Spratelloides* may depend on energy reserves in the liver for spawning. A comparative study of sardines, anchovies, and sprats showed intra-seasonal variation of batch fecundity is large and more pronounced than interannual variation (Alheit 1989).

The review by Beverton (1963) of clupeids and engraulids showed that the length of clupeoids at first reproduction ( $L_m$ ) was proportional to their asymptotic length ( $L_\infty$ ) - but see Pauly (1984, 2021).



In a multiple spawning fish with asynchronous oocyte development, histological analysis is necessary to distinguish developing ovaries from those which finished the individual spawning season and are regressing and to differentiate maturing ovaries from those which are already partially spent. The contemporary occurrence of postovulatory follicles and vitellogenic oocytes together in one ovary indicates that the studied species is a batch spawner. The high proportion of reproductively active females, their presence over the whole study time, and the demonstrated oocyte-size-frequency-distribution (OSFM) of females indicate that *E. punctifer* is an indeterminate batch spawner. An extended spawning period of several months, or during the whole year, with possible bimodal intensity, is a characteristic of an indeterminate serial spawning fish (George 1998). According to Hunter *et al.* (1992) multiple spawning fish are called 'indeterminate serial' or 'batch spawners,' if the annual fecundity is not fixed at the beginning of spawning and the standing stock of present oocytes in the ovary is continuously replaced by new developing oocytes during one spawning cycle. Any time of the year, a particular fraction of the anchovies are able to spawn.

A constant biotic environment is necessary for this ability, which is the case in tropical coastal waters off West Sumatra (Maack and George 1999) Serial spawners produce more eggs than a total spawner of comparable size. Small fish like anchovies usually do not have enough space in the body cavity necessary to contain the total amount of oocytes produced per year at the same time. The hydration of the oocytes has to be divided into portions (Lozan 1985).

Additional knowledge about spawning grounds is important to quantify the effect of variation in prey density to spawning biomass and indirectly to recruitment. Tzeng and Wang (1992) found spawning areas for *E. punctifer* in a mangrove estuary in Taiwan. Their study indicated that the standing stock of *E. punctifer* is affected not only by the fishery impact, but also by the human utilization of the mangrove estuaries, and variation in prey density.

Rao (1988a, 1988b) described the reproductive biology of *Encrasicholina devisi* and *Stolephorus bataviensis* caught by purse seiners and trawlers in Mangalore waters of India. *E. devisi* attains first maturity at a length of 62 mm. The major spawning is from October to February. Juveniles are found from February to May, and fecundity estimates are positively correlated to fish length. A steep fall in condition factor at 62 mm coincides with the length at first maturity. The low values for condition factor values beyond the length at first maturity appears to be due to the protracted spawning season of this species.

Rao (1988b) observed that *S. bataviensis* reaches a length of 77 mm at six months and 101 mm at the end of one year. The sexes are uniformly distributed over most of the study period. The length at first maturity is estimated as 77 mm. The major spawning period is from November to March, however mature fish are found throughout the year. Juveniles are abundant from April to June. Fecundity estimates are poorly correlated to the total length of the species. The condition factor fluctuated beyond the length at first maturity may be due to protracted spawning season of the species.

In Sri Lanka, Navarathne and Disanyake (2016) studied the coastal waters off Negombo, Sri Lanka, and the biology of *E. heteroloba* at Negombo and Kuttiduwa fish landing sites. Reproductive activity was assessed using macroscopic and microscopic observations of gonad characteristics, trends of gonad indices, size at first sexual maturity and differences in the monthly sex ratio. The sex ratio of *E. heteroloba*

population fluctuated seasonally, and a significantly high male to female sex ratio was observed in April, May, June, October, and November.

The fishery, reproductive biology and the gillnet selectivity pattern of *E. heteroloba* were assessed using the data collected from the Negombo fish landing site on the west coast of Sri Lanka (Navarathne and Disanyake 2016). *E. heteroloba* are mainly exploited using drift gillnets of 1.1 cm, 1.2 cm, and 1.8 cm stretched mesh sizes. Females spawn throughout the year with a peak spawning reported in July.

The sizes at first sexual maturity of *E. heteroloba* male and female are 7.40 cm and 7.45 cm, respectively. The gillnet selectivity study revealed that the optimum length ( $L_{opt}$ ) and selection range of *E. heteroloba* varied with mesh sizes and estimated  $L_{opt}$  for 1.0 cm, 1.2 cm, and 1.8 cm mesh sizes were 5.6 cm, 6.4 cm, and 9.2 cm, respectively. The study concluded that the use of 1.8 cm mesh gill nets should be promoted, as a higher percentage of immature individuals are landed when smaller mesh (<1.2 cm) gill nets are used.

*Encrasicholina punctifer* is one of the dominant small pelagics and economically most important fishes of the Arabian Gulf, especially in Qeshm Island's coastal waters. Reproductive studies showed that the maturity season of the fish occurs in August and the length at first maturity of 84 mm (Salarpouri *et al.* 2007).<sup>4</sup>

### Food and Feeding Behavior

Summaries of the food of seven species of stolephorid anchovies are shown in Table 13. The seven species span a geographic range from the Middle East to the South Pacific. Crustaceans are the primary food of the stolephorids, especially copepods. Care should be exercised in drawing too much from comparisons of the spectrum of food items found in these stolephorid anchovies. Some studies were part of larger studies on the biology and ecology of species of stolephorid anchovies, while others were directed at their trophic ecology. There are methodological differences and differences in the duration of observations between these various studies. Nonetheless, it clear that stolephorids are zooplankton feeders and copepods are one of the most important food items.

Suspension feeding generally involves the generation of water currents that carry small food particles (such as bacteria, protists, microalgae) towards the mouth. Bornbusch and Lee (1992) made a detailed study of the mouth parts of several anchovy genera, including *Coilia*, *Lycotrissa*, *Setipinna*, *Thryssa*, *Stolephorus*, *Encrasicholina*, and *Papuengraulis* using scanning electron microscopy. They concluded that, jointly with gut contents analyses, their results indicate that the coiliids, *Stolephorus* and

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<sup>4</sup> Scientists at the NOAA Pacific Islands Fisheries Science Center based in Hawai'i have completed an opportunistic ichthyoplankton survey in 2023 spanning the EEZ of the Hawaiian Archipelago from Hōlanikū (Kure Atoll) through Hawai'i Island. At the time of this writing, several subsamples from this effort have been examined, with preliminary findings of relevance to this chapter in that large numbers of larval pelagic anchovy (*Encrasicholina punctifer*) were observed at survey stations spanning the western main Hawaiian Islands (O'ahu and Kaua'i) through much of the Papahānaumokuākea Marine National Monument. Schools of baitfish were observed from the ship but could not be sampled to verify species identification. Further sample processing and results from eDNA samples should prove enlightening in identifying relative larval densities of *E. punctifer* and their environmental associations throughout this survey. In similar context, anecdotal observations from pelagic fishers in the main Hawaiian Islands in 2023 have also included mention of large schools of baitfish, presumably *E. punctifer*, in nearshore pelagic areas. *Encrasicholina punctifer* does not regularly occur in Hawaii's waters, and larval *E. punctifer* have been relatively uncommon or absent in previous ichthyoplankton surveys, suggesting that the 2023 observations indicate a bloom of anchovy abundance in that year. Point of contact for this work is Dr. Justin Suca, Cooperative Institute for Marine and Atmospheric Research at the University of Hawai'i at Mānoa, working with NOAA scientists at the Pacific Islands Fisheries Science Center. Additional text is provided in Appendix A

*Encrasicolina* are not suspension feeders. Engrauloids for which data reliably indicate a suspension-feeding behavior include *Engraulis* (Leong and O'Connell 1969), *Cetengraulis mysticetus* (Bayliff 1964), and *Anchovia surinamensis* (Sousa *et al.* 2022). Non-suspension feeding clupeiforms actively seek out prey, rather than non-selectively filtering prey. Indeed, members of the genus *Thryssa*, most notably *T. baelama*, were observed to actively feeding on larval and juvenile stolephorids from baitfish samples collected in Papua New Guinea (P. Dalzell, pers. obs.), and may consume even larger prey.

With respect to inter-species competition for food, the distributional ranges of Cape anchovy, *Engraulis encrasicolus/capensis*, and Natal anchovy, *Stolephorus holodon*, presently overlap at their eastern and western extremes, respectively, off South Africa's east coast. Horton and van der Lingen (2019) suggested that they might become more strongly sympatric as a consequence of changed distributions caused by climate change, possibly leading to intensified interspecific competition for trophic and other resources. A comparative analysis of the trophodynamics of the two species demonstrated that interspecific competitive release between the two engraulids is facilitated through differential branchial-basket morphology, which allows size-based resource partitioning and mitigation against interspecific competition (Egan *et al.* 2017, 2018; Hajisame and Ibrahim 2008; Horinouchi *et al.* 2012).

On a broader scale Egan *et al.* (2017, 2018), looked at the biotic and abiotic forces that govern the evolution of trophic niches, which profoundly impact ecological and evolutionary processes and aspects of species biology. The diets and trophic guilds of small fishes from Taiwan's marine sandy beaches and estuaries (including *S. indicus* and *S. insularis*) showed that copepods were the most frequently identified item in fish guts, indicating they are key prey for the fish assemblages studied. Piscivore, crustacivore, detritivore, omnivore, zooplanktivore, and terrestrial invertivore trophic guilds were identified. The zooplanktivore guild contained the most fish species. Maximum prey size consumption was positively correlated with standard length in seven species and at the assemblage level and negatively correlated with standard length in a single detritivorous species.

Egan *et al.* (2018) investigated trophic niche evolution in Clupeoidei (anchovies, sardines, herrings, and their relatives). This most comprehensive phylogenetic hypothesis for Clupeoidei contains 153 of approximately 400 clupeoid species (Bloom and Lovejoy 2014). The study, investigated the evolution of herbivory and associations between herbivory and habitat in clupeoid fishes. This was accomplished by using an updated molecular dataset to reconstruct a new clupeoid phylogeny with more representative sampling of Indo-Pacific trophic diversity. This phylogeny was used to estimate the history of trophic niche evolution in clupeoids and test the hypotheses that herbivory is negatively correlated with salinity and latitude.

**Table 13.** Summary of the food items consumed by the most abundant and commonest stolephorid anchovies in Southeast and South Asia, and the South Pacific.

Species	Location	Food items and seasonal feeding cycles	Source
<i>Stolephorus indicus</i>	Singapore	Feeds on <i>Coscinodiscus</i> diatoms, polychaetes, small squids, and a wide range of crustaceans from copepods to decapod larvae, as well as fish larvae. Feeds heavily on <i>Leptochela</i> shrimp and calanids. Occasional heavy feeding on mysids, <i>Acetes</i> , <i>Squilla</i> larvae, brachyuran zoea and megalopa, as well as stolephorid larvae has been observed for <i>S. indicus</i> . <i>Lucifer</i> , <i>Porcellana</i> larvae, and other decapod larvae have been found occasionally in small numbers in the food.	Tham (1950) Tham (1953)
<i>S. indicus</i>	Kerala Coast, India	<i>Leptochela</i> appears to be the main food, while ostracods, <i>Cypris</i> larvae, calanids, mysids, brachyuran zoea, and <i>Stolephorus</i> larvae comprise subsidiary foods.	Gopal <i>et al.</i> (2018)
<i>S. insularis</i>	Singapore	Crustaceans, including copepods, lucifers, mysids, <i>Acetes</i> , and amphipods. Other preferred prey items were molluscs (bivalves and gastropods), small fishes, tintinnids, and dinoflagellates. Uniform feeding preferences with copepods being the preferred food item throughout the three climatic seasons. Indicated that the abundance of the prey items reflected a stable potential fishery and ecosystem.	Tham (1950) Tham (1953)
<i>S. commersonii</i>	South Andaman Sea	<i>S. commersonii</i> feeds chiefly on planktonic crustaceans, bivalves, gastropods, and other miscellaneous food items. The copepods formed the main prey item, contributing to between 24-48% of the diet. Smaller fish fed mainly on planktonic copepods and amphipods, whereas the larger fish fed mainly on post-larval shrimps and planktonic crustaceans like <i>Lucifer</i> spp. and <i>Acetes</i> spp.	Kumar <i>et al.</i> (2015)
<i>Encrasicholina punctifer</i> (now <i>E. gloria</i> with more gillrakers)	Arabian Gulf	Diet dominated by copepods and their eggs, nauplius, and semi-digested copepods constituting 54% of the diet. The next major food groups found in the diet of this fish were Cyanophyceae 21%, Bacillariophyceae 11%, fish egg and scale 6%, Dinophyceae 4%, with Euglenahycaeae, Chlorophyta, dinoflagellates, and other items comprising only 4% of the diet. Monthly variation in the stomach fullness indicated that feeding intensity fluctuated throughout the year, with the highest value in winter.	Salarpouri <i>et al.</i> (2007)
<i>Stolephorus heterolobus</i> (now <i>E. pseudoheteroloba</i> ; see Tables 3 and 4)	Papua New Guinea	In Papua New Guinea, <i>E. heterolobus</i> fed mainly on three plankton groups, which accounted for 88.5% of its diet. These were copepods 45.2%, pericardians 21.9%, and decapods 21.4%.	Chapau (1983)
<i>S. heterolobus</i> (now <i>E. pseudoheteroloba</i> ; See Table 3)	Singapore	Calanoid copepods always dominate the food of <i>S. heterolobus</i> , and <i>Leptochela</i> to a lesser extent, in Singapore Straits. Phytoplankton was also common in its food, especially in the smaller specimens up to 40 mm in length. However, only the diatoms of the various <i>Coscinodiscus</i> spp., are recognizable. <i>S. heterolobus</i> over 50 mm in length have been found to feed on polychaetes, mysids, <i>Squilla</i> larvae, <i>Lucifer</i> shrimps, brachyuran, and other decapod larvae, as well as stolephorid larvae.	Tham (1950) Tham (1953)
<i>S. heterolobus</i> (now <i>E. pseudoheteroloba</i> ; See Table 3)	Jakarta Bay	The food of <i>E. heterolobus</i> consisted mainly of zooplankton; however, phytoplankton such as <i>Coscinodiscus</i> and dinoflagellates were occasionally observed. Some other food items such as fish eggs and molluscs were periodically abundant for a limited period of time.	Burhanuddin <i>et al.</i> (1975)
<i>Stolephorus devisi</i> (now <i>E. heteroloba</i> ; see Table 3)	Papua New Guinea	In northern PNG, <i>S. devisi</i> fed mainly on two components of the plankton, namely copepods and decapods, collectively accounting for 88.9% of its diet, and individually 53.6% and 35.3% respectively of its diet.	Chapau (1983)
<i>E. devisi</i> (see above) (now <i>E. heteroloba</i> ; see Table 3)	Jakarta Bay	The food of this species is similar to that of <i>E. heterolobus</i> . Fragments of crustacea and copepods dominated the food items. The phytoplankton were also found in small quantities, and consisted of <i>Coscinodiscus</i> and dinoflagellates.	Burhanuddin <i>et al.</i> (1975)

## Age and Growth

Fitting growth curves to modal progressions has so far proved to be the most common way to estimate von Bertalanffy growth function (VBGF). The von Bertalanffy growth function (VBGF) takes the following form for length:

$$L_t = L_\infty(1 - e^{-K(t-t_0)})$$

where length at time  $t$  ( $L_t$ ) is a function of the asymptotic length ( $L_\infty$ ) and the growth parameter  $K$  is a measure of how fast asymptotic length is approached, while the difference between  $t = 0$  and  $t_0$  anchors the growth curve origin on the x-axis.

Tham (1966) used modal progression analysis to fit von Bertalanffy age at length curves to three stolephorids, using a fitting technique developed by Gulland and Holt (1959). The results for these growth curves are shown in Table 14. Burhanuddin *et al.* (1975) used similar techniques to estimate the VBGF's parameters for three stolephorid species in Jakarta Bay (see Table 3).

In the early 1970s, the potential for ageing fish through daily growth increments of the otoliths or ear stones was recognized (Pannella 1971, 1974). Daily increments were used to age *E. purpureus* in Hawai'i (Struhsaker and Uchiyama 1976). However, no VBGF was fitted to the data. At about the same time, Muller (1976) analysed length data for *Stolephorus heterolobus* (*E. pseudoheteroloba*, see Table 3) using length frequencies processed through a computer program that separated out the modes in polymodal length frequency data. A verification of the growth parameters obtained from modal progression analysis was made by counting presumed daily growth increments in the otoliths of ten *E. pseudoheteroloba*.

Larval *Encrasicholina purpurea* (*nehu*) exhibited exponential growth to a length of about 15-17 mm. At about 20 mm, the population enters an almost linear growth phase to about 60 mm. According to Struhsaker and Uchiyama (1976), the major inflection in *nehu* growth rate at about 17 mm reflects that this species begins to exhibit exponential growth in body depth at this size. Thus, much growth of individual *nehu* is directed to allometric growth of body depth, rather than body length.

From the early 1980s, the ELEFAN stock assessment package became available to determine age and growth parameters, mortalities, and recruitment patterns from length-frequency data (Pauly 1987).

Dalzell (1984b, 1990) analysed data for *E. heteroloba*, *E. devisi*, and *S. waitei* from three tuna baitfishing locations in Papua New Guinea; Ysabel Passage, Cape Lambert, and Fairfax Harbour. Two examples of ELEFAN outputs, redrawn for the purposes of this contribution, are shown in Figure 7. The first example shows the growth of two cohorts at Ysabel Passage, through seven consecutive months of 1972. A larger analysis in Figure 7 shows data for six cohorts moving through the fishery. The gap in the middle of the data set is a combination of a fishing season that typically closed in December and reopened in February/March. This was due to the Okinawan pole-and-line boats returning to Japan during a period of typically unfavorable weather and sea conditions for catching tuna.

In order to compare growth in fishes and invertebrates whose growth described by the VBGF, comparison of growth performance is facilitated by an index developed by Pauly and Munro (1984), for the comparison of growth curves,  $\varphi'$ , defined as:

$$\varphi' = 2 \cdot \log(L_\infty) + \log(K)$$

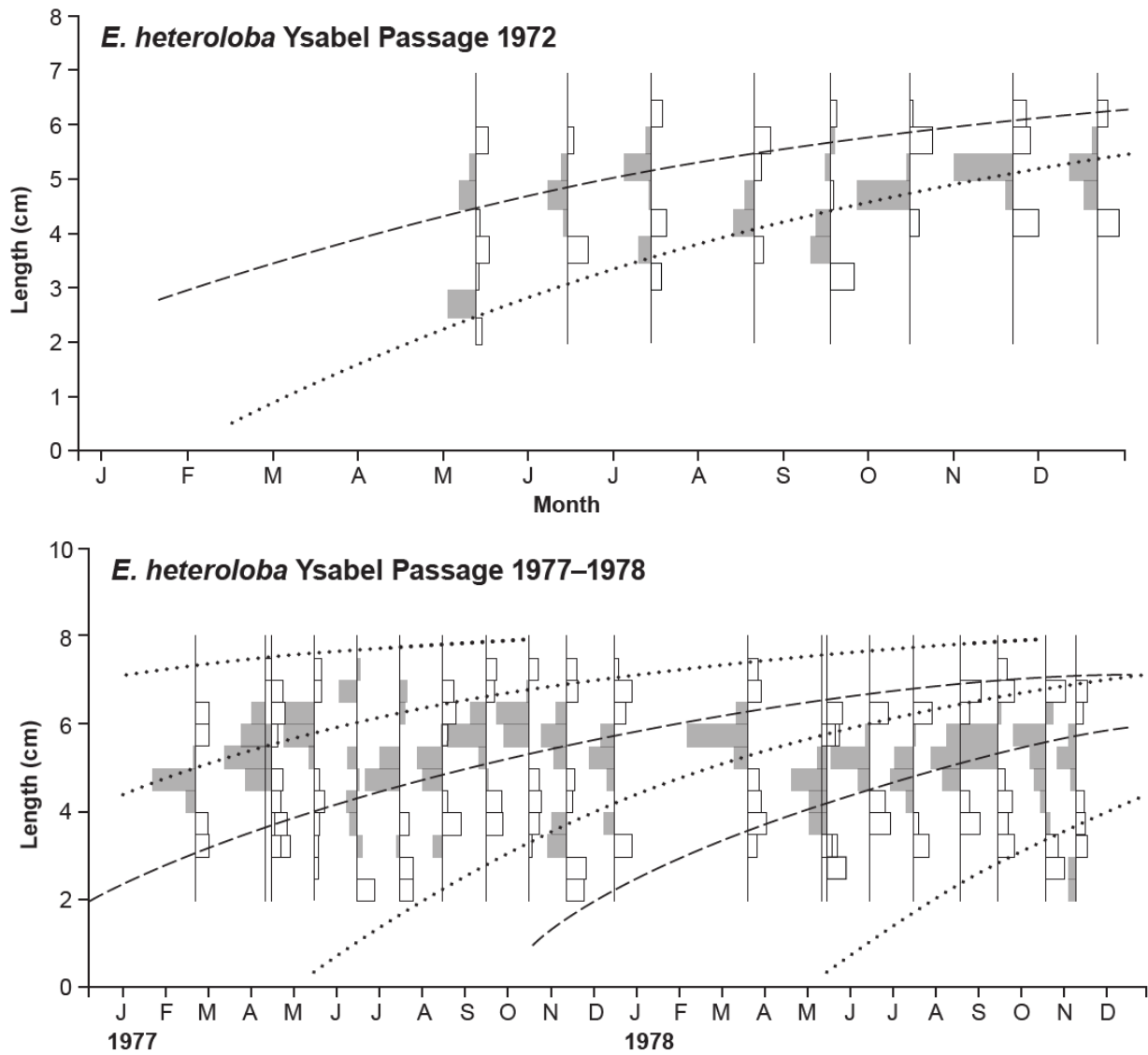
A frequency plot of  $\phi'$  (Figure 7) values based on 94 examples in Table 14 shows that most of the  $\phi'$  values for stolephorid anchovies are tightly clustered between values of 2.25 and 2.5 and a mean of 2.34 (standard error  $\pm$  0.670). The online database, FishBase ([www.fishbase.org](http://www.fishbase.org)) has 312 engraulid species primarily from tropical and sub-tropical locations in nine genera (*Thryssa*, *Stolephorus*, *Setipinna*, *Lycengraulis*, *Engraulis*, *Enchrasicholina*, *Coilia*, *Centengraulis*, and *Anchoa*) with a mean of 2.23 (standard error  $\pm$  0.431). Values which fall outside the estimates of  $\phi'$  for a given taxon may suggest that the corresponding growth parameters may be erroneous.

**Table 14.** A summary of von Bertalanffy growth parameters for stolephorid anchovies in the Indo-Pacific.

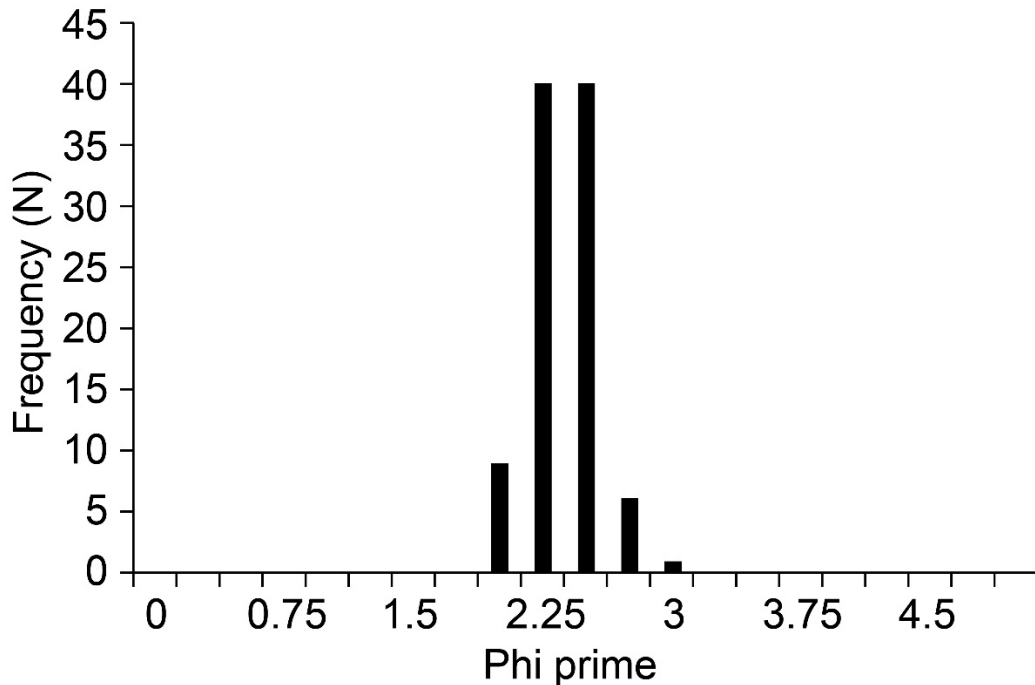
Species Names	Location	K (year <sup>-1</sup> )	L <sub>∞</sub> (cm)	Φ'	Source
<i>Encrasicholina heteroloba</i>	Ysabel Passage, PNG	2.60	7.90	2.21	Dalzell (1990)
<i>E. heteroloba</i>	Cape Lambert, PNG	2.40	8.70	2.26	Dalzell (1990)
<i>E. devisi</i>	Ysabel Passage, PNG	2.10	7.40	2.06	Dalzell (1990)
<i>E. devisi</i>	Cape Lambert, PNG	2.40	7.40	2.12	Dalzell (1990)
<i>E. devisi</i>	Fairfax Harbour, PNG	2.00	7.80	2.09	Dalzell (1990)
<i>Stolephorus waitei</i>	Fairfax Harbour, PNG	1.70	10.9	2.31	Dalzell (1990)
<i>S. commersonii</i>	Manila Bay, Philippines	0.96	11.3	2.09	Ingles and Pauly (1984)
<i>E. heteroloba</i>	Manila Bay, Philippines	1.60	12.1	2.37	Ingles and Pauly (1984)
<i>E. heteroloba</i>	Manila Bay, Philippines	0.95	11.4	2.09	Ingles and Pauly (1984)
<i>S. indicus</i>	Manila Bay, Philippines	1.42	16.3	2.58	Ingles and Pauly (1984)
<i>S. indicus</i>	Manila Bay, Philippines	1.08	15.7	1.26	Ingles and Pauly (1984)
<i>E. punctifer</i>	Manila Bay, Philippines	1.10	10.1	2.05	Ingles and Pauly (1984)
<i>E. punctifer</i>	Manila Bay, Philippines	1.85	10.6	2.32	Ingles and Pauly (1984)
<i>E. punctifer</i>	Manila Bay, Philippines	1.15	9.2	1.99	Ingles and Pauly (1984)
<i>E. punctifer</i>	Manila Bay, Philippines	1.08	15.7	2.43	Ingles and Pauly (1984)
<i>E. punctifer</i>	Manila Bay, Philippines	1.10	10.1	2.05	Ingles and Pauly (1984)
<i>E. punctifer</i>	Manila Bay, Philippines	1.85	10.6	2.32	Ingles and Pauly (1984)
<i>E. punctifer</i>	Manila Bay, Philippines	1.15	9.2	1.99	Ingles and Pauly (1984)
<i>E. heteroloba</i>	Jakarta Bay, Indonesia	2.40	9.7	2.35	Burhanuddin <i>et al.</i> (1975)
<i>S. insularis</i>	Jakarta Bay, Indonesia	1.66	8.6	2.09	Burhanuddin <i>et al.</i> (1975)
<i>E. devisi</i>	Jakarta Bay, Indonesia	3.35	8.80	2.41	Burhanuddin <i>et al.</i> (1975)
<i>E. heteroloba</i>	Jepara, Indonesia	1.17	9.80	2.05	Wright <i>et al.</i> (1990)
<i>E. heteroloba</i>	Jepara, Indonesia	2.12	9.80	2.31	Wright <i>et al.</i> (1990)
<i>E. heteroloba</i>	Palau	2.08	9.80	2.30	Muller (1976)
<i>S. nelsoni</i>	Northern Australia	2.10	9.70	2.30	Hoedt (2002)
<i>S. nelsoni</i>	Northern Australia	2.16	10.5	2.38	Hoedt (2002)
<i>E. heteroloba</i>	Munda, Solomon Islands	2.40	8.20	2.21	Tiroba <i>et al.</i> (1990)
<i>E. heteroloba</i>	Munda, Solomon Islands	2.40	8.20	2.21	Tiroba <i>et al.</i> (1990)
<i>E. heteroloba</i>	Munda, Solomon Islands	2.40	8.15	2.20	Tiroba <i>et al.</i> (1990)
<i>E. heteroloba</i>	Munda, Solomon Islands	2.40	8.15	2.20	Tiroba <i>et al.</i> (1990)
<i>E. heteroloba</i>	Munda, Solomon Islands	2.40	8.15	2.20	Tiroba <i>et al.</i> (1990)
<i>E. heteroloba</i>	Vona Vona, Solomon Is.	2.10	8.1	2.14	Tiroba <i>et al.</i> (1990)
<i>E. heteroloba</i>	Vona Vona Solomon Is.	2.10	8.1	2.14	Tiroba <i>et al.</i> (1990)
<i>E. heteroloba</i>	Vona Vona Solomon Is.	2.10	8.05	2.13	Tiroba <i>et al.</i> (1990)
<i>E. heteroloba</i>	Vona Vona Solomon Is.	2.00	8.05	2.11	Tiroba <i>et al.</i> (1990)
<i>E. heteroloba</i>	Vona Vona, Solomon Is.	2	8.0	4.11	Tiroba <i>et al.</i> (1990)
<i>E. heteroloba</i>	Tulagi, Solomon Islands	3	8.3	2.32	Tiroba <i>et al.</i> (1990)
<i>E. heteroloba</i>	Tulagi, Solomon Islands	3	8.3	2.32	Tiroba <i>et al.</i> (1990)
<i>E. devisi</i>	Tulagi, Solomon Islands	3.1	8.1	2.31	Tiroba <i>et al.</i> (1990)
<i>E. devisi</i>	Munda, Solomon Islands	2.3	7	2.05	Milton <i>et al.</i> (1990b)
<i>E. devisi</i>	Munda, Solomon Islands	2.3	7	2.05	Milton <i>et al.</i> (1990b)
<i>E. devisi</i>	Munda, Solomon Islands	2	7	1.99	Milton <i>et al.</i> (1990b)
<i>E. devisi</i>	Munda, Solomon Islands	2	7	1.99	Milton <i>et al.</i> (1990b)
<i>E. devisi</i>	Munda, Solomon Islands	2.2	7.3	2.07	Milton <i>et al.</i> (1990b)
<i>E. devisi</i>	Munda, Solomon Islands	2.2	7.3	2.07	Milton <i>et al.</i> (1990b)
<i>E. devisi</i>	Vona Vona, Solomon Is.	2	7.5	2.05	Milton <i>et al.</i> (1990b)
<i>E. devisi</i>	Vona Vona, Solomon Is.	2	7.5	2.05	Milton <i>et al.</i> (1990b)
<i>E. devisi</i>	Vona Vona, Solomon Is.	2	6.7	1.95	Milton <i>et al.</i> (1990b)
<i>E. devisi</i>	Vona Vona, Solomon Is.	2	6.7	1.95	Milton <i>et al.</i> (1990b)
<i>E. devisi</i>	Vona Vona, Solomon Is.	2	6.7	1.95	Milton <i>et al.</i> (1990b)
<i>E. devisi</i>	Tulagi, Solomon Islands	2.2	7.8	2.13	Milton <i>et al.</i> (1990b)
<i>E. devisi</i>	Tulagi, Solomon Islands	2.2	7.8	2.13	Milton <i>et al.</i> (1990b)
<i>E. devisi</i>	Tulagi, Solomon Islands	2.2	7.4	2.08	Milton <i>et al.</i> (1990b)
<i>E. devisi</i>	Tulagi, Solomon Islands	2.2	7.4	2.08	Milton <i>et al.</i> (1990b)
<i>E. devisi</i>	Tulagi, Solomon Islands	2.3	7.5	2.11	Milton <i>et al.</i> (1990b)
<i>E. heteroloba</i>	Kien Giang, Vietnam	4.38	9.4	2.59	Pham (2022)
<i>E. devisi</i>	Mangalore, India	2	11.3	2.41	Luther (1990)
<i>E. devisi</i>	Visakhapatnam, India	1.8	10.1	2.26	Luther (1990)
<i>S. waitei</i>	Mangalore, India	1.97	11.6	2.42	Luther (1990)
<i>S. waitei</i>	India Visakhapatnam	1.56	13.4	4.45	Luther (1990)
<i>E. devisi</i>	India East Coast	1.60	10.4	2.24	Gopakumar and Pillai (2000)
<i>E. devisi</i>	India West Coast	1.60	10.4	2.24	Gopakumar and Pillai (2000)
<i>S. waitei</i>	India East Coast	1.20	13.5	2.34	Gopakumar and Pillai (2000)
<i>S. waitei</i>	India West Coast	1.40	13.0	2.37	Gopakumar and Pillai (2000)
<i>E. devisi</i>	Kutai Kartanegara, Indonesia	1.3	13	2.34	Juliani <i>et al.</i> (2019)
<i>E. devisi</i>	Kei Islands, Indonesia	0.74	8.9	1.77	Supeni and Dobo (2017)
<i>S. indicus</i>	Peninsula Malaysia	-	16	2.39	Mohsin and Ambak (1996)
<i>E. heteroloba</i>	Dumbea, New Caledonia	4.8	10.7	2.74	Conand (1988)

Species Names	Location	K (year <sup>-1</sup> )	L <sub>∞</sub> (cm)	Φ'	Source
<i>E. heteroloba</i>	Dumbea, New Caledonia	3.7	10.7	2.63	Conand (1988)
<i>E. heteroloba</i>	Dumbea, New Caledonia	4.5	11	2.74	Conand (1988)
<i>E. punctifer</i>	Philippines, Sibuyan Sea	1.1	11.3	2.15	Bayate <i>et al.</i> (2018)
<i>E. punctifer</i>	Taiwan	2.32	17.6	2.86	Huang <i>et al.</i> (2018)
<i>E. punctifer</i>	Arabian Gulf and Oman Sea	1.4	11.5	2.27	Salarpouri <i>et al.</i> (2007)
<i>E. heteroloba</i>	Singapore Straits	2.1	8.9	2.22	Tham (1967)
<i>S. insularis</i>	Singapore Straits	2.1	9.9	2.31	Tham (1967)
<i>S. indicus</i>	Singapore Straits	0.71	19	2.41	Tham (1967)
<i>E. heteroloba</i>	Gulf of Thailand	1.81	10.54	2.30	Supongpan <i>et al.</i> (2000)
<i>S. baganesis</i>	Selangor, Malaysia	1.39	8	1.95	Supongpan <i>et al.</i> (2000)
<i>E. devisi</i>	Mercedes, Philippines	1.45	10.2	2.18	Dalzell (1988)
<i>E. heteroloba</i>	Zamboanga Philippines	1.5	12.7	2.38	Dalzell (1988)
<i>E. heteroloba</i>	Mercedes Philippines	1.51	10.15	2.19	Dalzell (1988)
<i>E. heteroloba</i>	Dalahican Philippines	1.65	11.8	2.36	Dalzell (1988)
<i>E. heteroloba</i>	Silay Philippines	1.56	11.5	2.31	Dalzell (1988)
<i>E. heteroloba</i>	Silay Philippines	1.71	11.5	2.35	Dalzell (1988)
<i>E. punctifer</i>	Zamboanga Philippines	1.65	11.7	2.35	Dalzell (1988)
<i>E. punctifer</i>	Dalahican Philippines	1.47	11.9	2.32	Dalzell (1988)
<i>E. punctifer</i>	Dalahican Philippines	1.42	11.8	2.30	Dalzell (1988)
<i>S. waitei</i>	Mercedes, Philippines	1.29	13	2.34	Dalzell (1988)
<i>E. heteroloba</i>	SW Vietnam	1.82	8.6	2.13	Pham (2022)
<i>S. commersonii</i>	SW India	0.98	15.4	2.39	Nair <i>et al.</i> (2021)
<i>E. devisi</i>	W. India	2.04	11.3	2.42	Doddamani <i>et al.</i> (2002)
<i>E. devisi</i>	Mangalore, India	1.10	12.2	2.21	Rohit and Gupta (2008)
<i>E. punctifer</i>	Mangalore, India	1.60	11.8	2.35	Rohit and Gupta (2008)
<i>S. waitei</i>	Mangalore, India	1.10	12.2	2.21	Rohit and Gupta (2008)





**Figure 7.** Growth curves for *Encrasicholina heteroloba*, from the Ysabel Passage (PNG), as generated by ELEFAN. The top panel is from 1972 showing the progression of a cohort (dotted line) and remnants of an older cohort (dashed line). The bottom panel shows the progression of six cohorts in 1977 and 1978. Estimates of curve parameters are shown in Table 14.



**Figure 7.** Frequency distribution of phi prime ( $\phi'$ ) estimates for stolephorid anchovies with a mode between 2.25 and 2.5 (Source: Table 14).

Milton *et al.* (1990b) conducted observations on daily micro-increments in sagittal otoliths of *Stolephorus heterolobus* (*E. pseudoheteroloba*) and parallel analysis of length frequencies with ELEFAN.

Observations were conducted from sites in the Solomon Islands and the Maldives, where stolephorid anchovies are used for tuna baitfish in pole-and-line fisheries. Milton *et al.* (1990b). also conducted validation experiments to demonstrate the daily deposition of micro-increments, but were unable to obtain meaningful results for *E. pseudoheteroloba*.

Milton *et al.* (1990b) observed that growth curves for *E. pseudoheteroloba* derived from otolith micro-increment counts were not inconsistent with those inferred from a length-frequency analysis using ELEFAN. Nevertheless, *E. pseudoheteroloba* appear to have maximum lifespans of 9-10 months and the VBGFs have growth constants (K) of 2.08-2.6 year<sup>-1</sup> (see Table 14). Various authors (Struhsaker and Uchiyama 1976; Milton *et al.* 1990b; Dalzell 1990) have noted that age and growth of stolephorids is variable between locations, which would indicate that extension of age and growth to other areas beyond the study sites should be conducted cautiously.

Results using otolith micro-increments and length frequency analysis to determine age and growth of stolephorids have been variable, confounded by difficulties in interpreting microincrement structure. However, Hoedt (1990) developed growth curves for *Stolephorus nelsoni*, including counts of otolith micro-increments in the sagittal otolith and length frequency data collected in 1984, 1988 and 1989. Calculated values of K and L<sub>∞</sub> were 2.16 year<sup>-1</sup> and 105 mm for the otolith derived growth curve. These compared favourably with mean values of K = 2.1 year<sup>-1</sup> and L<sub>∞</sub> = 97.3 mm obtained from length frequency data. This study suggests that otolith increments provide a useful estimate of age in days for adult *Stolephorus nelsoni*.

Gøjsaeter *et al.* (1976) examined otoliths from *Stolephorus* spp. from the Arabian Gulf. The otoliths were difficult to read because they appeared to contain two kinds of zonation; narrow increments, 2-4 micrometers thick, but there were also broader, more diffuse increments with thickness of 6-10 micrometers. From 1 to 5 of the narrow increments could be counted within the broader rings. If the thinner increments were daily, they would predict a growth rate considerably slower than the estimated growth of the species reported in the literature. If, instead, the thicker increments were daily, the growth would be similar to or a little faster than *E. heteroloba* and *E. pseudoheteroloba* from the Western Central Pacific and the Eastern Indian Ocean.

Despite the difficulty in reading stolephorid anchovy otolith micro-increments without extensive grinding and polishing, Dalzell and Wankowski (1980) were able to make counts of two adult *E. heteroloba* (*E. pseudoheteroloba*) specimens, and eleven juvenile stolephorids from the Ysabel Passage. This limited data indicated that juvenile stolephorids of about 20 mm in length were about 30 days old. An adult specimen of *E. heteroloba* of about 60 mm was 90 days old.

Ageing stolephorids still poses challenges, including interpreting large and small increments in otoliths (Wright 1990; Milton *et al.* 1990b; Hoedt 1990). The smaller increments in the otoliths appear to be deposited daily and have been validated using otolith marking techniques and ancillary studies using length frequency distributions (Milton *et al.* 1990b). Wright (1990) suggests that additional studies be conducted by scanning electronic microscopy to achieve accurate counts of the very thin rings on the otolith margin. Nevertheless, older fish often possess extremely narrow rings which can lead to underestimates of the true age of the fish (Morales-Nin 1992).

### **Morbidity and Mortality**

Morbidity (*sensu stricto*) is the condition of suffering from a disease or other pathological condition. Few studies have been conducted on morbidity in stolephorid anchovies, and those that have focused on external and internal parasites.

Schäperclaus (1986) reported a case of infection by lernaeid copepods. Bennet and Chellam (1979) observed *Pteroderma tasselum* parasitizing *Stolephorus commersonii* from Tuticorin, southeast coast of India. Rajkumar *et al.* (2006) reported on a double parasitism by crustacean parasites, namely a copepod (*Lernaeenicus sprattae*) and an isopod (*Nerocila phaiopleura*) on *S. commersonii* from the coastal waters of Tamil Nadu, India. The female of a copepod parasite, (*Peroderma tasselum*) was found on *S. commersonii* from Tuticorin, on the southeast coast of India.

An examination of parasites obtained from 2,511 specimens of 6 species of anchovies, i.e., *Stolephorus heterolobus*, *S. devisi*, *S. chinensis*, *S. indicus*, *S. bataviensis*, and *S. baganensis* from the inner and western coast of the Gulf of Thailand during January 1989 to December 1989 was conducted by Premkit (1999). Several parasites were found, which comprised 3 species of copepod, 1 species of nematode and 3 species of trematode. Six species of internal parasites comprised 2 species of nematode and 4 species of digenetic trematode. The predominant species were flukes, *Hemiurus* spp., found in 86.4 % of the stolephorids. The highest overall abundance of parasites was observed from March to June.

A single external copepod parasite was observed on a stolephorid anchovy during the collection of over 100,000 specimens of fish from the Ysabel Passage between 1973 and 1985 (Dalzell, unpublished data), suggesting that external copepod infestations of stolephorids may be rare.

The agents of natural mortality, other than senescence and illness, are the other range of marine biota that prey on stolephorid anchovies. Andamari *et al.* (2002) estimated that *Encrasicholina* species hatch between 15 and 24 hours after spawning at Bacan, Indonesia. Iwata *et al.* (2017) describe in detail the feeding of Bryde's whales in the upper reaches of the Gulf of Thailand, where waters at shallow depths are hypoxic, and anchovies are restricted to the oxygenated layers near the surface. The Bryde's whales take advantage of the restricted distribution of the anchovies and prey on them by widely opening their mouths and causing ingress of water and anchovies. Cetaceans are often seen actively feeding on schools of *E. punctifer* in the tropical western Pacific Ocean as observed by purse seine fishers pursuing tuna schools also feeding on the anchovies. These associations are described in Hampton and Bailey (1993). Predation by cetaceans on stolephorid anchovies has been observed by purse seiners in the tropical western Pacific Ocean (Hampton and Bailey 1993). Blaber *et al.* (1990) recorded that a range of species preyed on stolephorid anchovies, mostly larger pelagics consisting of scads, jacks, coastal scombrids, as well as snappers, barracudas, and slipmouths (Leiognathidae).

Stolephorid anchovies are important prey for many species of seabirds (Major 1978; Blaber *et al.* 1990; Muzaffar *et al.* 2017). For example, the Indian anchovy *Stolephorus indicus* was a predominant prey species of the brown booby, *Sula leucogaster*, from Northwestern Australia (Cannell *et al.* 2022). In New Caledonia, the black noddy (*Anous minutus*) ate small pelagic fishes inhabiting the reef and the lagoon, mainly round herrings (*Spratelloides* spp.), while the brown noddy (*Anous stolidus*) mainly preyed on offshore species including buccaneer anchovy (*Encrasicholina punctifer*), pelagic fishes (Exocoetidae) and squid (Villard *et al.* 2015).

Muzaffar *et al.* (2017) observed the inter-annual variation in the diet of the Socotra cormorant, *Phalacrocorax nigrogularis*, whereby *Encrasicholina* spp. were the dominant prey item in a given year, while the gold spot herring *Herklotsichthys quadrimaculatus* or flying fish, *Parexocoetus mento*, predominated in other years.

Predation of stolephorid anchovies by cetaceans, fish, seabirds and other predators, coupled with the short life span of stolephorid anchovies, results in high rates of natural mortality for these anchovy species. Species with high natural mortality rates tend to be resilient to the imposition of additional mortality through fishing (Beverton and Holt 1957).

A typical approach to measuring fishery impacts is to measure the annual total mortality rate ( $Z$ ) and then partition this into natural ( $M$ ) and fishing ( $F$ ) mortality rates. (Beverton and Holt 1957; Ricker 1975) Fishery impacts can be ascertained from the ratio of  $F/Z$ , i.e., the exploitation rate ( $E$ ). In the past, a common fishery management target reference point has been that a stock is at the maximum sustainable yield (MSY) when fishing mortality is equal to natural mortality or  $E = 0.5 = F/Z$ . Patterson (1992) observed that long-term management targets based on MSY are inappropriate for small pelagic fish because of the possibility of stock collapse due to impaired recruitment at low biomasses. Rather, Patterson suggested that pelagic stocks appeared to be in equilibrium at an exploitation rate  $F/Z = 0.4$ , which may be used as a guideline for the appropriate exploitation of pelagic stocks (Gulland 1983), though more elaborate guidelines have been elaborated since (Pikitch *et al.* 2012).

Estimating natural mortality ( $M$ ) may be problematic if a stock of fish has been fished for decades and in some cases centuries and millennia (Dalzell 1998). Natural mortality is one of the most influential quantities in fisheries stock assessment and management. The magnitude of natural mortality relates

directly to the productivity of the stock, the yields that can be obtained, as well as optimal exploitation rates, management quantities, and reference points (Beverton and Holt 1957; Jørgensen and Holt 2012). It is generally accepted that natural mortality is very high during the larval stages, and decreases as the age of the fish increases (Figure 8), approaching a low, steady rate (Jennings and Beverton 1991). The rate then increases when the fish nears maximum age. Natural mortality may also vary with size, sex, parasite load, density, food availability, and predator numbers. There is, however, a variety of empirical models available for estimating the instantaneous natural mortality. Vetter (1998) published a review of those methods, and Siegfried and Sansó (2014) reviewed the methods available to estimate natural mortality since Vetter's review.

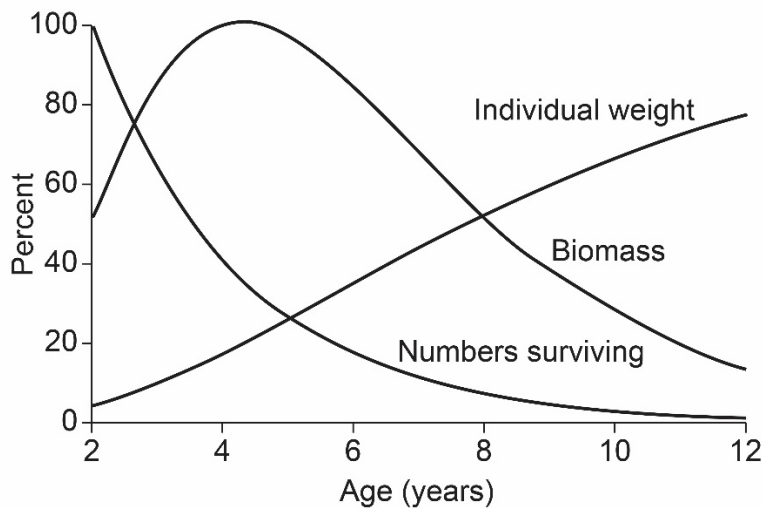
Pauly (1980) showed that  $M$  in fish was related to the constants,  $L_{\infty}$  (in cm) and  $K$  ( $\text{year}^{-1}$ ) from the von Bertalanffy growth function (VBGF) and ambient water temperature ( $T$  in  $^{\circ}\text{C}$ ):

$$\log M = -0.0152 - 0.279 \cdot \log L_{\infty} + 0.6543 \cdot \log K + 0.463 \cdot \log T$$

Hoening (1993) showed that total mortality ( $Z$ ;  $\text{year}^{-1}$ ) was related to the maximum age ( $t_{\max}$ ; year) in fish, cetacean, and mollusc populations. The generalized form of the model is as follows:

$$\ln(Z) = 1.44 - 0.987 \cdot \ln t_{\max}$$

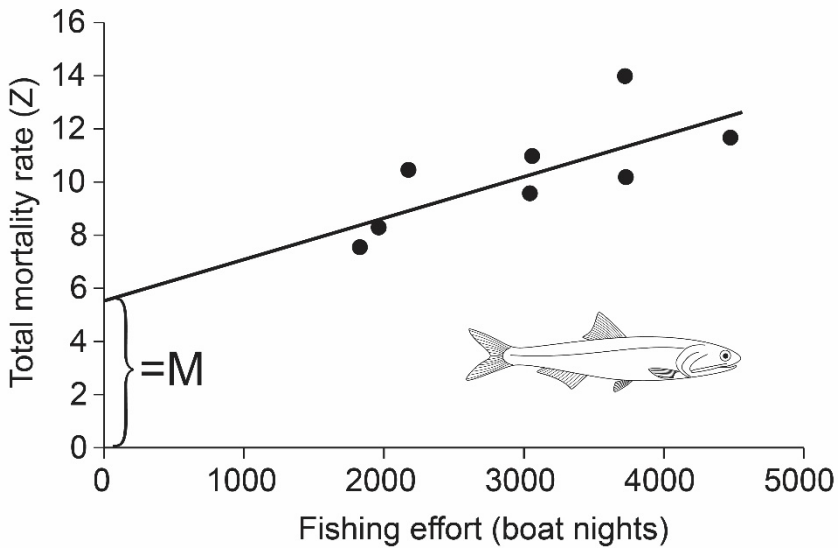
Table 15 lists data from three baitgrounds in Papua New Guinea used to generate  $M$ ; from plots of eight years of data on  $Z$  and fishing effort ( $f$ ) in the Ysabel Passage (Figure 9), from simultaneous equations for Cape Lambert where only two years of data was available, and from a previously unfished stock in Fairfax Harbour.



**Figure 8.** Simplified graphical model of factors influencing fish population in terms of growth, survivorship, and biomass. Adapted from King (2007). Perusal of the literature for other studies on stolephorid anchovy life histories and population dynamics (see Table 14)

**Table 15.** Derivation of natural mortality rates for *E. heteroloba* and *E. devisi* in Papua New Guinea. M1 is derived by method outlined in Table 14; M2 derived from Pauly's 1980 method. See Table 3 for up-to-date nomenclature.

Location	Species	Method	M <sub>1</sub>	M <sub>2</sub>	Catchability (q)
Ysabel Passage	<i>E. heteroloba</i>	Regression analysis of annual Z on f	5.5	5.8	0.0015
Ysabel Passage	<i>E. devisi</i>	Regression analysis of annual Z on f	4.4	7.0	0.0007
Cape Lambert	<i>E. heteroloba</i>	Simultaneous equations	4.6	6.2	0.0007
Cape Lambert	<i>E. devisi</i>	Simultaneous equations	4.8	7.4	0.0011
Fairfax Harbor	<i>E. devisi</i>	Unfished stock	4.4	7.5	N.A.



**Figure 9.** An example of total mortality plotted against annual fishing effort for *E. heteroloba* (= *E. pseudoheteroloba*) in The Ysabel Passage, Papua New Guinea. Source: Dalzell (1984b, 1986)

Pauly (1980) presented his empirical equation for estimating natural mortality method, it has been the subject of several critical studies. Then *et al.* (2015) evaluated the predictive performance of empirical estimators of natural mortality rate using information on over 200 fish species. The study recommended the use of the updated Hoenig's estimator where:

$$M \approx 4.9 \cdot t_{\max}^{-0.92}$$

when maximum age ( $t_{\max}$ ) is available. Where age is not available, the study recommended the simplified Pauly estimator.

$$M \approx 4.1K^{-0.73}L_{\infty}^{-0.33}$$

Pauly's 1980 method included average water temperature (T) in the equation. However, it has been claimed that the effects of temperature in predicting M may be taxon-specific (Griffiths and Harrod 2007).

### Stock and Recruitment

A proportion of the anchovies removed in a fishery are sexually mature adults and hence potential spawners. Two general stock-recruitment models were formulated by Ricker (1954) and Beverton and Holt (1957), which considered recruitment as a density-dependent function of the parent stock size. Muller (1976) fitted a Ricker model to stock and recruitment data for *E. heteroloba* from Palau. The fit of the model was improved by adding a term in the model for rainfall. Muller (1976) observed that rainfall can wash potential nutrients for primary production in the form of leaf litter and other decaying vegetation, accumulated bird droppings or guano, and leached phosphate from the limestone rock into the lagoon. This nutrient enrichment is reflected in the zooplankton abundance. As noted elsewhere in this review, the role of allochthonous fresh water for stolephorid anchovy and biomass spawning and recruitment cannot be overstated.

Dalzell (1984b) fitted Beverton and Holt and Ricker models for *E. heteroloba* and *E. devisi* from the Ysabel Passage. A linear rather than curvilinear model gave the best fit to the data. This was not surprising as Cushing (1971) suggested that near-linear relationship between parental stock size and the magnitude of recruitment was probably the most applicable for clupeoid fishes. It follows from this that the lack of a density-dependent relationship in the stolephorid anchovy stocks indicates that they and other clupeoids have little capacity for stabilizing their populations, unlike longer-lived fish such as the gadoids. The strong fluctuations in the stolephorid anchovy stocks from year to year may then be explained partly by their high vulnerability to both adverse environmental conditions and fishing pressure, which directly affects recruitment.

It has been demonstrated that recruitment can be predicted from knowledge of the parental stock size and the biomass of predators in aquaculture and natural systems (Pauly 1980, 1982; Hopkins *et al.* 1982). Dalzell (1984b) developed a series of linear predictive models for *E. heteroloba* and *E. devisi* stock and recruitment at the Ysabel Passage. The inclusion of *S. gracilis* in the model for the anchovies was thought to be particularly important, given that over 30% of the diet of *S. gracilis* comprises fish eggs (Chapau 1983). Further, both anchovies and round herrings have been found in the stomachs of other small pelagic species, namely *Rastrelliger kanagurta* and *Thryssa balaema* (Dalzell 1984a).

Milton *et al.* (1996) studied the temporal and spatial patterns of recruitment of the anchovies *Encrasicholina devisi* and *Encrasicholina heterolobus*, and the round herrings or sprats, *Spratelloides delicatulus*, *Spratelloides gracilis*, and *Spratelloides lewisi*. Milton *et al.* (1996) conducted *in-situ* research in the Solomon Islands and Maldives, and used the data included in Dalzell (1984a and b, 1986).

At all sites all species recruited throughout the year. There was no difference between months in the proportion of recruits in the fished population of any species at any site. The relative abundance of recruits of *E. devisi*, *E. heterolobus*, *S. delicatulus*, and *S. gracilis* between 1984 and 1989 was examined at Munda and Tulagi in the Solomon Islands.

There were no detectable differences between months or sites for any species, although the interannual variability in recruitment in some months was quite high. Both the relative abundance of recruits and variation in recruitment of both *Encrasicholina* species were correlated at both sites (Milton *et al.* 1996). Adult stock size was the most important factor that explained variation in recruitment two months later and accounted for between 30 and 85% of the variation in recruitment of each species at the two sites. Environmental factors such as zooplankton biomass, wind or monthly rainfall, were not correlated with recruitment of any species at either site.

Nor was predation by adults an important source of egg or larval mortality. All species preyed on *Encrasicholina* eggs and larvae at some time during the year and *Encrasicholina* species were the most important predators at both sites. However, unlike some temperate clupeoids, these species ate less than 1% of the estimated daily egg production each month during the study.

Overall, there was little variation in recruitment of *Encrasicholina* or *Spratelloides* species. Most of the monthly estimates of the relative abundance of recruits of each species did not differ from the long-term mean at each site by more than an order of magnitude. Milton *et al.* (1996) hypothesized that lower variability in recruitment of these tropical clupeoids compared with temperate clupeoids results from a combination of their multiple-spawning reproductive strategy, rapid growth and early recruitment. For these species, pre-recruit mortality appears to be relatively constant.

Finally, as Beverton (1990) observed, fisheries for small pelagics should be managed by direct conservation of an adequate spawning stock, neither catch nor fishing effort alone being reliable indicators, and by taking timely and, if necessary, drastic action to that end.

## **Ecological and Social Impacts of fisheries catching *Encrasicholina* and *Stolephorus* anchovies**

### **Ecological impacts**

Tuna fisheries and their bait catch is of specific interest here, given that several fleets, Palau, Papua New Guinea, and the Solomon Islands catch or caught predominantly *Encrasicholina* and *Stolephorus* anchovies. As noted earlier these anchovies are considered the best tuna baitfish in relation to low post-capture mortality and favourable behaviour when chummed (Smith 1977). *Encrasicholina heteroloba*/*E. pseudoheteroloba* and *E. devisi*/*E. heteroloba* were unrivalled in importance in Papua New Guinea. Both species are active swimmers with a tendency to return and school close to tuna vessels. However, tension may develop between fisheries for live bait for tuna fisheries and food fisheries such as in eastern Indonesia.

Rocliffe (2012) has summarized bait fisheries for tuna fisheries around the globe and their potential ecological and social impacts. These include a reduction in the amount of forage available for the larger piscivorous species on which subsistence and commercial fisheries depend, incidental and deliberate capture of juveniles and of species targeted by artisanal fisheries, overexploitation of live baitfish fisheries and conflict between bait fishers and local communities exploiting the same resource. Several of these



impacts have already been covered in this paper. Further, an earlier review of Pacific Islands bait fisheries conducted by Lewis *et al.* (1983) concluded that it seemed unlikely that bait fisheries are having any significant impact on coastal fisheries in island states. Lewis *et al.* (1983) also noted that in Fiji many of the important baitfishes are unknown to coastal fishermen and have no local names, which is evidence that they are not directly fished or targeted.

With respect to ecosystem impacts, small pelagic fishes are generally found in coastal marine ecosystems, and are particularly abundant in upwelling regions, although they can range several hundred kilometres offshore (Dalzell and Ganaden 1987). Such ecosystems are often characterised as ‘wasp-waist’ systems (Rice 1995). That is to say that while lower and upper trophic levels typically comprise a large number and diversity of species, the intermediate level is rather different. There is often a crucial intermediate trophic level, occupied by small, plankton-feeding pelagic fish dominated by one or a few schooling species.

Their massive populations may vary radically in size under intensive exploitation (Cury *et al.* 2000). They have been shown to exert top-down control on their prey species and bottom-up control on their predators and, in this way, appear to induce unsuspected ecosystem dynamics impacts (Shannon *et al.* 2009).

Studies in Eastern Indonesia provided data for a trophodynamic Ecopath/Ecosim ecosystem model of the Raja Ampat archipelago on the west coast of New Guinea (Ainsworth *et al.* 2008). Among other issues, the authors evaluate the exploitation status of stolephorid and other anchovies, and tuna, and report on the ecosystem effects of these fisheries. Located mainly in coastal areas adjacent to the central upwelling region of Dampier Strait, a large anchovy fishery is conducted in Raja Ampat by mobile lift nets (*bagan*) fleet in which paired vessels use lanterns at night to attract fish. Ainsworth *et al.* (2008) suggest that anchovies provide an ecosystem service: a large anchovy population may buffer fluctuations in large pelagic fish biomass under climate variation. Anchovies are only moderately exploited in Raja Ampat. Eliminating the fishery for them would cause their biomass to increase close to the unexploited level,  $B_0$ , which is 11% higher than the current stock size. There will be negligible changes in the biomass of predators like birds and pelagic fish, but there may be a beneficial stabilizing effect on fisheries for more valuable large pelagic fish. If a limited fishery is allowed, at or below current exploitation rates, the stock will remain safe from recruitment overfishing and it will be more resilient to climate variation than under a  $F_{MSY}$  policy. The multi-species optimal fishing effort lies near  $F_{0.1}$  as defined by Gulland and Boerema (1973).

An increase in fishing effort beyond this will reduce total income from pelagic resources; a large increase would cause a noticeable decline in bird and piscivore populations.

Blaber *et al.* (1990) examined the diets of lagoon fishes of the Solomon Islands. The objective of the study was to evaluate the impacts of the bait fishery on baitfish predators and on subsistence reef fishing by Solomon Islanders. The authors concluded that most of the fish caught by Solomon Islanders subsistence fishery do not eat baitfish. However, some pelagic species, mainly Scombridae, are baitfish predators, caught by trolling. Unless there is a marked increase in trolling among subsistence fishermen, there is little evidence that the commercial baitfishery at present directly affects the food chain on which the subsistence reef fishery depends (Blaber 1990).

## **Social Impacts**

Social and economic issues of baitfisheries and food fisheries for stolephorid anchovies include tourist and dive enterprises asserting that baitfishing depleted some of the more colourful reef species (Huang and Coelho 2017). Further, fisheries for stolephorid anchovies and other species are conducted entirely in the inshore coastal zone, which can create tension between the fisheries and local communities (Lewis 1990). The areas that produce stolephorid anchovies are in lagoons and bays frequently have village communities living along the margins. In some locations in the Pacific Islands, pole-and line tuna fleets and tuna canneries have been built to process domestically caught tuna or tuna shipped in from reefer vessels from tuna fisheries across the Western Pacific.

Several Pacific Island countries have canneries, including Papua New Guinea, Solomon Islands, Fiji, Marshall Islands, and American Samoa. Pole and line fleet were operated in Papua New Guinea and the Solomon Islands, which in turn led to baitfishing operations in these two countries fishing on stolephorid anchovy resources as reported in this review.

A pole-and-line baitfishery in coastal waters of Papua New Guinea, (Otto 1990; Turner 1990), operated in waters over which the local habitats claimed traditional marine tenure. This led to demands from local inhabitants that there be some compensation for fishing within their traditional fishing grounds. A rapid solution to generating royalties was to impose a 2.5% levy, based on the price of skipjack landed to US canneries, and then disburse this to the Papua New Guineans living along the margins of the bait ground (Otto 1990). However, the user rights to a single embayment between two headlands may be a dynamic mosaic of user rights based on clan membership, kinship, inter-marriage, residence, and whether resources are passed on through matrilineal or patrilineal custom. This can eventuate with user rights for villagers not living on the coastal margins of a bait ground, but who have a legitimate claim for a share of the bait royalties (Turner 1990).

Unfortunately, this was not well understood by fishery managers, who didn't have the social or anthropological background to understand the complex mixture of traditional user rights in PNG's coastal zone. There was much unhappiness about the dispersal of funds and of the individual Papua New Guineans who benefited. Otto (1990) provided a detailed account of the baitfish royalties program in Papua New Guinea, and the problems of such initiatives that are conducted in the absence of detailed sociological and anthropological research.

The Solomon Islands Government (SIG) worked with the pole-and-line fishing companies to develop an integrated method by which bait catches were monitored for management and also documented by Solomon Islander crew for volume of fish for bait royalty estimates (Nichols and Rawlinson 1990). Though there were some periods of strife, by and large, this program did not commit the same mistakes as in Papua New Guinea, which led to much dissatisfaction by the traditional owners of the bait grounds and their resources.

Barclay (2010) documented the negative social aspects of tuna fisheries and tuna canning in Pacific Island Countries and the Solomon Islands in particular. The Solomon Islands had both canneries and a domestic pole-and-line tuna fleet. The negative aspects of the fishery and canning industry ranged from alcoholism, an increase in sexually transmitted diseases, and other social ills. Further, women working at the canneries were still obliged to provide food to their families following their cannery shift, with concomitant nutritional problems. Further, cannery and fishery workers experienced deracination from

their village culture, reassimilation into which, they found difficult, sometimes leading to further social problems. Moreover, Barclay (2010) noted that negative impacts are thus double sided in that they act as resistance against the undesired parts of development, yet can threaten the viability of businesses, including the desired aspects of their operations.

Research on the social conditions of stolephorid anchovy fisheries in Indonesia by the NGO Verité (2016) reported on Indonesian fishing platforms (*jermals*) and Indonesian small fishing vessels targeting stolephorid anchovies. On *jermals*, workers were subject to harsh conditions and physical abuse from supervisors, used to force workers to work harder and longer hours. Workers are dependent on the *jermal* supervisor for their bleak housing on the platform itself and meager food rations. In short, fishing crews are reduced to conditions of near slavery, sometimes for decades at a time (Verité 2012; Nur 2021).

Similar circumstances are also evident on vessels fishing for stolephorid anchovies targeting tunas by pole-and-line fishing in North Sumatra are involved in a traditional fishing system in which power is concentrated with boat owners and their ‘admirals.’ Fishers must maintain good relationships with these powerful individuals to maintain the right to continue fishing with them. To some degree, workers are mobile and have the ability to leave a bad ‘admiral’ or boat owner. However, the overarching concern is the ability to maintain a viable livelihood, and that may mean accepting less than ideal working conditions. Poor working conditions, including long hours for low pay, are somewhat standard in the fishing sector in Indonesia. Hammond (2021) states areas of particular concern include the presence of child labour, hazardous adult labour, and opaque lending practices between boat ‘admirals’ and their workers, and excessive hours of work. These horrendous working conditions are not just confined to Asia, but are global in dimension, and exists in nations with explicit anti-slavery legislation (Nur 2021; Yuliantiningsih and Barkhuizen 2021).

Conservation initiatives may also have unforeseen impacts to stolephorid anchovy fisheries for bait and food. The Indonesian Archipelago forms the base for what is called the ‘Coral Triangle.’ The Coral Triangle Initiative on Coral Reefs, Fisheries, and Food Security (CTI-CFF), also simply known as the Coral Triangle Initiative (CTI), is a multilateral partnership of six countries (Indonesia, Malaysia, Philippines, Papua New Guinea, Solomon Islands, and Timor-Leste) working together to sustain marine and coastal resources by addressing crucial issues such as food security, climate change, and marine biodiversity (Briggs 2005). The CTI is establishing an extensive marine protected area (MPA) network, 166 to date, enclosing 187,227 km<sup>2</sup> within its boundaries, within which stolephorid anchovy fisheries are excluded (Asaad *et al.* 2018).

Further changes that may impinge on stolephorid anchovy fisheries include the rapid economic and income growth, urbanization, and globalization are leading to a dramatic shift of Asian diets away from staples and increasingly towards livestock and dairy products, vegetables and fruit, and fats and oils (Pingali 2006). While the diversification of diets away from the traditional dominance of rice with rising incomes is expected and observed, current food consumption patterns are showing signs of convergence towards a Western diet. The diet transition is characterized by increased consumption of wheat, fruits and vegetables, and high protein and energy-dense food. Globalization and the consequent global interconnectedness of the urban middle class, is the driving force behind the convergence of diets. The rapid spread of global supermarket chains and fast-food restaurants are reinforcing the above trends. The growing demand for diet diversity cannot be met solely by the traditional food supply chain. It requires the modernisation of the food retail sector, and the vertical integration of the food supply chain.

## ENVIRONMENTAL DRIVERS AND IMPACTS

### Hydrology and oceanography

Tropical and sub-tropical Pacific Islands typically have monsoon seasons and trade wind seasons, the former being the wettest period of the year. In the larger islands like Papua New Guinea, extensive estuarine regions, such as the Gulf of Papua, support a range of the larger stolephorids including *Stolephorus indicus*, *S. bataviensis*, *S. commersonii*, *S. tri*, *S. carpenteriae*, and *S. brachycephalus* (Kailola and Wilson 1978). The rivers of the Gulf of Papua, including the Fly River, drain from the mountainous interior of Papua New Guinea, and the organic matter sediment load is carried north and east (Brunskill *et al.* 1995), enriching the South Papuan Coast with nutrients.

Similarly, shelf areas and estuaries of Southeast Asia, such as the Mekong, Irrawaddy, and Yangon form major estuaries on the east of the Bay of Bengal, and which is itself an immense deltaic estuarine system formed by the confluence of the Ganges, Brahmaputra, and Meghna rivers. However, high salinity water masses from the Red Sea, Persian Gulf, and east and southeast Arabian Sea periodically flow into the Bay of Bengal and play an important role in its water column structure (Varkey *et al.* 1996). Whitehead *et al.* (1988) list *Stolephorus waitei*, *S. insularis*, *S. commersonii*, *S. dubious*, and possibly *S. andhraensis* as found there. Species of *Encrasicholina* and *Stolephorus* are found along the West and East Coasts of India both of which are influenced by monsoons.

South East Asia includes the archipelagos of the Philippines and Indonesia, both of which can be impacted by tropical storms and typhoons. The Philippines in particular is very vulnerable to typhoons, due to its North-South orientation over 1850 km. Records of the Philippine Atmospheric, Geophysical and Astronomical Services Administration (PAGASA [www.pagasa.dost.gov.ph/](http://www.pagasa.dost.gov.ph/)) records between 20-25 typhoons and tropical storms annually crossing the Philippines Archipelago. Indonesia's archipelago is East-West oriented for about 5,100 km, and has far fewer typhoons and tropical storms annually, due to its proximity to the equator. The Indonesian Agency for Meteorology, Climatology and Geophysics ([www.bmkg.go.id](http://www.bmkg.go.id)) estimates that on average about 7 typhoons and tropical storms pass through Indonesia, primarily hitting the Lesser Sunda Islands and Moluccas.

Whitehead *et al.* (1989) listed the following stolephorid anchovies which occur in either the Philippines or Indonesia, or in both archipelagos: *Encrasicholina heteroloba*, *E. pseudoheteroloba*, *E. oligobranchus*, *E. punctifer*, *Stolephorus andhraensis*, *S. baganensis*, *S. commersonii*, *S. dubiosus*, *S. indicus*, *S. insularis*, *S. ronquilloi*, *S. tri*, and *S. waitei*. To these should be added *E. sigma*, *S. barbarini*, *S. balinensis*, *S. mercurius*, *S. rex*, *S. baganensis*, *S. bataviensis*, *S. baweanensis*, *S. continentalis*, *S. oceanicus*, *S. celsior*, *S. bengalensis*, and *S. teghui* (see Table 3).

The Indian subcontinent is the eastern extent of the Arabian Sea, into which flows the Indus River forming a delta, most of which is in Pakistan. The coastal regions of the Arabian Sea are for the most part arid desert and include the Persian Gulf, the Gulf of Oman, and the Red Sea. The Tigris and Euphrates rivers flow into northern Arabian Gulf via the Shatt Al Arab delta system. This is the only major source of freshwater flowing into the Gulf. Where allochthonous nutrient input is lacking, upwelling may take on its fertilizing role. Upwelling is a dominant mechanism in the Arabian Sea that occurs annually during southwest monsoon summer season (Ajith *et al.* 2019). This results in abundance of phytoplankton and zooplankton in the region and has profound influence on the coastal fisheries. During the southwest monsoon, an intense low-level wind jet blows diagonally across the Arabian Sea generating coastal upwelling along the coasts of Somalia, Oman and the southeastern Arabian Sea.

Upwelling in the Arabian Sea is not homogeneous across the basin despite being driven by monsoon winds. A study by Ajith *et al.* (2019) shows that, Ekman transport and sea Surface temperature displayed positive trends with time, whereas chlorophyll-a showed a negative trend. Increased Ekman transport has not generated increased productivity, indicating the role of other mechanisms on the availability of nutrients in the region.

Whitehead *et al.* (1988) list *E. devisi* (now *E. heteroloba*, see Table 3) as widespread in the northern part of Indian Ocean (the Arabian Gulf, Gulf of Aden, but apparently not the Red Sea and not to the Kenya Coast or the Andaman Islands). It is found widely in the western and central Pacific (Southeast Asia to Western and Central Pacific archipelagoes to French Polynesia). *Encrasicholina heteroloba* (*E. pseudoheteroloba* - see Table 3) is widespread in the Indian Ocean (Red Sea, East African coast to at least northern Madagascar, and eastward to the Bay of Bengal) and equally widespread in western Pacific (Indonesia, Thailand) north to southern Japan; southward to northern coasts of Australia; eastward to Solomon Islands, New Caledonia, Fiji, Tonga, Samoa, and also Palau to Kosrae (FSM)).

Both these species form most of the pole and line baitfish resource for those countries using this method to catch tunas. Similarly, widespread is *E. punctifer*, but only in the Western and Central Pacific. In the Indian Ocean the close congener *Encrasicholina intermedia* reportedly dominates in the Indian Ocean, while *Encrasicholina gloria* is confined to the Arabian Gulf and Red Sea (see Table 3).

The Red Sea lies between arid land, desert and semi-desert, and exchanges water with the Arabian Sea and Indian Ocean via the Gulf of Aden. The southern Gulf of Aden is bordered by the coast of Somalia, which has a desert and semi-desert climate under the Köppen climate classification. To the south of Somalia are Kenya, Tanzania, Mozambique, and northern South Africa, which include greater range of climate types and have rivers which drain into the Indian Ocean.

The hydrology of the Western Indian Ocean Islands, apart from Madagascar is related to small islands, such as Mayotte or the Seychelles. These islands have limited freshwater catchments and have barrier reefs and fringing reefs. The rivers of Madagascar rise in the highlands and flow towards the coast, dominantly to the west, south and east. There are few rivers in the north (Rakotondrainibe 2006). The rivers flowing west carry large amounts of sediment, draining across muddy plains and mangrove swamps into the Mozambique Channel. The rivers flowing east are generally short, but can have high flows. The rivers flowing south are typically ephemeral, or ‘wadis’ – dry in the dry season, flowing only after heavy rains (Rakotondrainibe 2006).

The diversity of stolephorid anchovies in the far west of the Indo-Pacific appears to be low (see Briggs 1999) apart from Somalia (Hata and Motomura 2017b; Whitehead *et al.* 1988), include *E. macrocephala*, *E. heteroloba*, *E. pseudoheteroloba*, *E. intermedia*, *S. commersonii*, *S. indicus*, and *S. insularis*. Fricke *et al.* (2018) record only *E. heteroloba* and *S. commersonii* from Madagascar. Similarly, only three species of stolephorid anchovies – *E. punctifer*, *S. commersonii*, and *S. indicus* – were reported by Sekadende *et al.* (2020) from Tanzanian small pelagic fisheries. Based on Whitehead *et al.* (1988) *E. punctifer*, *S. commersonii*, and *S. indicus* are found in Mozambique waters. Only the endemic *S. holodon* and widespread *S. indicus* are found in the coastal waters of eastern South Africa.

The most widely distributed coastal stolephorid anchovy, *E. pseudoheteroloba*, is not ubiquitous in Indo-Pacific waters. It is found inshore from East Africa to Fiji and offshore in the shallow seas near Indonesia.

However, this species has not been recorded from most coral atolls or from platform islands which lack extensive shallow water such as the Mariana Islands. It does however occur in other "high" islands such as Pohnpei and Palau.

As noted previously, the common denominator in the areas where *E. pseudoheteroloba* and *E. heteroloba* have been reported, is high primary productivity. This also explains why *E. pseudoheteroloba* is found in high island lagoons, but not in near coral atolls, nor around platform islands without lagoons. However, *Encraicholina* anchovies are not entirely absent from atolls as suggested by the work of Milton *et al.* (1990a) on the comparative biology of *E. heteroloba* from the waters around high islands of the Solomon Islands and the lagoons of the Maldive atolls. Monsoon driven upwelling leads to high primary production in the Maldive lagoons, sufficient to support populations of *E. heteroloba* and other stolephorid anchovies.

Jebri *et al.* (2020) showed that annual variations of fisheries yield (including stolephorid anchovies) parallel those of chlorophyll-a (an index of phytoplankton biomass) for East African small pelagic stocks. This region's climate and oceanography is influenced by two monsoon seasons. Enhanced phytoplankton biomass during the Northeast monsoon is triggered by wind-driven upwelling. During the Southeast monsoon, upwelling driven by two current induced mechanisms: coastal 'dynamic uplift' upwelling; and westward advection of nutrients. This biological response to the Southeast monsoon is greater than that to the Northeast monsoon. For years, unaffected by the alternance of El-Niño and La-Niña events, the Southeast monsoon wind strength over the south tropical Indian Ocean has been the main driver of year-to-year variability.

In the equatorial Pacific, the El Niño Southern Oscillation (ENSO) is a major oceanographic factor determined by wind pressure from west to east. A weakening of the wind pressure from the West results in a cold tongue of water resulting from ocean upwelling off the coasts of Peru and Chile, spreading out along the equator (Wyrtki 1981). This cold tongue comes into the region of the eastern extent of the Indo-Pacific Warm Pool, a mass of ocean water located in the western Pacific Ocean and eastern Indian Ocean which consistently exhibits the highest water temperatures over the largest expanse of the Earth's surface. This tongue of cool water stretches from the Galapagos Islands to the date line. The merging of these two oceanic water masses, results in substantial upwelling along the equator, with concomitant enrichment of surface waters, leading planktonic blooms which in turn provides forage to oceanic plankton feeders such as *E. punctifer* (Lehodey *et al.* 2010, 2020). These nutrient rich waters spread north and south of the equator by a progression of gyres driven from the equator by a process known as Ekman transport (Price *et al.* 1987).

The Mangalore coast of India is well known for its multi-species and multi-gear fisheries. A ten-year study (1995–2004) of oceanographic parameters was conducted on the inshore waters off Mangalore to understand their seasonal and interannual variation and influences on the pelagic fisheries of the region (Krishnakumar and Bhat 2008). Attempts have also been made to understand the influence of local and global environmental conditions on the alternating patterns of abundance between the Indian mackerel and oil sardine. Field and satellite-derived oceanographic data have shown that coastal upwelling occurs during July–September with a peak in August, and results in high nutrient concentrations and biological productivity along the coast.

Nearly 70% of the pelagic fish catch, dominated by oil sardine and mackerel, was obtained during September–December, during or immediately after the upwelling season (Krishnakumar and Bhat 2008). Catches of scombroid fishes were significantly related to cold sea surface temperature (SST), while such relationships were not observed for sardines and *Stolephorus* and *Encrasicholina* anchovies (species not given). Significant positive correlations were observed among the ENSO events, the Multivariate ENSO Index (MEI) and seawater temperature from the study area. The extreme oceanographic events associated with the cold La Niña condition, which preceded the exceptional 1997–1998 El Niño event, were responsible for the collapse of the pelagic fishery, especially the mackerel fishery, along the southwest coast of India (Krishnakumar and Bhat 2008). The fishery revived during 1999–2000 all along the southwest coast of India.

Chiu et al (1997) observed that monthly abundance (CPUE) of larval anchovy in the coastal waters off south-western Taiwan from 1980 to 1992 fluctuated at intervals corresponding to the 4.3- and 2.2-year cycles of ENSO. Further, CPUE was significantly correlated with sea surface temperature, with a time lag of 3 months, and a suggestive correlation with river flow with a time lag of 4 months, which in turn correlated with ENSO at lags of 13–14 month). Moreover, Chu *et al.* (2003) state that the Kuroshio Current, which is the western extension of the North Equatorial Current, may be one of the important mechanisms of ENSO's teleconnections affecting local climate and fisheries in the western Pacific region. A comprehensive review of ENSO and its impacts on the Pacific Ocean and the teleconnections by which it influences other seas and water bodies is given by Santoso *et al.* (2017).

Further, anchovy larval recruitment in the Tanshui River estuary in northern Taiwan, including *S. insularis*, *E. punctifer*, and *E. heteroloba*, showed a distinct temporal succession in association with sea surface temperature (Wang and Tzeng 1997). Larval recruitment of *S. insularis* occurred in mid-September, *Encrasicholina heteroloba* in early October, and *E. punctifer* in mid-November. According to Wang and Tzeng (1997) the larvae of these sympatric clupeoid species tended to reduce competition for habitat and thus to maximize the utilization of resources.

In the Gulf of Bone, Indonesia, environmental factors play an important role in the stolephorid anchovy distribution in this location. High anchovy biomass in the Gulf of Bone corresponded with sea surface temperature 29.5–30.5 °C, and sea surface chlorophyll-a, 0.5–1.0 mg/m<sup>3</sup>. As noted above, in northern Papua New Guinea spawning of *Stolephorus devisi* and *S. heterolobus* (now *E. heteroloba* and *E. pseudoheteroloba*), were associated with twin peaks in plankton biomass, itself related to the monsoonal rainfall pattern (Figure 6).

The monsoons are one of the important factors influencing the salinity and turbidity in South and Southeast Asia. Butcher (2004) summarises the changes wrought by the tropical monsoons on the great rivers of the mainland, the Irrawady, Salween, Chao Praya, and Mekong. Further, the rivers on large Indonesian islands such as the Rokan and the Kamparin Sumatra and the Kapuas in Borneo discharge enormous quantities of silt (in total more than twice by all the other rivers of the world) making the sea shallower, less saline and more turbid over time. The annual cycle of changes, in currents and salinity that take place provides a good example of the impact of the monsoons. During the wet monsoon, beginning in November, a current flow from the South China Seas into the Java Sea and then the Banda Sea. As this happens and fresh rain falls on the Sea and, more importantly, rivers discharge fresh water into the sea, the current reverses and thereby the salinity drops.

Butcher (2004) noted that during the dry monsoon the current reverses direction bringing oceanic water that causes a rise in the salinity of the Java Sea. The migration of round scads (*Decapterus*) species from the Java Sea is a historically important resource. One large group of round scads moves from the Flores Sea into the Java Sea as the salinity rises and then returns to the Flores Seas as salinity drops. Further, other species, among them stolephorid anchovies, appear to thrive on the plankton blooms caused by extra nutrients. Indeed, the composition of species helped to sustain catches — or at least prevent them from falling more drastically — in areas subjected to intensive trawling such as the Gulf of Thailand.

### Climate Change

The issue of climate change and its influence on biota through various biological processes has been studied in detail by The Intergovernmental Panel on Climate Change (IPCC); the United Nations body for assessing the science related to climate change. A technical report on the scientific basis of climate change can be found at [www.ipcc.ch/report/ar6/wg1/downloads](http://www.ipcc.ch/report/ar6/wg1/downloads) (Accessed on June 19, 2022).

The technical report states that “[o]bservations, models, and paleo-evidence indicate that recently observed changes in the ocean are unprecedented for centuries to millennia. Over the past four to six decades, it is virtually certain that the global ocean has warmed, with human influence extremely likely the main driver since the 1970s. The amount of ocean warming observed since 1971 will likely at least double by 2100 under a low warming scenario and will increase by 4–8 times under a high warming scenario (SSP5-8.5). Greater ocean stratification with depth is virtually certain, as is acidification, deoxygenation and marine heatwave frequency.” Also, a comprehensive review of climate change impacts to tropical fisheries is given in Booth *et al.* (2018).

Our intention in this section is to show the extremes in which stolephorid anchovies live, and type of trade-offs that may occur with stolephorid anchovies with ocean warming. As noted earlier, there is some evidence that the tropical genus *Encrasicholina* is extending northwards in the north-western Pacific, possibly through the effects of global warming (Hata *et al.* 2012).

The trend of sea surface temperature anomalies in the context of the spatial and temporal aspects of anchovy (*Stolephorus* spp.) fisheries along southwest coast of India were investigated by Bharti and Jayasankar (2019). The impact of climate change on *Stolephorus* fisheries was evident in both vertical and horizontal shifting of the catch. As in many cases such as this, there appears to be a trade-off where stolephorid anchovies tend to remain on the southwest coast during the pre-monsoon season, but shifted into deeper water, possibly to avoid high temperatures on the southwest and southeast coastal region. This was beneficial for offshore mechanised gears like trawls and ringnets which experienced increasing catch rates. By contrast, gears catching stolephorids in shallower waters decreased. It remains to be seen if similar trade-offs are observed in other large multi-gear stolephorid fisheries.

As noted earlier, environmental factors play an important role in the stolephorid anchovy distribution in this location in the Gulf of Bone, Indonesia (Saffrudin and Zainuddin 2018). High anchovy biomass in the Gulf of Bone corresponded with sea surface temperature 29.5–30.5 °C, and sea surface chlorophyll-a, 0.5–1.0 mg/m<sup>-3</sup>. As noted above, in northern Papua New Guinea spawning of *Stolephorus devisi* and *S. heterolobus* (now *E. heteroloba* and *E. pseudoheteroloba*), were associated with twin peaks in plankton biomass; itself related to the monsoonal rainfall pattern (Figure 6).



From a global perspective, small pelagic fishes such as those directed to stolephorid anchovies, support some of the highest yield fisheries worldwide, but the impacts of climate change on the distribution, recruitment and sustainability of these species remain largely uncertain (Muhling *et al.* 2017). Several projected changes to the world's oceans are highly relevant to pelagic fishes, including warming, changes in circulation patterns and altered pelagic foodwebs. These are likely to drive changes in species distributions, spawning and migration behaviors, early life survival, and recruitment. In many marine ecosystems, climate change will result in environmental conditions which are beyond the range of variability experienced since the advent of industrialized fishing. Climate change will also influence the availability of target species to fishing fleets as fish distributions shift, as well as sustainable harvest rates as stock dynamics change. Management strategies will likely need to be more adaptive, flexible, and environmentally explicit in the future if populations are to be sustainably managed, and the communities and livelihoods that they support are to be preserved.

Additional studies on stolephorid anchovies and climate change could not be found. However, the habitats of the European anchovy (*Engraulis encrasicolus*), Cape anchovy (*E. capensis*) Australian anchovy (*E. australasicus*), and Japanese anchovy (*E. japonicus*) extend between temperate to tropical and equatorial waters. These *Engraulis* species are so closely related that their morphological diagnostic features are indistinguishable (Whitehead *et al.* 1988). The only reason these are designated as separate species may be because they live in different regions. Studies on these four species may provide some insights into how stolephorids may respond to climate change. Raybaud *et al.* (2017) modelled populations of *E. encrasicolus* in the Eastern North and Central Atlantic (coasts of Europe south from about Bergen, Norway, but not Baltic and rare in the north; whole Mediterranean and Black and Azov Seas). Their results indicated that substantial poleward shifts in the probability of anchovy occurrence are very likely and highlight areas where European anchovy fisheries are forecasted to change most.

Jung *et al.* (2016) reported on recent studies in the western North Pacific which showed declining standing stock biomass of anchovy (*E. japonicus*) in the Yellow Sea and a climate-driven southward shift of anchovy catch in Korean waters. The effects of a warming ocean on the latitudinal shift of anchovy catch were investigated by developing and applying individual-based models (IBMs) based on a regional ocean circulation model and an IPCC climate change scenario. Despite the greater uncertainty, the two IBMs projected that, by the 2030s, the strengthened Tsushima Warm Current in the Korea Strait and the Japan Sea, driven by global warming, and the subsequent confinement of the relatively cold-water masses within the Yellow Sea will decrease larval anchovy biomass in the Yellow Sea, but will increase it in the Korea Strait and the Japan Sea. Shifts of engraulid anchovies and the impacts such range shifts will have on the marine ecosystems and fisheries in the region, may also provide some clues as to the potential reactions of stolephorid anchovies as the climate shifts oceans and freshwaters to a warmer regime.

Finally, potential climate change ramifications that affect major changes to freshwater input to the coastal zone across the Indo-West Pacific needs to be examined in terms of likely impacts to stolephorid populations. Moreover, the stolephorid anchovies' role as a forage base especially *E. punctifer*, for tuna and other pelagics needs to be understood by the Indian Ocean Tuna Commission and the Western and Central Pacific Tuna Commission.

### **Pollutants in the marine realm and impacts on stolephorid anchovies**

As human populations have expanded over the past two centuries, there has been increasing pollution of the marine environment (Halpern *et al.* 2015). One of the major pollutants is plastic. The source of much

of the plastic pollution is discharge from 10 major rivers in Asia and Africa. Eight of the ten major rivers are in Asia and include: the Yangtze, Indus, Yellow, Hai He, Ganges, Pearl, Amur, and Mekong rivers (Schmidt *et al.* 2017).

Microplastics in stolephorid anchovies risk exposing humans with a high seafood diet to potentially plastic debris (fragments of any type of plastic less than 5 mm in length, according to the U.S. National Oceanic and Atmospheric Administration (NOAA) and the European Chemicals Agency (ECA). Studies of ingestion of microplastics by stolephorid anchovies from Lombok Island, Indonesia were conducted by Ningrum and Patrial (2019). They observed that the contaminated anchovies had a mean number of 88 particles in their alimentary tract, with microplastic particle sizes ranging from 20-50  $\mu\text{m}$ , 50-500  $\mu\text{m}$ , 500-1000  $\mu\text{m}$ , and >1000  $\mu\text{m}$ . Most of the microplastic fragments are fibre (51%) and film (30%). The microplastic fragments were comprised of polypropylene, polystyrene, low density polyethylene, high-density polyethylene, thermoplastic polyester, and foamed polystyrene nylon.

Additional studies of ingested microplastics include Guntur *et al.* (2021) on *Stolephorus indicus*, *S. insularis*, and *S. commersonnii* from Madura, Indonesia. Other studies of microplastics in Indonesia include Hardianti *et al.* (2021) on *S. indicus*; Ningrum and Patrial (2019) on various stolephorids from Lombok; Ningrum *et al.* (2019) on various stolephorids from Eastern Kalimantan, and Tahir and Rochman (2015) on *S. heterolobus* (*E. heteroloba*) from Makassar.

Alizada *et al.* (2020) reported on the bioaccumulation of heavy metals in tissues of Indian anchovy (*Stolephorus indicus*) from the United Arab Emirates and Arabian Gulf coasts. The concentrations of cadmium, chromium, copper, and zinc exceeded the recommended safe value provided by the European Community, World Health Organization and the Food and Agriculture Organization. Cadmium and copper were also found in muscle and exceeded international Maximum Permissible Levels (MPLs) from fishing landing sites at Ajman, Sharjah, and Umm Al Quwain, raising concerns about heavy metals in the marine food web as well as impacts on human consumers. It is important to note that the presence of some of these heavy metals in diets could create serious health problems ranging from neurological, carcinogenic, nephrological, and immunological disorders, if ingested over a long period of time.

Regionally, the concentration of selected elements in Indian anchovy from Umm Al Quwain was lower compared to Ajman and Sharjah, which can be considered as essential hotspots of heavy metal pollution. These hotspots were identified in localized areas that can be influenced by textile industry, wastewaters discharged from detergent industries, oil pollution from refineries, dredging, petrochemical, and reclamation activities. Alizada *et al.* (2020) concluded that industrial activities and the discharge of their municipal wastewater should be controlled and monitored and regular monitoring of heavy metal levels in fish species is necessary to understand the associated health risks to humans.

Sampling of seawater by Dehm *et al.* (2021) found seventy-two pharmaceuticals quantified in coastal water of southern Viti Levu, Fiji. Pharmaceutical concentrations ranged from 0.04 nanograms (ng)/L to 760 ng/L. The pharmaceutical concentrations likely result from turbulent mixing on the coastline, and these pollutants are not necessarily restricted to highly populated areas.

Organic pollution and its danger to human life by food-borne illnesses have major social and economic impacts. *Vibrio parahaemolyticus* has recently been recognized as one of the most important food borne pathogens as the leading causal agent of human acute gastroenteritis, and also it has the biofilm forming

capacity (Costerton *et al.* 1999). The Vijayan *et al.* (2017) study was conducted to detect the biofilms producing *V. parahaemolyticus* found on *Stolephorus indicus* sold in markets in Puducherry (formerly Pondicherry). Forty percent of the samples tested positive for the bacteria and out of these, 75% had biofilms, which as noted by the authors are highly resistant to cleaning, antimicrobial agents and reduce the efficiency of chemicals on sanitization of food processing equipments in the food industry.

### **Ecosystem Impacts and Socio-Economic Factors Influencing Stolephorid Anchovy Fisheries**

Impacts of stolephorid anchovy catches on other fisheries within an archipelago have not been studied exhaustively. Studies conducted on species other than sprats and anchovies in Papua New Guinea's baitfisheries identified a wide range of associated juvenile reef and pelagic species, amounting to between 10-20% of the catch (Dalzell 1990).

In the absence of upwelling, primary productivity in coastal lagoons inhabited by stolephorid anchovies is driven primarily by allochthonous freshwater flow. Anthropogenic influences on upwelling are largely so small that they may be ignored. Freshwater influx, however, may be influenced by land-based activities, such as mangrove clearances, irrigation demand, and landscaping.

Many locations where stolephorid anchovies occur may be in areas of high natural beauty, and which may attract developers catering to domestic housing demands and hotels offering a range of leisure activities for tourists such as golf, tennis, and snorkelling and SCUBA diving. The potential for the reduction of freshwater influxes into stolephorid anchovy habitat is significant since maturation and spawning seems to depend on an adequate food supply.

This is something that national governments in Indo-Pacific region should be aware of, especially as maturation and spawning is dependent on high primary productivity. Further, the drive for terrestrial development will likely marginalize local fisheries based on stolephorid anchovies, leading to internal strife and antagonism between different communities. Catching stolephorids are among those fisheries which 'hide in plain sight,' i.e., are unnoticeable, in a setting that masks their presence. Indeed, they may 'hide' so successfully that they are entirely absent from a book describing India's marine fisheries by Bal and Rao (1984), despite stolephorid anchovies or "whitebait" being a major national fishery (Pravin and Meenakumari 2016). Thus, the first step for improving stolephorid anchovy fishery statistics may be to recognize and describe these fisheries. Otherwise, developers, planners, and politicians may not factor-in the impacts and consequences to local fisheries targeting stolephorid anchovies, or with a high anchovy incidental catch.

Small scale fisheries and poverty are strongly correlated in the lower latitudes of the Indo-Pacific Region. The small-scale fisheries sector tends to be firmly rooted in local communities, traditions, and values. Many small-scale fishers are self-employed and usually provide fish for direct consumption within their households or communities. Women are significant participants in the sector, particularly in post-harvest and processing activities. It is estimated that about 90 percent of all people directly dependent on capture fisheries work in the small-scale fisheries sector (World Bank/FAO/WorldFish 2012). As such, small-scale fisheries serve as an economic and social engine, providing food and nutrition security, employment and other multiplier effects to local economies while underpinning the livelihoods of fishing communities (FAO 2015). Moreover, the political power of such marginalized communities is limited and may be easily

bypassed. These remarks are not limited to just stolephorid anchovy fisheries, but to tropical and sub-tropical small-scale fisheries sectors as a whole.

As noted earlier (Pingali 2006), the rapid spread of global supermarket chains and fast food restaurants is reinforcing the above trends. The advent of Western fast foods does not appear yet to have displaced the demand for traditional stolephorid anchovy products. However, as the major fast-food chains expand and become entrenched in the Asia-Pacific Region, it may lead to young people consuming less traditional foods in favor of chain restaurant burgers, pizzas, noodles, and tacos. Besides shifts in preferences among the young, there is also increasing urbanization across the region, which may also promote not just fast foods, but also convenience foods which require a minimum of preparation ([www.worldometers.info/population/countries-in-asia-by-population/](http://www.worldometers.info/population/countries-in-asia-by-population/); accessed on May, 2023).

## Concluding Remarks

1. Stolephorid anchovies potentially contribute to the food security of between 30-50% of the global human population. Apart from stolephorid anchovies as food, some countries harvest large volumes of stolephorid anchovies for animal feed, most notably Pakistan. The role of stolephorid anchovies as animal feed and the social and economic characteristics of these enterprises need to be comprehensively evaluated.
2. The role of freshwater in the ecology of stolephorid anchovies needs to be understood not just by fisheries scientists and managers, but also ecologists investigating terrestrial impacts of land-based developments, such as agriculture, tourism, irrigation, and dams for water supply and electrical power generation.
3. Stolephorid anchovies are important species which are largely overlooked, except for regional agencies such as the Southeast Asian Fisheries Development Center (SEAFDEC). It is timely that the various tuna commissions in the Indo-West Pacific also take further account of these species in their research, model forecasts and management decisions, given the importance of the stolephorids as a forage base for fish in coastal and oceanic waters, where they indirectly support the tuna fisheries.
4. The stolephorid anchovies by and large are a cheap source of nutrition in the poorer South, while the tropical tuna they help capture (as bait) and provide a forage base for, are consumed principally in the wealthier North.
5. Living and working conditions for fishers targeting stolephorid anchovies vary widely by country; however, the accumulation of evidence, primarily from vessels in Southeast Asia indicates that many anchovy fishermen are forced to endure slavery-like conditions, such as beatings and starvation (Yea 2014). Clearly, the countries with substantial anchovy fisheries need to enforce legislation and statutes that protect anchovy fishers.
6. Low environmental impact tropical and subtropical pole-and-line tuna fishing industries in the Indian Ocean and Western Pacific, are supported primarily by stolephorid anchovies which have their own complex population and fishery dynamics. Moreover, in the Western Pacific (*E. punctifer*) and eastern Indian Ocean *E. gloria* and *E. intermedia*) offshore anchovies serves as a critical trophic link in the pelagic ecosystem as a forage base for the largest tropical tuna stocks in both oceans. A positive relationship has been noted between intense surface feeding activity of mature yellowfin tuna on this stolephorid and an increased vulnerability to surface fisheries, especially purse seine.
7. There remain many avenues for study of these anchovies and their ecology, especially in this era of global climate change. More broadly, this includes other fisheries for clupeoid fish in the tropics and subtropics, which support major human populations and industries.

## Acknowledgements

In September 2023, my co-author and great friend, Tony Lewis died, following a bout of illness. Tony was a major force in advancing our knowledge of tuna biology and ecology in the Western and Central Pacific and Southeast Asia. His passing will be felt across the region. Tony's knowledge also encompassed the often-bewildering species diversity of reef and lagoon fishes, including the stolephorid anchovies. When I proposed writing the present review, Tony was extremely supportive, providing much information and guidance on the many drafts, and to my relief, finally agreeing to a co-authorship, given the complexities of stolephorid anchovy taxonomy and biology. Tony was an acknowledged expert in fish identification throughout the Pacific. He had the keen eye of a naturalist that allowed him to discern new species that were hiding in plain sight. His work in this area was acknowledged with several new fish species bearing his name, for example, the Lewis round herring (*Spratelloides lewisi*). He is greatly missed.

Many people provided help in sourcing information and publications on stolephorid anchovies in the Indo-Pacific. First and foremost, I am extremely grateful to my friend and colleague, Dr. Daniel Pauly for agreeing to publish this monograph under the auspices of the *Seas Around Us* Project of the University of British Columbia's Institute for the Oceans and Fisheries. I am beholden to Jacquelyn Crossman, NOAA/NCEI Librarian and Information Retrieval Specialist for her unstinting and invaluable support in obtaining stolephorid articles from little known journals and grey literature.

Other colleagues across the region and beyond that responded to my requests for information and publications on stolephorid anchovy fisheries and biology include: Ali Salarpouri (Iran), Alamin Mohamed (Sudan), Katya Popova (UK and Tanzania), Pratap K. Mohanty (India), Sujeewa Haputhantri and Longomani Gathray (Sri Lanka), Zarrien Ayub (Pakistan), Pham Viet Anh and Ho Thong (Vietnam) and Ton Otto (Denmark and Papua New Guinea, David Itano (Hawai'i, Western Pacific and SE Asia.) Thanks are due to Don Kobayashi and his colleague is Justin Suca for observations and information on the *E. punctifer* mass spawning event around the Hawaiian Islands in 2023. I am very grateful to Dr. Harutaka Hata (Kagoshima University, Japan) for reviewing the stolephorid nomenclature in this article to minimize any discrepancies between this contribution and the taxonomic literature. I am grateful for the edits by two referees, by Ms. Elaine Chu of the *Sea Around Us*, and by the former Editor of the *Oceanography and Marine Biology: An Annual Review*. Also, I gratefully acknowledge the help I received from my wife Nellie Saupa Dalzell with reviewing the references. Finally, this paper is dedicated to my late mother Mary Dalzell, who sadly died as this paper was being completed.

## References

- Abdullahi, M.D. 2001. Culture and Customs of Somalia. Greenwood Press Westport, Connecticut. 223 p.
- Ainsworth, C., D. Varkey and T. Pitcher. 2008. Ecosystem simulations supporting ecosystem-based fisheries management in the Coral Triangle, Indonesia. *Ecological Modelling*, 214: 361–374.
- Ajith J., C. Jayaram, A. Nair, M. George, A. Balchand, and L. Pettersson. 2019. Remote Sensing of Upwelling in the Arabian Sea and Adjacent Near-Coastal Regions, p. 467-483. In: V. Barale and M. Gade (eds). *Remote Sensing of the Asian Seas*. Springer, Cham. [doi.org/10.1007/978-3-319-94067-0\\_26](https://doi.org/10.1007/978-3-319-94067-0_26)
- Alheit, J. 1989. Comparative spawning biology of anchovies, sardines, and sprats. *Rapports et Proces-verbaux des Réunions. Conseil International pour l'Exploration de la Mer*, 191: 7-14.
- Alizada, N., S. Malik and S.B. Muzaffar. 2020. Bioaccumulation of heavy metals in tissues of Indian anchovy (*Stolephorus indicus*) from the UAE coast, Arabian Gulf. *Marine Pollution Bulletin* 154: 111033.
- Al-Abdulrazzak, D. 2013. Total fishery extractions for Qatar: 1950-2010, p. 31-37. In: D. Al-Abdulrazzak and D. Pauly (eds). *From dhows to trawlers: a recent history of fisheries in the Gulf countries, 1950 to 2010*. Fisheries Centre Research Reports 21(2). Fisheries Centre, University of British Columbia.
- Andamari, R., D.A. Milton, and T. Zubaidi. 2002. Reproductive biology of five species of anchovy (Engraulidae) from Bima Bay, Sumbawa, Nusa Tenggara. *Indonesia Journal of Agriculture Science*, 3(2): 37-42.
- Anderson, C. 1997. The Maldivian Tuna Livebait Fishery: status and trends. In: D.J. Nickerson, M.H. Maniku (eds). *Workshop on Integrated Reef Resources Management in the Maldives*. Bay of Bengal Programme, FAO, Madras, India.
- Anderson, R.C., M.S. Adam, and J.I. Goes. 2011. From monsoons to Mantas: seasonal distribution of *Manta alfredi* in the Maldives. *Fisheries Oceanography*, 20 (2): 104–113.
- Argue, A.W. and R.E. Kearney. 1982. An assessment of the skipjack and baitfish resources of Solomon Islands. Noumea, New Caledonia: South Pacific Commission. 73 p.
- Ariansyach, I. 2017. Fisheries Country Profile: Indonesia. The Southeast Asian Fisheries Development Center (SEAFDEC), Chatuchak, Bangkok, Thailand. Available at: [www.seafdec.org/fisheries-country-profile-indonesia/](http://www.seafdec.org/fisheries-country-profile-indonesia/) (Accessed June 26, 2022)
- Arim, M. and P.A. Marquet. 2004. Intraguild predation: a widespread interaction related to species biology. *Ecological Letters*, 7: 557–564.
- Asaad, I., C.J. Lundquist, M.V. Erdmann, R. Van Hooidek, and M.J. Costello. 2018. Designating Spatial Priorities for Marine Biodiversity Conservation in the Coral Triangle. *Frontiers in Marine Science*, 5:400 [doi.org/10.3389/fmars.2018.00400](https://doi.org/10.3389/fmars.2018.00400)
- Babu Rao, M. 1966. A new species of *Stolephorus* Lacépède from the East coast of India (Pisces: Engraulidae). *Annals and Magazine of Natural History*, 9: 101-110.
- Bailey, C., A. Dwiponggo, and F. Marahudin. 1987. Indonesian marine capture fisheries. ICLARM Studies and Reviews 10. International Center for Living Aquatic Resource Management, Manila, Philippines; Directorate General of Fisheries, and Marine Fisheries Research Institute, Ministry of Agriculture, Jakarta, Indonesia. 196 p.
- Bal, D.V. and K.V. Rao. 1984. Marine Fisheries of India. Tata McGraw Hill Publishing Company Limited, New Delhi. 470 p.
- Baldwin, W.J. 1984. *Stolephorus pacificus*, a new species of tropical anchovy (Engraulidae) from the Western Pacific Ocean. *Micronesica*, 19(1-2): 151-156.
- Barclay, K. 2010. Impacts of tuna industries on coastal communities in Pacific Island countries. *Marine Policy*, 34(3): 406-413.
- Barua, S., E. Karim, and N. Humayun. 2014. Present status and species composition of commercially important finfish in landed trawl catch from Bangladesh marine waters. *International Journal of Pure and Applied Zoology*, 2: 150-159.
- Bat, N.K. and V.C. Tran. 2017. Stock Information of Anchovy, Indo-Pacific Mackerel and Blue Swimming Crab (AIB) Species in the Southwest Sea of Viet Nam, Annex 6. In SEAFDEC. *Report of the Experts Group Meeting on Stock Status and Geographical Distribution of Anchovy, Indo-Pacific Mackerel and Blue Swimming Crab (AIB) Species in the Gulf of Thailand*. Bangkok, Thailand, 22-23 September 2016. Southeast Asian Fisheries Development Center.

- Baust, S., L. Teh, S. Harper, and D. Zeller. 2015. South Africa's marine fisheries catches (1950–2010), p. 129–150. In: F. Le Manach and D. Pauly (eds). *Fisheries catch reconstructions in the Western Indian Ocean, 1950–2010*. Fisheries Centre Research Reports 23(2). Fisheries Centre, University of British Columbia.
- Bayate, D., J. Regalado, M. Guanco, and S. Mesa. 2018. Aspects of the population biology of the Buccaneer Anchovy, *Encrasicholina punctifer* (Fowler 1938) in Southern Sibuyan Sea, Philippines. *Philippines Scientist*, 53: 1–13.
- Bayliff, W.H. 1964. Some Aspects of the Age and Growth of The Anchoveta, *Cetengraulis mysticetus*, in the Gulf of Panama. *Inter-American Tropical Tuna Commission Bulletin* 9(1): 3-27.
- Beamish, R.J. 1995. Climate Change and Northern Fish Populations. Canadian Special Publication of Fisheries and Aquatic Sciences 121. National Research Council, Ottawa, Canada. 739 p.
- Beckley, E. 1904. Hawaiian Fisheries and Methods of Fishing with an Account of The Fishing Implements used by The Natives of the Hawaiian Islands." Honolulu: Advertiser Steam Print, 1883 (on microfilm, Hamilton Library, UH at Manoa).
- Beckley, L. and S.T. Fennessy. 1996. The beach-seine fishery off Durban, Kwazulu-Natal. *South African Journal of Zoology*, 31: 186-192.
- Bennet, P.S. and A. Chellam. 1979 *Peroderma tasselum* sp. nov. (Lernaeoceriforms; Copepoda) parasitic on the fish *Stolephorus commersonii* Lacepede. *Indian Journal of Fisheries*, 22(1-2): 279-282.
- Beverton, R.J.H. and S.J. Holt. 1957. On the Dynamics of Exploited Fish Populations. Fisheries Investigations Series 2, vol 19. Ministry of Agriculture and Fisheries, U.K. 533 p.
- Beverton, R.J.H. 1963. Maturation, growth and mortality of Clupeid and Engraulid stocks in relation to fishing. *Proces-verbaux des Réunions. Conseil International pour l'Exploration de la Mer*, 154: 44-67.
- Beverton, R.J.H. 1990. Small marine pelagic fish and the threat of fishing; are they 'endangered? *Journal of Fish Biology*, 37(sA): 5-16.
- Bharti, V. and J. Jayasankar. 2019. Life cycle of anchovy and climate driven changes in its distribution on the southwest coast of India. *ICAR-Central Marine Fisheries Research Institute, Marine Fisheries Information Service Technical and Extension Series*, 239: 7-10.
- Blaber, S.J.M. and J.W. Copland (ed). 1990. Tuna Baitfish in the Indo-Pacific Region. Proceedings of a workshop, Honiara. Solomon Islands, 11-13 December 1989. Australian Centre for International Agricultural Research Proceedings No. 30.
- Blaber, S.J.M., D.A. Milton, N.J.F. Rawlinson, G. Tiroba, and P.V. Nichols. 1990. Diets of lagoon fishes of the Solomon Islands: predators of tuna baitfish and trophic effects of baitfishing on the subsistence fishery. *Fisheries Research*, 8: 263-286.
- Blackburn, M. 1966. Synopsis of biological information on the Australian anchovy *Engraulis australis* (White). *California Cooperative Oceanic Fisheries Investigations Reports*, 11.
- Bleeker, P. 1848. A contribution to the ichthyology of Sumbawa. *The Journal of the Indian Archipelago and Eastern Asia*, 2(9): 632 – 639.
- Bleeker, P. 1852. Bijdrage tot de kennis der Haringachtige visschen [Clupeoïden on cover] van den Soenda-Molukschen Archipel. *Verhandelingen van het Bataviaasch Genootschap van Kunsten en Wetenschappen*, 24 (8): 1-48 + 49-52.
- Bloom, D.D. and N.R. Lovejoy. 2014. The evolutionary origins of diadromy inferred from a time-calibrated phylogeny for Clupeiformes (herring and allies). *Proceedings of the Royal Society B, Biological Sciences*, 281. [dx.doi.org/10.1098/rspb.2013.2081](https://doi.org/10.1098/rspb.2013.2081).
- Bloom, D.D., M.D. Burns, and T.A. Schriever. 2018. Evolution of body size and trophic position in migratory fishes: a phylogenetic comparative analysis of Clupeiformes (anchovies, herring, shads and allies). *Biological Journal of the Linnean Society*, 125(2): 302-314.
- BoBP. 2018a. Profile of Marine Fisheries of India. Bay of Bengal Programme, Abhiramapuram Chennai Tamil Nadu, India.
- BoBP. 2018b. Profile of Marine Fisheries Profile of Marine Fisheries of Bangladesh. Bay of Bengal Programme, Abhiramapuram Chennai Tamil Nadu, India.
- Bodiguel, C. and C. Breuil. 2015. Report of the Meeting on Marine Small Pelagic Fishery in the United Republic of Tanzania, Bagamoyo, Tanzania. SFFAO/2015/34, IOC-SmartFish Programme. FAO, Rome. 96 p.
- Boggs, C.H. and R.Y. Ito. 1993. Hawai'i's Pelagic Fisheries. *Marine Fisheries Review*, 55(2): 69-82.
- Boistol, L., S. Harper, S. Booth, and D. Zeller. 2011. Reconstruction of marine fisheries catches for Mauritius and its outer islands, 1950-2008, p. 39-61. In: S. Harper and D. Zeller (eds). *Fisheries*



- catch reconstructions: Islands, Part II*. Fisheries Centre Research Reports 19(4). Fisheries Centre, University of British Columbia.
- Boldrocchi, G. and R. Bettinetti. 2019. Whale shark foraging on baitfish off Djibouti. *Marine Biodiversity*, 49: 2013–2016.
- Booth, D., D. Feary, D. Kobayashi, O. Luiz, and Y. Nakamura. 2018. Tropical Marine Fishes and Fisheries and Climate Change, p. 875-896. In: B.F. Phillips and M. Pérez-Ramírez (eds). *Climate Change Impacts on Fisheries and Aquaculture*. John Wiley and Sons Ltd. England, UK.
- Bornbusch, A.H. and M. Lee. 1992. Gill Raker Structure and development in Indo-Pacific Anchovies (Teleostei: Engrauloidea), with a discussion of the structural evolution of engrauloid gill rakers. *Journal of Morphology*, 214: 109-119.
- Boulenger, G.A. 1900. Descriptions of new fishes from the Cape of Good Hope. *Marine Investigations in South Africa*, 8: 10–12.
- Breuil, C. and D. Grima. 2014. *Baseline Report Somalia*. SmartFish Programme of the Indian Ocean Commission, Fisheries Management FAO component, Ebene, Mauritius. 21 p.
- Briggs, J. 1999. Coincident biogeographic patterns: Indo-West Pacific Ocean. *Evolution*, 53(2): 326-335.
- Briggs, J.C. 2005. Coral reefs: Conserving the evolutionary sources. *Biological Conservation* 126: 297–305
- Brunskill, G.J., I. Zagorskis, K.J. Woolfe. 1995. Distribution of riverine sediment chemistry on the shelf, slope and rise of the Gulf of Papua. *Geo-Marine Letters*, 15: 160–165.
- Burhanuddin, S.M., S. Martosewojo, and M. Hutomocea. 1975. A preliminary study on growth and food of *Stolephorus* spp. from Jakarta Bay. *Marine Research in Indonesia*, 14: 1-31.
- Butcher, J.G. 2004. The Closing of the Frontier: A History of the marine fisheries of Southeast Asia c.1850-2000. Institute of Southeast Asian Studies (ISEAS), Singapore. 442 p.
- CAE. 2018. Trends in Marine Resources and Fisheries Management in Indonesia. California Environmental Associates (CAE), San Francisco, USA. 145 p.
- Cannell B.L, P.J.D. Allen, E.M. Wiley, B. Radford, C.A. Surman, and A.R. Ridley. 2022. Diet of brown boobies at a globally significant breeding ground is influenced by sex, breeding, sub-colony and year. *Marine Ecology Progress Series*, 681: 227-245.
- Cashion, T., S. Glaser, M. Sarah, P. Lo, P. Roberts, and D. Zeller. 2018. Fisheries in Somali waters. Reconstruction of domestic and foreign catches for 1950–2015. *Marine Policy*, 87: 275-283
- Castillo, S. and J. Mendo. 1987. Estimation of unregistered Peruvian anchoveta (*Engraulis ringens*) catch statistics, 1951 to 1982, p. 109-116. In: D. Pauly and I. Tsukayama (eds). *The Peruvian anchoveta and its upwelling ecosystem: three decades of change*. ICLARM Studies and Reviews 15. Instituto del Mar del Peru (IMARPE), Callao, Peru; Deutsche Gesellschaft fdr TechnLsche Zusammenarbeit (G72), GmbH, Eschbom, Federal Republic of Germany; and International Center for Living Aquatic Resources Management, Manila, Philippines.
- Castro, B.F., M. Peña, E. Nogueira, M. Gilcoto, E. Broullón, A. Comesaña, D. Bouffard, A.C.N. Garabato, and B. Mourriño-Carballido. 2022. Intense upper ocean mixing due to large aggregations of spawning fish. *Nature Geoscience*, 15(4): 287-292.
- Cawthra, H., F.H. Neumann, R. Uken, A. Smith, L. Guastella, and A. Yates. 2012. Sedimentation on the narrow (8 km wide), oceanic current-influenced continental shelf off Durban, Kwazulu-Natal, South Africa. *Marine Geology*, 323–325: 107-122.
- Chaitiamvong, S. 1999. Identification of cephalopods found in the Gulf of Thailand. Marine fishery technical reports 1990-1998 Part 1: Invertebrates. Bangkok Marine Fisheries Development Center, Thailand. 78 p.
- Chapau, M. 1983. The Plankton and Hydrology of the Ysabel Passage. Res. Rep. 83-06. Fisheries Research and Surveys Branch, Department of Primary Industry, Port Moresby, Papua New Guinea. 46 p.
- Chassot, E., F. Melin, O. LePape, and D. Gascuel. 2007. Bottom-up control regulates fisheries production at the scale of eco-regions in European seas. *Marine Ecology Progress Series*, 343: 45–55.
- Cheung, W.W.L., V.W.Y. Lam, J.L. Sarmiento, K. Kearney R. Watson and D. Pauly. 2009. Projecting global marine biodiversity impacts under climate change scenarios. *Fish and Fisheries*, 10: 235-251. [doi.org/10.1111/j.1467-2979.2008.00315.x](https://doi.org/10.1111/j.1467-2979.2008.00315.x)
- Chittick, N. 1980. Sewn Boats in the Western Indian Ocean, and a Survival in Somalia. *International Journal of Nautical Archaeology*, 9(4): 297–309.
- Chiu, T.S., S.S. Young, and C.S. Chen. 1997. Monthly variation of larval anchovy fishery in Ilan Bay, NE Taiwan, with an evaluation for optimal fishing season. *Journal of the Fisheries Society of Taiwan*, 24: 273–282.

- Chu, X., C. Dong, and Y. Qi. 2017. The influence of ENSO on an oceanic eddy pair in the South China Sea. *Journal of Geophysical Research: Oceans*, 122: 1643–1652. [doi.org/10.1002/2016JC012642](https://doi.org/10.1002/2016JC012642)
- Clark, M. 2015. Deforestation in Madagascar: Consequences of Population Growth and Unsustainable Agricultural Processes. *Global Majority e-Journal*, 3(1): 61–71.
- Clarke, T.A. 1987. Fecundity and spawning frequency of the Hawaiian anchovy. *Encrasicholina purpureus*. *Fisheries Bulletin*, 85: 127-197.
- Colléter, M., A. Darar Djibril, G. Hosch, P. Labrosse, Y. Yvergniaux, F. Le Manach, and D. Pauly. 2015. Le développement soutenu des pêcheries artisanales : reconstruction des captures marines à Djibouti de 1950 à 2010, p. 13–25. In: F. Le Manach and D. Pauly (eds). *Fisheries catch reconstructions in the Western Indian Ocean, 1950–2010*. Fisheries Centre Research Reports 23(2). Fisheries Centre, University of British Columbia
- Conand, F. 1988. Biologie et écologie des poissons pélagiques du lagon de Nouvelle Calédonie utilisables comme appât thonier. PhD Thesis, Université de Bretagne Occidentale, Editions de l'ORSTOM. Paris. 224 p.
- Corpus, L. 2014. Reconstructing Singapore's marine fisheries catch, 1950-2010, p. 137-146. In: K. Zylich, D. Zeller, M. Ang, and D. Pauly (eds). *Fisheries catch reconstructions: Islands, Part IV*. Fisheries Centre Research Reports 22(2). Fisheries Centre, University of British Columbia.
- Costerton, J.W., S.E. Stewart, and P. Greenberg. 1999. Bacterial biofilms: a common cause of persistent infections. *Science*, 284: 1318-1322.
- Cury, P., A. Bakun, R.J.M. Crawford, A. Jarre-Teichmann, R.A. Quiñones, L.J. Shannon, and H.M. Verheye. 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in “waspwaist” ecosystems. *ICES Journal of Marine Society*, 57: 603–618.
- Cushing, D.H. 1971. The dependence of recruitment on parent stock in different groups of fishes *Journal Conseil international pour l'Exploration de la Mer.*, 33(3): 340-362.
- Cushing, D.H. and F.R. Harden–Jones. 1968. Why Do Fish School? *Nature*, 218: 918–920
- Daly, J.C. and B.J. Richardson. 1980. Allozyme variation between populations of baitfish species *Stolephorus heterolobus* and *St. devisi* (Pisces: Engraulidae) and *Spratelloides gracilis* (Pisces: Dussumieriidae) from Papua New Guinea waters. *Australian Journal of Marine and Freshwater Research*, 31(5): 701 – 711.
- Dalzell, P.J. 1983a. Raw data and preliminary results for an analysis of the population dynamics of PNG baitfish. Res. Rep. 83-04. Fisheries Research and Surveys Branch, Department of Primary Industry, Port Moresby, Papua New Guinea. 79 p.
- Dalzell, P.J. 1983b. The distribution and production of anchovies in PNG waters. Res. Rep. 83-03. Fisheries Research and Surveys Branch, Department of Primary Industry, Port Moresby, Papua New Guinea. 24 p.
- Dalzell, P.J. 1984a. The influence of rainfall on catches of stolephorid anchovies in Papua New Guinea waters. Res. Rep. 84-04. Fisheries Research and Surveys Branch, Department of Primary Industry, Port Moresby, Papua New Guinea. 18 p.
- Dalzell, P.J. 1984b. The population biology and management of baitfish in Papua New Guinea waters. Res. Rep. 84-05. Fisheries Research and Surveys Branch, Department of Primary Industry, Port Moresby, Papua New Guinea. 51 p.
- Dalzell, P.J. 1986. The distribution and production of anchovies in Papua New Guinea waters. *Papua New Guinea Journal of Agriculture, Forestry and Fisheries*, 34(1-4): 59-70.
- Dalzell, P.J. 1987a. Notes on the biology of *Spratelloides lewisi* (Wongratana 1983), a recently described species of sprat from Papua New Guinea waters. *Journal of Fish Biology*, 30: 691-700.
- Dalzell, P.J. 1987b. Some aspects of the reproductive biology of stolephorid anchovies from northern Papua New Guinea. *Asian Fisheries Science*, 1(1): 91-106.
- Dalzell, P. 1988. An atlas of the growth, mortality, and recruitment of Philippine small pelagic fishes. International Center for Living Aquatic Resources Management, Manila, Unpublished Report.
- Dalzell, P.J. 1990. Biology and population dynamics of small schooling fishes used for tuna baitfish in Papua New Guinea, p. 100-114. In: S.J.M. Blaber and J.W. Copeland (eds). *Tuna baitfish in the Indo Pacific region*, ACIAR Workshop Proceedings 30.
- Dalzell, P.J. 1993. Small Pelagic Fishes, p. 97-133. In: A. Wright and L. Hill (eds). *Nearshore Marine Resources of the South Pacific*. Forum Fisheries Agency Honiara, Institute of Pacific Studies Suva.
- Dalzell, P.J. 1998. The role of archaeological and cultural-historical records in long-range coastal fisheries resources management strategies and policies in the Pacific Islands. *Ocean and Coastal Management*, 40: 237-252.

- Dalzell, P.J. and R. Ganaden. 1987. A review of the fisheries for small pelagic fishes in Philippine waters. *Bureau of Fisheries and Aquatic Resources Technical Paper Series*, 10(1): 1-58.
- Dalzell, P.J. and A.D. Lewis. 1989. A Review of the South Pacific Tuna Baitfisheries: Small Pelagic Fisheries Associated with Coral-Reefs. *Marine Fisheries Review*, 51(4): 1-10.
- Dalzell, P.J. and J.W.J. Wankowski. 1980. The biology, population dynamics and fisheries dynamics of exploited stocks of three baitfish species *Stolephorus heterolobus*, *S. devisi* and *Spratelloides gracilis* in the Ysabel Passage, New Ireland Province, Papua New Guinea. Res. Bull. 22. Department of Primary Industry, Port Moresby, Papua New Guinea. 124 p.
- Dalzell, P.J., P. Corpuz, R. Ganaden, and F. Arce. 1990. Philippine small pelagic fisheries and their management. *Aquaculture and Fisheries Management*, 21: 77-94.
- Dalzell, P.J., P. Corpuz, R. Ganaden, and D. Pauly. 1987. Estimation of maximum sustainable yield and maximum economic rent from the Philippine small pelagic fisheries. *Bureau of Fisheries and Aquatic Resources Technical Paper Series*, 10(3): 1-23.
- Dalzell, P.J., T. Adams, and N. Polunin. 1996. Coastal fisheries in the Pacific Islands. *Oceanography and Marine Biology Annual Review*, 33: 395-531.
- Dehm, J., S. Singha, M. Ferreira, S. Piovano, and J. Fick. 2021. Screening of pharmaceuticals in coastal waters of the southern coast of Viti Levu in Fiji, South Pacific. *Chemosphere*, 276: 130161. [doi.org/10.1016/j.chemosphere.2021.130161](https://doi.org/10.1016/j.chemosphere.2021.130161)
- Delsman, H.C. 1931. Fish eggs and larvae from the Java Sea. 17. The genus *Stolephorus*. *Treubia*, 13: 217-243.
- de Vis, C.W. 1883. Description of three new species of fish of Queensland (*Oligurus goliath*, *Synaptura fitzroiensis*, *Engraulis carpentariae*). *Proceedings of the Linnean Society of New South Wales*, 7: 318-320.
- Doddamani, M.S., T.J. Ramesha, M.T. Laxmipathi, T.S. Annappaswamy, and S.L. Shanbhogue. 2002. Reproductive potential and growth of from Dakshina Kannada coast. *Indian Journal of Fisheries*, 9: 321-325.
- Doherty, B., M. Hauzer, and F. Le Manach. 2015a. Reconstructing catches for the Union of the Comoros: uniting historical sources of catch data for Ngazidja, Ndzuwani and Mwali from 1950–2010, p. 1-11. In: F. Le Manach and D. Pauly (eds). *Fisheries catch reconstructions in the Western Indian Ocean, 1950–2010*. Fisheries Centre Research Reports 23 (2). Fisheries Centre, University of British Columbia
- Doherty, B., J. Herfaut, F. Le Manach, S. Harper, and D. Zeller. 2015b. Reconstructing domestic marine fisheries in Mayotte from 1950–2010, p. 53–65. In: F. Le Manach and D. Pauly (eds). *Fisheries catch reconstructions in the Western Indian Ocean, 1950–2010*. Fisheries Centre Research Reports 23(2). Fisheries Centre, University of British Columbia.
- Doherty, B., M. McBride, A. Brito, F. Le Manach, L. Sousa, I. Chauca, and D. Zeller. 2015c. Marine fisheries in Mozambique: catches updated to 2010 and taxonomic disaggregation, p. 67-81. In: F. Le Manach and D. Pauly (eds). *Fisheries catch reconstructions in the Western Indian Ocean, 1950–2010*. Fisheries Centre Research Reports 23(2). Fisheries Centre, University of British Columbia.
- Dutt, S. and M. Babu Rao. 1959 Occurrence of *Anchoviella baganensis* Hardenberg off east coast of India. *Current Science*, 28:160–161.
- Dunne, R., N. Polunin, P. Sand, and M. Johnson. 2014. The creation of the Chagos Marine Protected Area: A fisheries perspective. *Advances in Marine Biology*, 69: 79-127.
- Edelist, D., A. Scheinin, O. Sonin, J. Shapiro, P. Salameh, G. Rilov, Y. Benayahu, D. Schulz, and D. Zeller. 2013. Israel: Reconstructed estimates of total fisheries removals in the Mediterranean, 1950–2010. *Acta Adriacta*, 54(2): 253 – 264.
- Egan, J.P., U.-S. Chew, C.-H. Kuo, V. Villarroel-Diaz, P.J. Hundt, N.G. Iwinski, M.P. Hammer, and A.M. Simons. 2017. Diets and trophic guilds of small fishes from coastal marine habitats in western Taiwan. *Journal of Fish Biology*, 91(1): 331-345.
- Egan, J.P., S. Gibbs, A.M. Simons. 2018. Trophic niches through ontogeny in twelve species of Indo-Pacific marine Clupeoidei (herrings, sardines, and anchovies). *Marine Biology*, 165(10): 153.
- Egan, J.P., D.D. Bloom, and A.M. Simons. 2022. Time for speciation and niche conservatism explain the latitudinal diversity gradient in clupeiform fishes. *Journal of Biogeography*, 49(11): 1952–1966.
- Ellway, C.P. and R.E. Kearney. 1981. Changes in the Fijian Baitfishery, 1974 – 1980. Skipjack Survey and Assessment Programme Technical Report No.5, South Pacific Commission, Noumea, New Caledonia. 24 p.

- FAO. 2003a. Fishery Country Profile – Pakistan. Available at: [www.fao.org/faolex/country-profiles/general-profile/en/?iso3=PAK](http://www.fao.org/faolex/country-profiles/general-profile/en/?iso3=PAK) (Accessed June 2, 2022)
- FAO. 2003b. Fishery Country Profile - Sultanate of Oman. Available at: [www.fao.org/fishery/docs/DOCUMENT/fcp/en/FI\\_CP\\_OM.pdf](http://www.fao.org/fishery/docs/DOCUMENT/fcp/en/FI_CP_OM.pdf) (Accessed on March 31, 2022)
- FAO. 2003c. Fishery Country Profile – Kuwait. Available at: [www.fao.org/fi/oldsite/FCP/en/KWT/profile.htm](http://www.fao.org/fi/oldsite/FCP/en/KWT/profile.htm) (Accessed on March 31, 2022)
- FAO. 2003d. Fishery Country Profile - Kingdom of Saudi Arabia. Available at: [www.fao.org/countryprofiles/maps/en/?iso3=SAU](http://www.fao.org/countryprofiles/maps/en/?iso3=SAU) (Accessed on March 31, 2022).
- FAO. 2003e. Fishery Country Profile - State of Qatar Available at: [www.fao.org/fi/oldsite/FCP/en/QAT/profile.htm](http://www.fao.org/fi/oldsite/FCP/en/QAT/profile.htm) (Accessed on March 31, 2022)
- FAO. 2003f. Fishery Country Profile - Hashemite Kingdom of Jordan. Available at: [www.fao.org/fi/oldsite/FCP/en/JOR/profile.htm](http://www.fao.org/fi/oldsite/FCP/en/JOR/profile.htm) (Accessed on March 31, 2022)
- FAO. 2004a. Fishery Country Profile – Republic of Iraq. Available at: [www.fao.org/fi/oldsite/FCP/en/IRQ/profile.htm](http://www.fao.org/fi/oldsite/FCP/en/IRQ/profile.htm) (Accessed on March 31, 2022)
- FAO. 2004b. Fishery Country Profile - United Arab Emirates. Available at: [www.fao.org/fi/oldsite/FCP/en/IRQ/profile.htm](http://www.fao.org/fi/oldsite/FCP/en/IRQ/profile.htm) (Accessed on March 31, 2022)
- FAO. 2004c. Fishery Country Profile - The Arabic Republic of Egypt. Available at: [www.fao.org/fi/oldsite/FCP/en/EGY/profile.htm](http://www.fao.org/fi/oldsite/FCP/en/EGY/profile.htm) (Accessed on March 31, 2022)
- FAO. 2005a. Fishery Country Profile – Islamic Republic of Iran. Available at: [www.fao.org/fi/oldsite/FCP/en/IRN/profile.htm](http://www.fao.org/fi/oldsite/FCP/en/IRN/profile.htm) (Accessed on March 31, 2022)
- FAO. 2005b. AQUASTAT Country Profile – Eritrea. Food and Agriculture Organization of the United Nations (FAO). Rome, Italy.
- FAO. 2006. Country Profile – Sri Lanka. Available at: [www.fao.org/faolex/country-profiles/general-profile/en/?iso3=LKA](http://www.fao.org/faolex/country-profiles/general-profile/en/?iso3=LKA) (Accessed on June 2, 2022)
- FAO. 2007. Country Profile – The State of Israel. Available at: [www.fao.org/fishery/docs/DOCUMENT/fcp/en/FI\\_CP\\_IL.pdf](http://www.fao.org/fishery/docs/DOCUMENT/fcp/en/FI_CP_IL.pdf) (Accessed on June 2, 2022)
- FAO. 2015. Voluntary Guidelines for Securing Sustainable Small-Scale Fisheries in the Context of Food Security and Poverty Eradication. Food and Agriculture Organization of the United Nations, Rome. 34 p.
- FAO. 2019. Fishery and Aquaculture Country Profiles of the Democratic Socialist Republic of Sri Lanka. Available at: [www.fao.org/fishery/facp/LKA/en](http://www.fao.org/fishery/facp/LKA/en) (Accessed 18 August 2021).
- FAO. 2020. Fishery Country Profile – Japan. Available at: [www.fao.org/faolex/country-profiles/general-profile/en/?iso3=JPN](http://www.fao.org/faolex/country-profiles/general-profile/en/?iso3=JPN) (Accessed on June 2, 2022.)
- FAO. 2022. Fishery Country Profile - Republic of Yemen. Available at: [www.fao.org/fi/oldsite/FCP/en/YEM/profile.htm](http://www.fao.org/fi/oldsite/FCP/en/YEM/profile.htm) (Accessed on March 31, 2022)
- FAO. 2023. Fishery and Aquaculture Statistics. Global capture production 1950-2021 (FishStatJ). FAO Fisheries and Aquaculture Division, Rome. Available at: [www.fao.org/fishery/en/statistics/software/fishstatj](http://www.fao.org/fishery/en/statistics/software/fishstatj)
- Fowler, H.W. 1900. Contributions to the ichthyology of the tropical Pacific. *Proceedings of Academy of Natural Sciences of Philadelphia*, 52: 493–528.
- Fowler, H.W. 1911. Notes on clupeoid fishes. *Proceedings of Academy of Natural Sciences of Philadelphia*, 63: 204–221.
- Fowler, H.W. 1938. The fishes of the George Vanderbilt South Pacific Expedition, 1937. *Monographs of the Academy of Natural Sciences of Philadelphia*, 2: 1–349.
- Fricke, R., D. Golani, and B. Appelbaum-Golani. 2012. First record of the Indian Ocean anchovy *Stolephorus insularis* Hardenberg, 1933 (Clupeiformes: Engraulidae) in the Mediterranean. *BioInvasions Records*, 1: 303–306.
- Fricke, R., J. Mahafina, F. Behivoke, H. Jaonalison, M. Léopold, and D. Ponton. 2018. Annotated checklist of the fishes of Madagascar, south western Indian Ocean, with 158 new records. *FishTaxa*, 3(1): 1-432.
- Gangan, S.S., A. Pavan-Kumar, S. Jahageerdar, A.K. Jaiswar. 2020. A new species of *Stolephorus* (Clupeiformes: Engraulidae) from the Bay of Bengal. *Zootaxa*, 4743: 561–574.
- Gascuel, D., S. Guenette, and D. Pauly. 2011. The trophic-level-based ecosystem modelling approach: Theoretical overview and practical uses. *ICES Journal of Marine Science*, 68: 1403-1416.
- Gayathry, L. 2020. Status of the anchovy fishery in Sri Lanka: based on data collected from 2011-2019, with special reference to the selected landing sites in the southern and western coastal regions.

- Unpublished paper. Marine Biological Resources Division, National Aquatic Resources Research and Development Agency (NARA), Colombo, Sri Lanka. 2 p.
- George, M.R. 1998. Die Fortpflanzungsbiologie zweier pelagischer Fischarten *Sardinops sagax* (Jenyns, 1842) (Clupeidae) und *Trachurus picturatus murphyi* Nichols 1920 (Carangidae) im Auftriebsgebiet Nordchiles. Verlag Natur und Wissenschaft, Solingen. 133 p.
- Gillett, R. 2004. *The Marine Fisheries of Cambodia*. FishCode Review No. 4. Food and Agriculture Organization, Rome.
- Gillett, R., A. Jauharee, and M. Adam. 2013. Maldives livebait fishery management plan. Marine Research Centre, Ministry of Fisheries and Agriculture, Maldives. 17 p.
- Gislason, H. and M.I. Sousa. 1985. Biology, stock size and catch of Small Pelagic Fish along the coast of Mozambique. *Revista de Investigacao Pesqueira Maputo*, 13: 27- 81.
- Gopall, V., V. Ramasubramanian, B. Santhosh, and M.A. Kurian. 2018. Food spectrum and dietary preferences of the Indian anchovy *Stolephorus indicus* (van Hasselt, 1823) from Thiruvananthapuram coast, Kerala. *Indian Journal of Fisheries*, 65(1): 15-19.
- Gopakumar, G. and N.G.K. Pillai. 2000. Whitebait, p. 296-309. In: V.N. Pillai and N.G. Menon (eds). *Marine Research and Management*. Central Marine Fisheries Research Institute, Cochin, India.
- Gøjsaeter, J., P.O.A. Dayaratne, O. Bergstad, I. Sousa, and I. Beck. 1976. Ageing Tropical Fishes by Growth Rings in the Otoliths. FAO Fisheries Circular 776. Food and Agriculture Organization, Rome. 54 p.
- Grantham, H., S.L. Petersen, and H. Possingham. 2008. Reducing bycatch in the South African pelagic longline fishery: the utility of different approaches to fisheries closures. *Endangered Species Research*, 5(201): 291-299.
- Groeneveld, J.C. and K.A. Koranteng (eds). 2017. The RV Dr Fridtjof Nansen in the Western Indian Ocean: Voyages of marine research and capacity development. Food and Agriculture Organization, Rome. 258 p.
- Gulland J.A. 1983. *Fish Stock Assessment. A Manual of Basic Methods*. John Wiley and Sons, New York. 236 p.
- Gulland, J.A. and L.K. Boerema. 1973. Scientific advice on catch levels. *Fishery Bulletin*, 71: 325-335.
- Gulland, J.A. and S.J. Holt. 1959. Estimation of growth parameters for data at unequal time intervals. *ICES Journal of Marine Science*, 25: 47-49.
- Guntur, G., M.A. Asadi, and K. Purba. 2021. Ingestion of microplastics by anchovies of the Madura Strait, Indonesia. *Aquaculture, Aquarium, Conservation and Legislation – International Journal of the Bioflux Society*, 14: 1163-1170.
- Günther, A. 1880. Report on the shore fishes procured during the voyage of H.M.S. Challenger in the years 1873-1876. Rep Sci Res Voy H. M. S. Challenger during the years 1873-76. *Zool*, 1 (pt 6):1-82, pls 1-32.
- Ha, V.V. and D.V. Thi. 2010. *Assessing reserves and sustainable exploitation of anchovies in Kien Giang waters and proposing solutions for resource management. Evaluation of reserves and sustainable exploitation of anchovies in Kien Giang waters*. Seafood Research Institute, Haiphong.
- Halpern, B.J.S., M. Frazier, J. Potapenko, K.S. Casey, K. Kenig, C. Longo, J.S. Lowdnes, R.C. Rockwood, E.R. Selig, K.A. Selkoe, and S. Walbridge. 2015. Spatial and temporal changes in cumulative human impacts on the world's ocean. *Nature Communications*, 6: 7615. [doi.org/10.1038/ncomms8615](https://doi.org/10.1038/ncomms8615)
- Hajisame, S. and S. Ibrahim. 2008. Seasonal and spatial variations of fish trophic guilds in a shallow, semi-enclosed tropical estuarine bay. *Environmental Biology of Fishes*, 82: 252-264.
- Hammond, D.R. 2021. Modern Slavery, Human Trafficking, and Child Labor in Corporate Supply Chains: Creating Oppression-Free Portfolios. Veriti Management LLC (Veriti), Boston, MA. 40 p.
- Hampton, J. and K. Bailey. 1993. Fishing for tunas associated with floating objects: A review of the Western Pacific fishery. Technical Report No. 31. Tuna and Billfish Assessment Programme, South Pacific Commission, Noumea, New Caledonia.
- Hardenberg, J.D.F. 1934. Some remarks on the genus *Stolephorus* Lacépède in the Indo-Australian archipelago. *Treubia*, 14: 313-375.
- Hardenberg, J.D.F. 1933a. Notes on some genera of the Engraulidae. *Natuurkundig Tijdschrift voor Nederlandsch-Indië*, 93: 230-257.
- Hardenberg, J.D.F. 1933b. New *Stolephorus* species of the Indo-Australian seas. *Natuurkundig Tijdschrift voor Nederlandsch-Indië*, 93: 258-263

- Hardianti, E., W. Wardhana and M.P. Patria. 2021. Microplastic abundance in anchovy *Stolephorus indicus* (Van Hasselt, 1823) in the Lada Bay, Pandeglang, Banten. *Journal of Physics: Conference Series*, 1725: 012050.
- Hassan, R.B.R. and A.R. Latun. 2016. Purse seine fisheries in Southeast Asian Countries: A regional synthesis. *Fish for the People*, 14: 7-15.
- Hata, H., S. Lavoué, S.V. Bogorodsky, T.J. Alpermann, and H. Motomura. 2023. A new *Stolephorus* (Teleostei: Clupeiformes: Engraulidae: Engraulinae) from the Red Sea. *Ichthyology and Herpetology*, 111(2): 191–203. [doi.org/10.1643/i2022064](https://doi.org/10.1643/i2022064)
- Hata, H., S. Lavoué, and H. Motomura. 2019. Taxonomic status of nominal species of the anchovy genus *Stolephorus* previously regarded as synonyms of *Stolephorus commersonnii* Lacepède 1803 and *Stolephorus indicus* (van Hasselt 1823), and descriptions of three new species (Clupeiformes: Engraulidae) *Ichthyological Research* 68: 327–372.
- Hata, H., S. Lavoué, and H. Motomura. 2020a. *Stolephorus babarani*, a new species of anchovy (Teleostei: Clupeiformes: Engraulidae) from Panay Island, central Philippines. *Zootaxa*, 4178: 509–520.
- Hata, H., S. Lavoué, and H. Motomura. 2020b. *Stolephorus acinaces*, a new anchovy from northern Borneo, and redescription of *Stolephorus andhraensis* Babu Rao, 1966 (Clupeiformes: Engraulidae). *Marine Biodiversity*, 50: 102. [doi.org/10.1007/s12526-020-01115-2](https://doi.org/10.1007/s12526-020-01115-2)
- Hata, H., S. Lavoué, and H. Motomura. 2021. Taxonomic status of nominal species of the anchovy genus *Stolephorus* previously regarded as synonyms of *Stolephorus commersonnii* Lacepède 1803 and *Stolephorus indicus* (van Hasselt 1823), and descriptions of three new species (Clupeiformes: Engraulidae). *Ichthyological Research*, 68: 327–372. [doi.org/10.1007/s10228-020-00792-0](https://doi.org/10.1007/s10228-020-00792-0)
- Hata, H., S. Lavoué, and H. Motomura. 2022b. Description of three new species previously identified as *Stolephorus bengalensis* (Dutt and Babu Rao, 1959) or *Stolephorus insularis* Hardenberg, 1933, and a redescription of *S. bengalensis* (Chordata, Osteichthyes, Clupeiformes, Engraulidae). *ZooKeys*, 1121: 145–173.
- Hata, H., S. Lavoué, and H. Motomura. 2022c. A new species of *Stolephorus* from the eastern Indian Ocean and redescription of *Stolephorus dubiosus* Wongratana, 1983, with comments on the evolution of prepelvic scute numbers within *Stolephorus* (Clupeiformes: Engraulidae). *Zoological Studies*, 61: e58. [doi.org/10.6620/zs.2022.61-58](https://doi.org/10.6620/zs.2022.61-58)
- Hata, H. and H. Motomura. 2015. A new species of anchovy, *Encrasicholina macrocephala* (Clupeiformes: Engraulidae), from the northwestern Indian Ocean. *Zootaxa*, 3941: 117-124.
- Hata, H. and H. Motomura. 2016a. Two new species of the genus *Encrasicholina* (Clupeiformes: Engraulidae): *E. intermedia* from the western Indian Ocean and *E. gloria* from the Persian Gulf, Red Sea and Mediterranean. *Raffles Bulletin of Zoology*, 64: 79–88.
- Hata, H. and H. Motomura. 2016b. Validity of *Encrasicholina pseudoheteroloba* (Hardenberg 1933) and redescription of *Encrasicholina heteroloba* (Rüppell 1837), a senior synonym of *Encrasicholina devisi* (Whitley 1940) (Clupeiformes: Engraulidae). *Ichthyological Research*, 64:18–28.
- Hata, H. and H. Motomura. 2017a. A new species of anchovy, *Encrasicholina auster* (Clupeiformes: Engraulidae), from Fiji, southwestern Pacific Ocean. *New Zealand Journal of Zoology*, 44: 122–128.
- Hata, H. and H. Motomura. 2017b. First record of the engraulid fish *Encrasicholina macrocephala* (Clupeiformes) from Somalia. *Check list the Journal of Biodiversity data*, 13: 47–51.
- Hata, H. and H. Motomura. 2018a. *Stolephorus insignis*, a new anchovy from the western Pacific, and redescription of *Stolephorus apiensis* (Jordan and Seale 1906) (Clupeiformes: Engraulidae). *Ichthyological Research*, 66: 280–288.
- Hata, H. and M. Motomura. 2018b. *Stolephorus continentalis*, a new anchovy from the northwestern South China Sea, and redescription of *Stolephorus chinensis* (Günther 1880) (Clupeiformes: Engraulidae). *Ichthyological Research*, 65: 374–382.
- Hata, H. and H. Motomura. 2018c. First reliable record of *Encrasicholina punctifer* (Clupeiformes: Engraulidae) from Shibushi Bay, east coast of the mainland of Kagoshima, southern Japan. *Nature of Kagoshima*, 44: 333–340.
- Hata, H. and H. Motomura. 2020a. A new species of anchovy, *Encrasicholina sigma* (Teleostei, Clupeiformes, Engraulidae), from Sulawesi, Indonesia. *Zootaxa*, 4750: 261–268.
- Hata, H. and H. Motomura. 2020b. First Northern Hemisphere records of the Samoan anchovy, *Stolephorus apiensis* (Actinopterygii: Clupeiformes: Engraulidae) *Acta Ichthyologica et Piscatoria*, 50: 367–372.

- Hata, H. and H. Motomura. 2021a. Two new species of *Stolephorus* (Teleostei: Clupeiformes: Engraulidae) from the western Pacific. *Raffles Bulletin of Zoology*, 69: 109–117.
- Hata, H. and Motomura, H. 2021b. Redescription of *Encrasicholina oligobranchus* (Wongratana 1983) (Clupeiformes: Engraulidae) and description of a new species of *Encrasicholina* from New Guinea. *Ichthyological Research*, 68: 277–286.
- Hata, H. and H. Motomura. 2021d. A New Species of the Anchovy Genus *Stolephorus* Lacepède 1803 from North Sumatra, Indonesia, and redescription of *Stolephorus pacificus* Baldwin 1984 and *Stolephorus teguhi* Kimura, Hori and Shibukawa 2009 (Teleostei: Clupeiformes: Engraulidae) *Zoological Studies*, 60: e65.
- Hata, H. and H. Motomura. 2022. *Stolephorus lotus*, a new anchovy (Teleostei: Clupeiformes: Engraulidae) from the Northern Territory, Australia. *Zoological Studies*, 61: e87. [doi.org/10.6620%2FZS.2022.61-87](https://doi.org/10.6620%2FZS.2022.61-87)
- Hata, H. and H. Motomura. 2023. Description of *Stolephorus horizon* n. sp. from Fiji and Tonga, and redescription of *Stolephorus scitulus* (Fowler, 1911) (Teleostei: Clupeiformes: Engraulidae). *Taxonomy*, 3(3): 356–380. [doi.org/10.3390/taxonomy3030021](https://doi.org/10.3390/taxonomy3030021)
- Hata, H., H. Motomura, and H. Ishimori. 2012. First Japanese record of an engraulid fish, *Encrasicholina devisi* (Clupeiformes), collected from Kagoshima Prefecture, southern Japan and comparisons with congeners. *Japanese Journal of Ichthyology*, 59 (2), 125–134.
- Hayasi, S. 1966. A note on the biology and fishery of the Japanese anchovy *Engraulis japonica* (Houttuyn). *California Cooperative Oceanic Fisheries Investigations Reports*, 11: 44–57
- Hayashi, M. and K. Nisiyama. 1980. Fishes collected by the stationary net in the west coast of Sagami Bay. *Kanagawa Nature Magazine*, 1: 15–27.
- Hemmings, M., S. Harper, and D. Zeller. 2014. Reconstruction of total marine catches for the Maldives, 1950–2010, p. 21–37. In: S. Harper and D. Zeller (eds). *Fisheries catch reconstructions: Islands, Part II*. Fisheries Centre Research Reports 19 (4). Fisheries Center, University of British Columbia.
- Heupel, M.R. and R.E. Hueter. 2002. Importance of prey density in relation to the movement patterns of juvenile blacktip sharks (*Carcharhinus limbatus*) within a coastal nursery area. *Marine and Freshwater Research*, 53: 543–550.
- Hida, T. 1973. Food of tunas and dolphins (Pisces: Scombridae and Coryphaenidae) with emphasis on the distribution and biology of their prey *Stolephorus buccaneeri*. *Fishery Bulletin*, 71: 135–143.
- Ho, T. 2019. Fishery performance indicators: Vietnam's anchovy fisheries. University of Economics, Ho Chi Minh City, Vietnam. 10 p.
- Hoang, N.S. and V.V. Ha. 2019. Overview of anchovy resources and anchovy fishing activities in Vietnam. Seafood Research Institute, Hai Phong.
- Hoedt, F.E. 1990. Growth of the tropical anchovy, *Stolephorus nelsoni*, in northern Australia, p. 147–149. In: S.J.M. Blaber, and J.W. CopJand (eds). *Tuna Baitfish in the Indo-Pacific Region: proceedings of a workshop, Honiara, Solomon Islands, 11–13 December 1989*. ACIAR Proceedings No. 30.
- Hoedt, F.E. 1994. A comparative study of the habitats, growth and reproduction of eight species of tropical anchovy from Cleveland and Bowling Green Bays, North Queensland. PhD thesis, James Cook University, Townsville, Australia. 230 p.
- Hoedt, F.E. 2002. Growth in eight species of tropical anchovy determined from primary otolith increments. *Marine and Freshwater Research*, 53: 859–867.
- Hoenig, J.M. 1983. Empirical use of longevity data to estimate mortality rates. *Fishery Bulletin*, 82: 898–903.
- Hong Kong Fish Net. 2022. Agriculture, Fisheries and Conservation, Government of Hong Kong Special Administration Region. Available at: [www.hk-fish.net/en](http://www.hk-fish.net/en) (Accessed on June 28, 2022)
- Hopkins, T.L., T.T. Sutton, and T.M. Lancraft. 1982. The trophic structure and predation impact of a low latitude midwater fish assemblage. *Progress in Oceanography*, 38(3): 205–239.
- Horinouchi, M., P. Tongnunui, K. Furumitsu, Y. Nakamura, K. Kanou, A. Yamaguchi, K. Okamoto, and M. Sano. 2012. Food habits of small fishes in seagrass habitats in Trang, southern Thailand. *Fisheris Science*, 78: 577–587.
- Horton, M. and C.D. van der Lingen. 2019. Comparative trophic ecology of Cape anchovy *Engraulis encrasicolus* and Natal anchovy *Stolephorus holodon* off South Africa's east coast. *African Journal of Marine Science*, 41: 269–279.

- Hsieh, C.-H., C.-S. Chen, T.-S. Chiu, K.-T. Lee, F.-J. Shieh, J.-Y. Pan, and M.-A. Lee. 2009. Time series analyses reveal transient relationships between abundance of larval anchovy and environmental variables in the coastal waters southwest of Taiwan. *Fisheries Oceanography*, 18(2): 102–117.
- Huang, C.-H., C.-S. Chen, and T.-S. Chiu. 2018. Growth of Buccaneer Anchovy (*Encrasicholina punctifer*) During Juvenile Stage in the Waters off Southwestern Taiwan. *Journal of Taiwan Fisheries Research*, 26(1): 53-61.
- Huang, V.R. and R. Coelho. 2017. Sustainability performance assessment focusing on coral reef protection by the tourism industry in the Coral Triangle region. *Tourism Management*, 59: 510-527.
- Hunter, J. R., B. J. Macewicz, N.C.H. Lo, and C.A. Kimbrell. 1992. Fecundity, spawning, and maturity of female Dover sole, *Microstomus pacificus*, with an evaluation of assumptions and precision. *Fisheries Bulletin*, 90: 101-128.
- Ikeda, H. and T. Nakabo. 2015. *Fishes of the Pacific coast of southern Japan*. Tokai University Press, Kanagawa. 597 p.
- Imran, Z. and M. Yamao. 2014. Factors contributing to the decline of the anchovy Fisheries in Krueng Raya Bay, Aceh, Indonesia. *Annals of Tropical Research*, 36(2): 22-43.
- Ingles, J. and D. Pauly. 1984. An atlas of the growth, mortality and recruitment of Philippine fishes. ICLARM Technical Reports 13. Institute of Fisheries Development and Research College of Fisheries, University of the Philippines in the Visayas, Quezon City. Philippines and International Center for Living Aquatic Resources Management, Manila, Philippines. 127 p.
- Itano, D.G. 2000. The Reproductive Biology of Yellowfin Tuna (*Thunnus albacares*) in Hawaiian Waters and the Western Tropical Pacific Ocean: Project Summary. University of Hawai'i School of Ocean and Earth Science and Technology Report 00-01, Honolulu, Hawai'i. 69 p.
- Iwakiri, S. and V. Ram. 1988. Types and Activities of Small Fishing Economies in the South Pacific —A Case Study of Fiji. *Memoirs of the Faculty of Fisheries, Kagoshima University*, 37: 57-96.
- Iwata, T., T. Akamatsu, S. Thongsukdee, P. Cherdskujai, K. Adulyanukosol, and K. Sato. 2017. Tread-water feeding of Bryde's whales. *Current Biology*, 27: 1141–1155.
- Jacquet, J., H. Fox, H. Motta, A. Ngusaru, and D. Zeller. 2010. Few data but many fish: marine small-scale fisheries catches for Mozambique and Tanzania. *African Journal of Marine Science*, 32(2): 197–206.
- Jauharee, A.R., K. Neal, and K.I. Miller. 2015. Maldives tuna Pole-and-line Tuna Fishery: Livebait Fishery Review. MRC, IPNLF and MSPEA, Maldives. 60 p.
- Jebri, F., Z. Jacobs, D.E. Raitsos, M. Srokosz, E. Popova, S.C. Painter, S. Kelly, M. Roberts, L. Scott, S. Taylor, M. Palmer, H. Kizenga, Y. Shaghude, and J. Wishgott. 2020. Interannual monsoon winds variability as a key driver of East African small pelagics. *Nature Scientific Reports*, 10: 13247. [doi.org/10.1038/s41598-020-70275-9](https://doi.org/10.1038/s41598-020-70275-9)
- Jennings, S. and R.J.H. Beverton. 1991. Intraspecific variation in the life history tactics of Atlantic herring (*Clupea harengus* L.) stocks. *ICES Journal of Marine Science*, 48: 117– 125.
- JFA. 2013. Japanese fisheries agency. Fishery and resource management of anchovy. The 18th Pacific wide-area fisheries adjustment committee material (in Japanese). Available at: [www.jfa.maff.go.jp/j/suisin/s\\_kouiki/taiheiyo/pdf/t18-3-1.pdf](http://www.jfa.maff.go.jp/j/suisin/s_kouiki/taiheiyo/pdf/t18-3-1.pdf) (Accessed on May 5, 2023)
- Jhawar, J., R.G. Morris, U.R. Amith-Kumar, M. Danny Raj, T. Rogers, H. Rajendran, and V. Guttal. 2020. Noise-induced schooling of fish. *Nature Physics*, 16: 488–493.
- Jiddawi, N.S. and M.C. Öhman. 2002. Marine Fisheries in Tanzania. *AMBIO: A Journal of the Human Environment*, 31(7): 518-527.
- Johannessen O., G. Subbaraju, and J. Blindheim. 1981. Seasonal variations of the oceanographic conditions off the southwest coast of India during 1971-1975. *Fiskeridirektoratets Skrifter*, 18(5): 247-261.
- Jordan, D.S. and A. Seale. 1906. The Fishes of Samoa. Description of the Species Found in the Archipelago, with a Provisional Check-List of The Fishes of Oceania. *Bulletin of the Bureau of Fisheries*, 25: 173-455.
- Jordan, D.S. and A. Seale. 1926. Review of the Engraulidae, with descriptions of new and rare species. *Harvard University Bulletin of the Museum of Comparative Zoology*, 67: 355-418.
- Jørgensen, C., E. Rebecca, and R.E. Holt. 2013. Natural mortality: Its ecology, how it shapes fish life histories, and why it may be increased by fishing. *Journal of Sea Research*, 75: 8-18.
- Juliani, S. Anggoro, S.W. Saputra, and Helminuddin. 2019. Sustainability assessment of Devis' anchovy (*Encrasicholina devisi* (Whitley, 1940)) (Clupeiformes: Engraulidae) fisheries based on biology



- aspects, Kutai Kartanegara, Indonesia. *Aquaculture, Aquarium, Conservation and Legislation - International Journal of the Bioflux Society*, 12(5): 1938-1950.
- Jung, S., I.-C. Pang, J. Lee, and K. Lee. 2016. Climate-change driven range shifts of anchovy biomass projected by bio-physical coupling individual-based model in the marginal seas of East Asia. *Ocean Science Journal*, 51: 563-580.
- Kailola, P.J. and M.A. Wilson. 1978. The trawl fishes of the Gulf of Papua. Res. Bull. 20. Department of Primary Industry, Port Moresby, Papua New Guinea.
- Kamsan, N. 2019. Country Fisheries Trade: Cambodia. The Southeast Asian Fisheries Development Center (SEAFDEC), Chatuchak, Bangkok, Thailand. Available at: [www.seafdec.org/fisheries-country-profile-cambodia/](http://www.seafdec.org/fisheries-country-profile-cambodia/) (Accessed on June 28, 2022)
- Kasumyana, A.O. and D.S. Pavlov. 2018. Evolution of Schooling Behavior in Fish. *Journal of Ichthyology*, 58(5): 670-678.
- Kearney, R.E., A.D. Lewis, and B.R. Smith. 1971. Cruise Report Tagula 71-1: Survey of skipjack tuna and bait resources in Papua New Guinea Waters. Res. Bull. 8. Department Agriculture Stocks and Fisheries, Port Moresby, Papua New Guinea. 145 p.
- King, M. 2007. *Fisheries Biology, Assessment and Management*. Blackwell Publishing Ltd, Oxford, England. 408 p.
- Kimura, S., K. Hori, and K. Shibukawa. 2009. A new anchovy, *Stolephorus teguhi* (Clupeiformes: Engraulidae), from North Sulawesi, Indonesia. *Ichthyological Research*, 56: 292-295.
- Koya, M.K., A. Azeez, P.P. Rohit, S. Ramanathan, K.M. Rajesh, and E.M. Abdussamad. 2019. Lakshadweep Livebait Fisheries Management Plan. CMFRI Marine Fisheries Policy Series No. 12. ICAR-CMFRI, India. 56 p.
- Krishnakumar, P.K. and G.S. Bhat. 2008. Seasonal and interannual variations of oceanographic conditions off Mangalore coast (Karnataka, India) in the Malabar upwelling system during 1995-2004 and their influences on the pelagic fishery. *Fisheries Oceanography*, 17: 45-60.
- Kumar, M.A., G. Padmavati, and S. Venu. 2015. Food and Feeding Dynamics of *Stolephorus commersonnii* (Lacepede, 1803) (Family: Engraulidae) from South Andaman, *Journal of Marine Biology*, 870919. [dx.doi.org/10.1155/2015/870919](https://doi.org/10.1155/2015/870919)
- Kwek, A. 2017. Annual 2017 Exporter Guide: Singapore. Global Agriculture Information Network, GAIN Report SN7017. US Department of Agriculture, Washington DC. 23 p.
- Lacepède, B.G.E. 1803. *Histoire naturelle, générale et particulière, des poissons*. Dufart, Paris.
- Lamarca, N. 2017. Fisheries Country Profile: The Philippines. The Southeast Asian Fisheries Development Center (SEAFDEC), Chatuchak, Bangkok, Thailand. Available at: [www.seafdec.org/fisheries-country-profile-philippines/](http://www.seafdec.org/fisheries-country-profile-philippines/) (Accessed on 18 August 2021)
- Larsson, M. 2012. Why do fish school? *Current Zoology*, 58(1): 116-128.
- Lavoué, S., M. Miya, P. Musikasinthorn, W.-J. Chen, and M. Nishida. 2013. Mitogenomic evidence for an Indo-West Pacific origin of the Clupeoidei (Teleostei: Clupeiformes). *PLoS ONE*. 8 (2): e56485. [doi.org/10.1371/journal.pone.0056485](https://doi.org/10.1371/journal.pone.0056485)
- Lavoué, S., J. Bertrand, H.-Y. Wang, W.-J. Chen, H.-C. Ho, H. Motomura, H. Hata, T. Sado, and M. Miya. 2017. Molecular systematics of the anchovy genus *Encrasicholina* in the Northwest Pacific. *PLoS ONE*, 12(7): e0181329. [doi.org/10.1371/journal.pone.0181329](https://doi.org/10.1371/journal.pone.0181329)
- Le Manach, F., C.A. Abunge, T.R. McClanahan, and D. Pauly. 2015a. Tentative reconstruction of Kenya's marine fisheries catch, 1950-2010, p. 37-51. In: F. Le Manach and D. Pauly (eds). *Fisheries catch reconstructions in the Western Indian Ocean, 1950-2010*. Fisheries Centre Research Reports 23(2). Fisheries Centre, University of British Columbia.
- Le Manach, F., P. Bach, L. Barret, D. Guyomard, P.-G. Fleury, P.S. Sabarros, and D. Pauly. 2015b. Reconstruction of the domestic and distantwater fisheries catch of La Réunion (France), 1950-2010, p. 83-98. In: F. Le Manach and D. Pauly (eds). *Fisheries catch reconstructions in the Western Indian Ocean, 1950-2010*. Fisheries Centre Research Reports 23(2). Fisheries Centre, University of British Columbia.
- Le Manach, F., P. Bach, L. Boistol, J. Robinson, and D. Pauly. 2015c. Artisanal fisheries in the world's second largest tuna fishing ground —Reconstruction of the Seychelles' marine fisheries catch, 1950-2010, p. 99-110. In: F. Le Manach and D. Pauly (eds). *Fisheries catch reconstructions in the Western Indian Ocean, 1950-2010*. Fisheries Centre Research Reports 23(2). Fisheries Centre, University of British Columbia.
- Le Manach, F., C. Gough, F. Humber, S. Harper, and D. Zeller. 2011. Reconstruction of total marine fisheries catches for Madagascar (1950-2008), p. 21-37. In: S. Harper and D. Zeller (eds).

- Fisheries catch reconstructions: Islands, Part II*. Fisheries Centre Research Reports 19 (4). Fisheries Centre, University of British Columbia.
- Leary, D.F., G.I. Murphy, and M. Miller. 1975. Fecundity and length at first spawning of the Hawaiian Anchovy, or Nehu (*Stolephorus purpureus* Fowler) in Kaneohe Bay, Oahu. *Pacific Science*, 29 (2): 171-180.
- Lee, R. 1973. Live bait research: Skipjack tuna fishery project in Fiji. *South Pacific Island Newsletter*, 9: 26-30.
- Lee, Y.-J., N.-J. Su, H.-T. Lee, W. Hsu, and C.-H. Liao. 2021. Application of Métier-Based Approaches for Spatial Planning and Management: A Case Study on a Mixed Trawl Fishery in Taiwan. *Journal of Marine Science and Engineering*, 9(5): 480. [doi.org/10.3390/jmse9050480](https://doi.org/10.3390/jmse9050480)
- Lehodey, P., J.-M. Andre, M. Bertignac, J. Hampton, A. Stoens, C. Menkes, L. Memery, and N. Grima. 1998. Predicting skipjack tuna forage distributions in the equatorial Pacific using a coupled dynamical bio-geochemical model. *Fisheries Oceanography*, 7(3/4): 317-325.
- Lehodey, P., A. Bertrand, A.J. Hobday, H. Kiyofuji, S. McClatchie, C.E. Menkès, G. Pilling, J. Polovina, and D. Tommasi. 2020. ENSO Impact on Marine Fisheries and Ecosystems, p. 429-251. In: J. McPhaden, A. Santoso, and W. Cai (eds). *El Niño Southern Oscillation in a Changing Climate*. Geophysical Monograph Series 253. American Geophysical Union, Hoboken, NJ.
- Lehodey, P., I. Senina, and R. Murtugudde. 2010. A spatial ecosystem and populations dynamics model (SEAPODYM) – modeling of tuna and tuna-like populations. *Progress in Oceanography*, 78: 304-318.
- Leong, R.J.H. and C.P. O'Connell. 1969. Laboratory Study of Particulate and Filter Feeding of The Northern Anchovy (*Engraulis mordax*). *Journal of The Fisheries Research Board of Canada*, 26(3): 557-582.
- Lewis, A.D. 1990. Tropical South Pacific Tuna Baitfisheries, p. 10-21. In: S.J.M. Blaber and J.W. Copland (eds). *Tuna Baitfish in the Indo-Pacific Region: proceedings of a workshop, Honiara, Solomon Islands, 11-13 December 1989*. ACIAR Proceedings No. 30. Australian Centre for International Research, Australia.
- Lewis, A.D. 2019. *A review of NFD operations*. Independent Report to the Government of the Solomon Islands' National Fisheries Development, Honiara, Solomon Islands.
- Lewis, A.D. and V. Allain. 2021. Tuna fisheries of the Bismarck Sea and adjacent waters, pag.var. In: FNHM (eds). *The Marine Fauna and Flora of the Bismarck Sea and Adjacent Waters*. French Natural History Museum, Paris, France.
- Lewis, A.D. and Heri. 2019. Panduan bergambar tentang ikan umpan pada perikanan di Indonesia Timur. AP2HI / IPNLF Handbook. 22 p.
- Lewis, A.D. and Heri 2020. Improving utilization of live baitfish resources by Indonesian vessels. Final Report to Walton Family Foundation, June 2020. 27 p.
- Lewis, A.D., B.R. Smith, and C.P. Ellway. 1983. A guide to the common tuna baitfishes of the South Pacific Commission area. Skipjack Survey and Assessment Program, Manual No. 23. South Pacific Commission, Noumea, New Caledonia. 82 p.
- Lewis, A.D., B.R. Smith, and R.E. Kearney. 1974. Studies on tuna and billfish in Papua New Guinea waters II. Res. Bull. 11. Department of Agriculture, Stocks and Fisheries, Port Moresby, Papua New Guinea. 122 p.
- Li, G.-L. 1978. *Anchoviella shantungensis* - a new anchovy from China. *Acta Zoologica Sinica*, 24(2): 193-195.
- Lopetcharat, K., Y.J. Choi, J.W. Park, and M.A. Daeschel. 2001. Fish sauce products and manufacturing: a review. *Food Reviews International*, 17 (1): 65-88.
- Lozan, J.L. 1985. *Wachstum, Rekrutierung, Netzselektion, Fortpflanzung und Fruchtbarkeit. Fischereibiologische Methoden*, Vol. III. Hamburg: Institut für Hydrobiologie und Fischerei.
- Low, M.E., and L.E. Neal. 2013. Dates of publication of the Zoology parts of the Report of the Scientific Results of the Voyage of H.M.S. Challenger During the Years 1873-76. *Zootaxa*, 3701(4): 401-420.
- Luther, G. 1990. Biology of whitebait anchovies of Indian Waters, p. 75-82. In: S.J.M. Blaber and J.W. Copland (eds). *Tuna Baitfish in the Indo-Pacific Region: proceedings of a workshop, Honiara, Solomon Islands, 11-13 December 1989*. ACIAR Proceedings No. 30. Australian Centre for International Research, Australia.
- Luther, G., K.V. Narayana Rao, G. Gopalakumar, C. Munthia, N.C. Gopalakrishna Pillai, P. Rohit, K. Knarayana Kurup, S. Reuben, P. Devadoss, G. Syda Rao, P. Sam Bennet, and N.S. Radhakrishnan.

1992. Resource characteristics and stock assessment of whitebaits. *Indian Journal of Fisheries*, 39(3,4): 152-168.
- Maack, G. 1997. Aspects of the reproductive cycle of *Encrasicholina punctifer* Fowler, 1938, from West-Sumatra. *Biology and Behavior* CM 1997/CC:19. International Council for the Exploration of the Sea. 10p.
- Maack, G. and M.R. George. 1999. Contributions to the reproductive biology of *Encrasicholina punctifer* Fowler, 1938 (Engraulidae) from West Sumatra. *Indonesian Fisheries Research Journal*, 44(2): 113-120.
- Major, P. 1978. Predator-prey interactions in two schooling fishes, *Caranx ignobilis* and *Stolephorus purpureus*. *Animal Behaviour*, 26(3): 760-777.
- Mar, M.K. 2017. Fisheries Country Profile: Myanmar. The Southeast Asian Fisheries Development Center (SEAFDEC), Chatuchak, Bangkok, Thailand. Available at: [www.seafdec.org/fisheries-country-profile-myanmar/](http://www.seafdec.org/fisheries-country-profile-myanmar/) (Accessed on August 20, 2021)
- Marramà, G. and G. Carnevale. 2016. An Eocene anchovy from Monte Bolca, Italy: The earliest known record for the family Engraulidae. *Geological Magazine*, 153: 84-94.
- Mendo, J. and C. Wosnitza-Mendo. 2016. Peru, p. 336. In: D. Pauly and D. Zeller (eds). *Global Atlas of Marine Fisheries: A critical appraisal of catches and ecosystem impacts*. Island Press, Washington D.C.
- Milton, D.A., S.J.M. Blaber, and N.J.F. Rawlinson. 1995. Fecundity and egg production of four species of short-lived clupeoid from Solomon Islands, tropical South Pacific. *ICES Journal of Marine Science*. Science, 52: 111-125.
- Milton, D.A., S. Blaber, N. Rawlinson, and A. Hafiz. 1990a. Reproductive Biology of *Spratelloides delicatulus*, *S. gracilis* and *Stolephorus heterolobus* from Solomon Islands and Maldives, p. 89-98. In: S.J.M. Blaber and J.W. Copland (eds). *Tuna Baitfish in the Indo-Pacific Region: proceedings of a workshop, Honiara. Solomon Islands, 11-13 December 1989*. ACIAR Proceedings No. 30. Australian Centre for International Research, Australia.
- Milton, D.A., S.J.M. Blaber, N.J.F. Rawlinson, A. Hafiz, and G. Tiroba. 1990b. Age and Growth of Major Baitfish Species in Solomon Islands and Maldives, p. 135-141. In: S.J.M. Blaber and J.W. Copland (eds). *Tuna Baitfish in the Indo-Pacific Region: proceedings of a workshop, Honiara. Solomon Islands, 11-13 December 1989*. ACIAR Proceedings No. 30. Australian Centre for International Research, Australia.
- Milton, D.A., N. Rawlinson, and S. Blaber. 1996. Recruitment patterns and factors affecting recruitment of five species of short-lived clupeoids in the tropical South Pacific. *Fisheries Research*, 26(3-4): 239-255.
- Mittelbach, G.G., D.W. Schemske, H.V. Cornell, A.P. Allen, J.M. Brown, M.B. Bush, S.P. Harrison, A.H. Hurlbert, N. Knowlton, H.A. Lessios, and C.M. McCain. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology letters*, 10: 315-331. [doi.org/10.1111/j.1461-0248.2007.01020.x](https://doi.org/10.1111/j.1461-0248.2007.01020.x)
- Mohanty P., S. Khora, U. Panda, G. Mohapatra, and P. Mishra. 2005. An overview of sardines and anchovies fishery along the Indian coasts. Department of Marine Sciences, Berhampur University, Berhampur, Odisha, India. 12 p.
- Mohsin, A.K.M., and A.A. Ambak. 1996. *Marine Fishes and Fisheries of Malaysia and Neighbouring Countries*. Universiti Pertanian Malaysia Press, Serdang, Malaysia. 744 p.
- Morales-Nin, B. 1992. Determination of growth in bony fishes from otolith microstructure. FAO Fisheries Technical Paper No. 322. Food and Agriculture Organization, Rome. 51 p.
- Morgan, G.R. and D.J. Staples. 2006. The history of industrial marine fisheries in Southeast Asia. Rap Publication 2006/12. Regional Office for Asia and The Pacific Bangkok, Food and Agriculture Organization, Thailand. 28 p.
- Muzaffar, S.B, R. Whelan, C. Clarke, R. Gubiani, and S. Benjamin. 2017. Breeding Population Biology in Socotra Cormorants (*Phalacrocorax nigrogularis*) in the United Arab Emirates. *Waterbirds*, 40 (1): 1-10.
- Muhling, B., M. Lindegren, L. Worsøe Clausen, A. Hobday, and P. Lehodey. 2017. Impacts of Climate Change on Pelagic Fish and Fisheries, p. 771-814. In: B.F. Phillips and M. Pérez-Ramírez (eds). *Climate change impacts on fisheries and aquaculture: A global analysis, vol II*. John Wiley & Sons Ltd, United Kingdom.
- Muller, R. 1976. Population biology of *Stolephorus heterolobus* (Pisces: Engraulidae) in Palau, Western Caroline Islands. Ph.D. thesis. University of Hawai'i. Honolulu. 174 p.

- Mustafa, A. 1983. Fisheries of the Andaman and Nicobar Islands. *ICLARM Newsletter*, 6: 7-9.
- Nair, P.G., S. Josepha, V. Kripaa, and V. Pillai. 2021. Population growth and maturity characteristics of Commerson's anchovy (*Stolephorus commersonnii* Lacepede, 1803) along the southwest coast of India. *Indian Journal of Geo Marine Sciences*, 50(2): 141-147.
- Narzary, Y., S. Das, A.K. Goyal, L.S. Shiung, H. Sarma, and D. Sharma. 2021. Fermented fish products in South and Southeast Asian cuisine: indigenous technology processes, nutrient composition and cultural significance. *Journal of Ethnic Food*, 8: 33. [doi.org/10.1186/s42779-021-00109-0](https://doi.org/10.1186/s42779-021-00109-0)
- Navarathne, N. and T.D. Dissanayake. 2016. Combining insights into reproduction and gear selectivity to enhance management advice for *Engrasicholina heteroloba* (Engraulidae) in the west coast of Sri Lanka. *Sri Lanka Journal of Aquatic Science*, 24(2): 77-88.
- Nazir, K, Y. Mu, K. Hussain, M. Kalhor, S. Kartika, and M.A. Mohsin. 2016. study on the assessment of fisheries resources in Pakistan and its potential to support marine ecology. *Indian Journal of Geo-Marine Sciences*, 45(9): 1181-1187.
- Nelson G.J. 1983. *Anchoa argentivittata*, with notes on other eastern Pacific anchovies and the Indo-Pacific genus *Engrasicholina*. *Copeia*, (1): 48-54.
- Nghia, N.V. 2017. Báo cáo tổng kết dự án I.9, “Đánh giá tổng thể hiện trạng và biến động nguồn lợi hải sản ở biển Việt Nam”. Project Review Report I.9. Overall Assessment of Status and Variables: seafood resources in the Sea of Vietnam. Seafood Research Institute-RIMF, Vietnam.
- Nguyen, T.B. 2015. Study on trawl fishery socio-economics and supply chains in Kien Giang, Viet Nam. Viet Nam Directorate of Fisheries, Ha Noi. 74 p.
- Nguyen, T.U. 2017. Fisheries Country Profile: Vietnam. The Southeast Asian Fisheries Development Center (SEAFDEC), Chatuchak, Bangkok, Thailand. Available at: [www.seafdec.org/fisheries-country-profile-viet-nam/](http://www.seafdec.org/fisheries-country-profile-viet-nam/) (Accessed on 22 August 2021)
- Nichols, P.V. and N.J.F. Rawlinson. 1990. Development of the fishery in Solomon Islands with reference to the baitfishery and its management, p. 30-45. In: S.J.M. Blaber and J.W. Copland (eds). *Tuna Baitfish in the Indo-Pacific Region: proceedings of a workshop, Honiara, Solomon Islands, 11-13 December 1989*. ACIAR Proceedings No. 30. Australian Centre for International Research, Australia.
- Ningrum, E.W. and M.P. Patrial. 2019. Ingestion of microplastics by anchovies from East Lombok Harbour, Lombok Island, Indonesia. *AIP Conference Proceedings*, 2120(1): 040002. [doi.org/10.1063/1.5115640](https://doi.org/10.1063/1.5115640)
- Ningrum, E.W., M.P. Patrial, and A. Sedayu. 2019. Ingestion of microplastics by anchovies from Talisayan Harbor, East Kalimantan, Indonesia. *Journal of Physics: Conference Series*, 1402: 033072. [doi.org/10.1088/1742-6596/1402/3/033072](https://doi.org/10.1088/1742-6596/1402/3/033072)
- Nur, M. 2021. Slavery of Indonesian Migrant Fishers: a review of regulation and its implementation. *Yustisia Jurnal Hukum*, 10(2): 145-162.
- O'Connor, S., R. Ono, and C. Clarkson. 2011. Pelagic Fishing at 42,000 Years Before the Present and the Maritime Skills of Modern Humans. *Science*, 334: 1117-1121.
- OECD. 2021. Fisheries and Aquaculture in Japan. Château de la Muette, Paris, France. Available at: [www.oecd.org/agriculture/topics/fisheries-and-aquaculture/documents/report\\_cn\\_fish\\_jpn.pdf](http://www.oecd.org/agriculture/topics/fisheries-and-aquaculture/documents/report_cn_fish_jpn.pdf)
- Oda, K., H. Hashimoto, Y. Masuda, Y., Imaizumi, H. Usuki, and K. Teruya. 2018. Resistance of Japanese anchovy, *Engraulis japonicus*, in captivity to high water temperature and hypoxia. *Journal of Fishery Technology*, 10: 1-7.
- Ogura, M., T. Tanabe, and M. Takahashi. 1999. Note on the distribution and size information of pelagic species, excluding skipjack and tunas, caught by the mid-water trawl net in the tropical waters of the Western Pacific. In: *12th Meeting of the Standing Committee on Tuna and Billfish*. Working Paper SKJ-3. National Research Institute of Far Seas Fisheries, Shimizu, Japan.
- Omar, A. 2017. Fisheries Country Profile: Malaysia. Fisheries Country Profile: Malaysia. The Southeast Asian Fisheries Development Center (SEAFDEC), Chatuchak, Bangkok, Thailand. Available at: [www.seafdec.org/fisheries-country-profile-malaysia/](http://www.seafdec.org/fisheries-country-profile-malaysia/) (Accessed on August 8 2021)
- Orlov, A.M. 1995. Aggregations of anchovy, *Engrasicholina punctifer* (Engraulidae), in the open Philippine Sea. *Journey of Ichthyology*, 35(3): 151-156.
- Otto, T. 1990. The sociology of baitfish royalties in Papua New Guinea, New Hanover and Tigak Islands (New Ireland), p. 1-18. In: T. Otto, J. Turner, and C. Filer (eds). *University of Papua New Guinea, Dept of Anthropology and Sociology Occasional Paper 6*. University of Papua New Guinea, Port Moresby.

- Ozawa, T. and H. Tsukahara. 1973. On the occurrence of the engraulid fish, *Stolephorus buccaneeri* Strasburg, in the oceanic region of the equatorial western Pacific. Life history and distribution. Kyushu University. *Journal of the Faculty of Agriculture*, 17: 151-171.
- Panha, T. 2019. Fisheries Country Profile: Cambodia. The Southeast Asian Fisheries Development Center (SEAFDEC), Chatuchak, Bangkok, Thailand. Available at: [www.seafdec.org/fisheries-country-profile-cambodia](http://www.seafdec.org/fisheries-country-profile-cambodia) (Accessed on August 28 2021)
- Pannella, G. 1971. Fish otoliths: Daily growth layers and periodical patterns. *Science*, 173: 1124-1127.
- Pannella, G. 1974. Otolith growth patterns: An aid in age determination in temperate and tropical fishes, p.28-39. In: T.B. Bagenal (ed). *The Ageing of Fish*. Unwin Brothers Ltd., Woking, England.
- Patadiya, D.S., P. Jawahar, N. Jayakumar, J.J. Pereira. 2018. Length: weight relationship and relative condition factor of Indian anchovy *Stolephorus indicus* (van Hasselt, 1823) from Thoothukudi coastal waters. *Journal of Entomology and Zoology Studies*, 6(2): 279-282.
- Patterson, K. 1992. Fisheries for small pelagic species: an empirical approach to management. *Reviews in Fish Biology and Fisheries*, 2: 321-338.
- Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *Journal du Conseil International pour l'Exploration de la Mer*, 39: 175-192.
- Pauly, D. 1982. Studying single-species dynamics in a tropical multispecies context, p. 33-70. In: D. Pauly and G.I. Murphy (eds). *Theory and management of tropical fisheries*. ICLARM Conference Proceedings 9. ICLARM, Manila, Philippines, and Division of Fisheries Research, Commonwealth Scientific and Industrial Research Organisation, Cronulla, Australia.
- Pauly, D. 1984. A mechanism for the juvenile-to-adult transition in fishes. *ICES Journal of Marine Science*, 41(3): 280-284. [doi.org/10.1093/icesjms/41.3.280](https://doi.org/10.1093/icesjms/41.3.280)
- Pauly, D. 1987. A review of the ELEFAN system for analysis of length-frequency data in fish and aquatic invertebrates, p. 7-34. In: D. Pauly and G.R. Morgan (eds). *Length-based methods in fisheries research*. ICLARM Conference Proceedings 13. ICLARM, Manila, Philippines, and Kuwait Institute for Scientific Research, Safat, Kuwait.
- Pauly, D. 1996. Fleet-operational, economic and cultural determinants of by-catch uses in Southeast Asia, p. 285-288. In: *Solving By-Catch: Considerations for Today and Tomorrow*. University of Alaska, Sea Grant College Program, Report No. 96-03, Fairbanks.
- Pauly, D. 2021. Why do fish reach first maturity when they do? *Journal of Fish Biology*. [doi.org/10.1111/jfb.14902](https://doi.org/10.1111/jfb.14902)
- Pauly, D., V. Christensen, and C.J. Walters. 2000. Ecopath, Ecosim and Ecospace as tools for evaluating ecosystem impact of fisheries. *ICES Journal of Marine Science*, 57: 697-706. [doi.org/10.1006/jmsc.2000.0726](https://doi.org/10.1006/jmsc.2000.0726)
- Pauly, D. and J.L. Munro. 1984. Once more on the comparison of growth in fish and invertebrates. *Fishbyte*, 2(1): 1-21.
- Pavlov D.S. and A.O. Kasumyan. 2000. Patterns and mechanisms of schooling behavior in fish: A Review. *Journal of Ichthyology*, 40: S163-S231.
- Pham, V.A., A. Folkvord, A. Johannessen, and V.-T. Dang. 2022. Growth patterns and reproductive biology of anchovy (*Engrasicholina heteroloba*) in southwestern sea of Vietnam. Unpublished paper. Department of Capture Fisheries and Resources Protection, Ha Noi city, Vietnam.
- Phan, L.T. and N.V. Luc. 1991. Biological characteristic of anchovy (*Stolephorus*) genus in the coastal Vietnam. *Proceedings of Marine Fisheries Research*, 3: 51-58.
- Pikitch, E., P.D. Boersma, I.L. Boyd, D.O. Conover, P. Cury, T. Essington, S.S. Heppell, E.D. Houde, M. Mangel, D. Pauly, É. Plagányi, K. Sainsbury, and K. Steneck. 2012. Little Fish, Big Impact: Managing a Crucial Link in Ocean Food Webs. Lenfest Ocean Program, Washington, DC. 108 p.
- Pinault, M. and J. Wickel. 2014. What appears to be a defensive behavior in the anchovy could also be a double-edged sword. *Coral Reefs*, 33: 343.
- Pingali, P. 2006. Westernization of Asian diets and the transformation of food systems: Implications for research and policy. *Food Policy*, 32: 281-298.
- Por, F.D. 1978. *Lessepsian Migration: The Influx of Red Sea Biota into the Mediterranean by Way of the Suez Canal*. Springer-Verlag Ecological Studies 23(1). Springer Book, Berlin. 228 p.
- Pravin, P. and B. Meenakumari. 2016. Purse seining in India - a review. *Indian Journal of Fisheries*, 63(3): 162-174.
- Price, J.F., A. Robert, R.A. Weller, and R.R. Schudlich. 1987. Wind-driven ocean currents and Ekman Transport. *Science*, 238(4833): 1534-1538.

- Pritchard, M., A. Gordon, G. Patterson, and A. Gray. 1996. Utilization of Small Pelagic Fish Species in Asia. Natural Resources Institute, Chatham, UK. 24 p.
- Premkit, W. 1999. Abundance of parasites of anchovies (*Stolephorus* spp.) from the inner and western coast of the gulf of Thailand. Marine fishery technical reports 1990-1998 part 2: Pelagic fishes. Department of Fisheries, Bangkok Marine Fisheries Development Center, Bangkok, Thailand. 41 p.
- Rajkumar, P., P. Perumal, and J.P. Trilles. 2006. On the occurrence of a double parasitism (copepod and isopod) on the anchovy fish in India. *Journal of Environmental Biology*, 27(3): 613-614.
- Rakotondrainibe, J.H. 2006. *Synthese de la geologie et de l'hydrogeologie de Madagascar*. Africa Groundwater Litterature Archive.
- Randall, J.E. 1998. Zoogeography of Shore Fishes of the Indo-Pacific Region. *Zoological Studies*, 37(4): 227-268.
- Rao, G.S. 1988a. Some aspects of biology of *Stolephorus bataviensis* Hardenberg, from Mangalore area, Dakshina Kannada. *Journal of the Marine Biology Association of India*, 30(1 and 2): 107-113.
- Rao, G.S. 1988b. Biology of *Stolephorus devisi* (Whitley) from Mangalore area, Dakshina Kannada, *Indian Journal of Fisheries*, 30: 28-36.
- Rawlinson, N.J.F. and P.V. Nichols. 1990. Analysis of catch and effort data for the Solomon Islands baitfishery. In: S.J.M. Blaber and J.W. Copland (eds). *Tuna Baitfish in the Indo-Pacific Region: proceedings of a workshop, Honiara, Solomon Islands, 11-13 December 1989*. ACIAR Proceedings No. 30. Australian Centre for International Research, Australia.
- Raybaud, V., M. Bacha, A. Rachid, and G. Beaugrand. 2017. Forecasting climate-driven changes in the geographical range of the European anchovy (*Engraulis encrasicolus*). *ICES Journal of Marine Science*, 74(5): 1288–1299.
- Retnowati, S. and F. Satria. 2013. Fishery Statistic Data Collection System in Indonesia. Indian Ocean, Tuna Commission, IOTC-2013-WPDCS09-17. Victoria, Seychelles. 5 p.
- Rice, J. 1995. Food web theory, marine food webs, and what climate change may do to northern marine fish populations, p. 561-568. In: R.J. Beamish (ed). *Climate change and northern fish populations*. Canadian Special Publication of Fisheries and Aquatic Sciences 121. National Research Council of Canada, Ottawa, Canada.
- Ricker, W.E. 1954. Stock and recruitment. *Journal of the Fisheries Research Board of Canada*, 11: 559-623.
- Ricker, W.E. 1975. *Computation and interpretation of biological statistics of fish populations*. Bulletin of the Fisheries Research Board of Canada, Bulletin 191. Ottawa, Canada.
- Rocliffe, S. 2012. Ensuring Sustainability of Livebait Fish. International Pole-and-line Foundation, London. 57 p.
- Rohit, P. and A.C. Gupta. 2008. Whitebait fishery of Mangalore - Malpe, Karnataka during 1997-2002. *Indian Journal of Fisheries*, 55 (3): 211-214.
- Ronquillo, I.A. and P. Dalzell. 1989. A review of Southeast Asian stolephorid anchovies with a key to species. *Fisheries Research Journal of the Philippines*, 14(1-2): 1-22.
- Ruddle, K. and N. Ishige. 2010. On the Origins, Diffusion and Cultural Context of Fermented Fish Products in Southeast Asia, p. 29-45. In: J. Farrer, R. Ceccarini, P. Yarrow, M. Neves, and K. Ray (eds). *Globalization, Food and Social Identities in the Asia Pacific Region*. Sophia University Institute of Comparative Culture, Tokyo, Japan.
- Rüppell, W. 1837. *Neue wirbelthiere zu der fauna von Abyssinien gehörig*. Siegmund Schmerber, Frankfurt am Main, Germany.
- Sætersdal, G., G. Bianchi, T. Strømme, and S.C. Venema. 1999. The Dr. Fridtjof Nansen Programme 1975–1993. Investigations of Fishery Resources in Developing Countries. History of the programme and review of results. FAO Fisheries Technical Paper No. 391. Rome, Fisheries and Agriculture Organization FAO. 434 p.
- Saffrudin, H.R. and M. Zainuddin. 2018. Effects of environmental factors on anchovies *Stolephorus* spp. distribution in Bone Gulf, Indonesia. *Aquaculture, Aquarium, Conservation and Legislation - International Journal of the Bioflux Society*, 11(2): 387-393.
- Saikliang, P. and V. Boonragsa. 1997. Pelagic fisheries and resources in Thai Waters. The Third Regional Workshop on Shared Stocks in The South China Sea Area, Kuala Terengganu, Malaysia 6 - 8 October. Country Status Report. Marine Fishery Resources Development and Management Department WS/97/CR.7. Southeast Asian Fisheries Development Center, Bangkok Thailand. 28 p.

- Salarpouri, A., M. Darvishi, S. Behzadi, and F. Seraji. 2007. Reproduction and feeding of buccaneer anchovy (*Encrasicholina punctifer*) from coastal waters of Qeshm Island, the Persian Gulf. *Iranian Journal of Scientific Fisheries*, 17(1): 1-10.
- Salarpouri, A., E. Kamrani, F. Kaymaram, and R. Mahdavi Najafabadi. 2018. Growth, mortality and exploitation of buccaneer anchovy (*Encrasicholina punctifer* Fowler, 1938) from the north Persian Gulf and Oman Sea. *Iranian Journal of Fisheries Sciences*, 17(2): 313-326.
- Samoilys, M.A., G. Maina, and K. Osuka. 2011. Artisanal fishing gears of the Kenyan coast. Mombasa. Coastal Ocean Research and Development–Indian Ocean, CORDIO East Africa, Mombasa, Kenya. 36 p.
- Santoso, A., M.J. Mcphaden, and W. Cai. 2017. The defining characteristics of ENSO extremes and the strong 2015/2016 El Niño. *Reviews of Geophysics*, 55: 1079–1129.
- Sapari, A. 2019. Country Fisheries Trade: Indonesia. The Southeast Asian Fisheries Development Center (SEAFDEC), Chatuchak, Bangkok, Thailand. Available at: [www.seafdec.org/fisheries-country-profile-indonesia/](http://www.seafdec.org/fisheries-country-profile-indonesia/) (Accessed on August 20, 2021).
- Schaperclaus, W. 1986. Fish Diseases. Oxonian Press Pvt Ltd, New Delhi.
- Schmidt, C., T. Orcid, and S. Wagners. 2017. Export of Plastic Debris by Rivers into the Sea. *Environmental Science Technology*, 51: 12246–12253.
- Schug, D.M. 2001. Hawai'i's Commercial Fishing Industry: 1820-1945. *The Hawaiian Journal of History*, 35: 15-34.
- Scott, J.M. 1969. Tuna schooling terminology. *California Fish and Game*, 55: 136-140.
- SEAFDEC. 2017a. Report of the Experts Group Meeting on Stock Status and Geographical Distribution of Anchovy, Indo-Pacific Mackerel and Blue Swimming Crab (AIB) Species in the Gulf of Thailand, Bangkok, Thailand, 22-23 September 2016. The Southeast Asian Fisheries Development Center, Bangkok, Thailand. 69 p.
- SEAFDEC. 2017b. Southeast Asian State of Fisheries and Aquaculture 2017. The Southeast Asian Fisheries Development Center, Bangkok, Thailand. 167 p.
- Sekadende, B., L. Scott, J. Anderson, S. Aswani, J. Francis, Z. Jacobs, F. Jebri, N. Jiddaw, A. Kamukuru, S. Kelly, H. Kizenga, B. Kugura, M. Kyewalyanga, M. Noyon, N. Nyandwi, S.C. Painter, M. Palmer, D.E. Raitsos, and E. Popova, E. 2020. The small pelagic fishery of the Pemba Channel, Tanzania: What we know and what we need to know for management under climate change. *Ocean and Coastal Management*, 197: 1-18.
- Siegfried, K.I. and B. Sansó. 2012. Estimating natural mortality in fish populations. NOAA Internal Report. 31p.
- Shannon, L., M. Coll, N. Sergio, P. Cury, and J.-P. Roux. 2009. The role of small pelagic fish in the ecosystem, p. 158-190. In: D. Checkley, C. Roy, J. Alheit, and Y. Oozeki (eds). *Climate Change and Small Pelagic Fish*, Cambridge University Press, United Kingdom.
- Sharma, S. 1988. *The Fijian Baitfishery*. SPC/Inshore Fish. Res./BP 14. South Pacific Commission Workshop on Inshore Fishery Resources. Noumea, New Caledonia. 18 p.
- El Sheikha, A.F., R. Ray, D. Montet, S. Panda, and W. Worawattanamateekul. 2014. African fermented fish products in scope of risks. *International Food Research Journal*, 21(2): 425-432.
- Shiriskar, A., G.D. Khedkar, and A. Dipty. 2010. Preparation of boiled and dried products from anchovies (*Stolephorus* sp.) and studies on quality changes during storage. *Journal of Food Processing and Preservation*, 34: 73–86.
- Smith, L. 1993. Trying to explain scale loss mortality: A continuing puzzle. *Reviews in Fisheries Science*, 1(4): 337-355. [doi.org/10.1080/10641269309388549](https://doi.org/10.1080/10641269309388549)
- Smith, B.R. 1977. Appraisal of the live-bait potential and handling characteristics of the common tuna bait species in Papua New Guinea, p. 95-103. In: R.S. Shomura (ed). *Collection of Tuna and Baitfish Papers*. NOAA Technical Report NMFS Circular 408. National Marine Fisheries Service, USA.
- Somerton, D. 1990. Baitfish Stock Assessment Using the Egg Production Method: an application on the Hawaiian anchovy or nehu (*Encrasicholina purpurea*), p. 152-158. In: S.J.M. Blaber and J.W. Copland (eds). *Tuna Baitfish in the Indo-Pacific Region: proceedings of a workshop, Honiara. Solomon Islands, 11-13 December 1989*. ACIAR Proceedings No. 30. Australian Centre for International Research, Australia.
- Sousa, R.G.C., J.A. Alves, R.V. Alves., and S.A. Lima. 2022. Seasonality of the feeding behavior and condition factor of *Anchovia surinamensis* in the floodplains of the Madeira River (Rondônia, Brazil). *Bulletin of the Institute of Fish*, 48: e682. [doi.org/10.20950/1678-2305/bip.2022.48.e682](https://doi.org/10.20950/1678-2305/bip.2022.48.e682)

- Spoehr, A. 1984. Change in Philippine capture fisheries: an historical overview. *Philippine Quarterly of Culture and Society*, 12 (1): 25-56.
- Springer, V.G. 1982. Pacific plate biogeography, with special reference to shorefishes. Smithsonian Institution Press, Washington DC. 182 p.
- SSAP. 1984a. *An assessment of the skipjack and baitfish resources of Papua New Guinea*. Skipjack Survey and Assessment Programme Final Country Report No. 12. South Pacific Commission, Noumea, New Caledonia. 91 p.
- SSAP. 1984b. *An Assessment of the Skipjack and Baitfish Resources of Northern Mariana Islands, Guam, Palau, Federated States of Micronesia, and the Marshall Islands*. Skipjack Survey and Assessment Programme Final Country Report No. 18. South Pacific Commission, Noumea, New Caledonia. 109 p.
- SSAP. 1985. *An assessment of the skipjack and baitfish resources of New Caledonia*. South Pacific Commission, Noumea, New Caledonia. 43 p.
- Steuert, B. and F. Marsac. 1989. Tropical tuna: surface fisheries in the Indian Ocean. FAO Fisheries Technical Paper 282. Food and Agriculture Organization, Rome. 238 p.
- Struhsaker, P. and J. Uchiyama. 1976. Age and growth of the nehu, *Stolephorus purpureus* (Pisces: Engraulidae) from the Hawaiian Islands as indicated by daily growth increments of sagittae. *Fishery Bulletin*, 74: 9-17.
- Sululu, J.S., A.T. Kamukuru, C. Sekadende, S.B. Mahongo, and M. Igulu. 2020. Reproductive biology of the anchovy (*Stolephorus commersonnii*, Lacepède, 1803) and spotted sardine (*Amblygaster sirm*, Walbaum, 1792) from Tanga Region, Tanzania. *Western Indian Ocean Journal of Marine Science*, Special Issue 1: 81-94.
- Supeni, E.A. and J. Dobo. 2017. Exploitation status of Devis' Anchovy in Kei Island Waters: based on total length data. *Institute of Physics Conference Series, Earth and Environmental Science*, 89: 012004. [doi.org/10.1088/1755-1315/89/1/012004](https://doi.org/10.1088/1755-1315/89/1/012004)
- Supongpan, M., C. Chamchang, S. Boongerd, and A. Laowapong. 2000. Technical report on the anchovy fisheries in the Gulf of Thailand. FAO/FISHCODE Project GCP/INT/648/NOR: Field report F-6 Suppl. Food and Agriculture Organization, Rome. 105 p.
- Suwannapoom, S. 2019. County Fisheries Trade: Thailand. The Southeast Asian Fisheries Development Center (SEAFDEC), Chatuchak, Bangkok, Thailand. Available at: [www.seafdec.org/country-fisheries-trade-thailand/](http://www.seafdec.org/country-fisheries-trade-thailand/) (Accessed on June 26, 2022)
- Suzuki, A. and H. Kawahata. 2003. Carbon budget of coral reefsystems: an overview of observations in fringing reefs, barrier reefs and atolls in the Indo-Pacific regions. *Tellus B: Chemical and Physical Meteorology*, 55(2): 428-444.
- Tahir, A. and C.M. Rochman. 2015. Plastic Particles in Silverside (*Stolephorus heterolobus*) Collected at Paotere Fish Market, Makassar. *International Journal of Agriculture System*, 2: 163-168.
- Teh, L., D. Shon, K. Zylich, and D. Zeller. 2014a. *Reconstructing Cambodia's Marine Fisheries Catch, 1950-2010*. Working Paper Series Number 2014-18, Fisheries Centre, University of British Columbia, Vancouver, Canada. 12 p.
- Teh, L., D. Zeller, K. Zylich, G. Nguyen, and S. Harper. 2014b. *Reconstructing Vietnam's Marine Fisheries Catch, 1950-2010*. Working Paper Series Number 2014-17, Fisheries Centre, University of British Columbia, Vancouver, Canada. 10 p.
- Tham, A.K. 1950. The food and feeding relationships of the fishes of Singapore Straits. Fisheries Publication Colonial Office 1(1). U.K. 35 p.
- Tham, A.K. 1953. A preliminary study of the physical and biological characteristics of Singapore Straits. Fisheries Publication Colonial Office 1(4). U.K. 65 p.
- Tham, A.K. 1966. Synopsis of biological data on the Malayan anchovy, *Stolephorus pseudoheterolobus*. *The Malaysian Agricultural Journal*, 45(31): 258-267.
- Tham, A.K. 1967. A contribution to the study of the growth of members of the genus *Stolephorus* Lacépède in Singapore Straits. *Proceedings of the Indo-Pacific Fisheries Council*, 12(2): 1-25.
- Tham, A.K. 1968. Synopsis of biological data on the Malay anchovy, *Stolephorus pseudoheterolobus* Hardenberg 1933. Fisheries Synopsis 37. Food and Agricultural Organization, Rome. 18 p.
- Thanh, V. 2019. County Fisheries Trade: Viet Nam. The Southeast Asian Fisheries Development Center (SEAFDEC), Chatuchak, Bangkok, Thailand. Available at: [www.seafdec.org/country-fisheries-trade-viet-nam/](http://www.seafdec.org/country-fisheries-trade-viet-nam/) (Accessed on July 7, 2022)



- Then, A., J. Hoenig, N. Hall, and D. Hewitt. 2015. Evaluating the predictive performance of empirical estimators of natural mortality rate using information on over 200 fish species. *ICES Journal of Marine Science*, 72(1): 82–92.
- Thuy, P.T.T. and O. Flaaten. 2013. The backward-bending supply curve in fisheries – revisited. *Journal of Sustainable Development*, 6(6): 15-29.
- Tiews, K., I.A. Ronquillo, and L.M. Santos. 1971. On the biology of the anchovies (*Stolephorus* Lacepede) in Philippine waters. *The Philippine Journal of Fisheries*, 9: 92-123.
- Tint, M.K. 2019. Country Fisheries Trade: Myanmar. The Southeast Asian Fisheries Development Center (SEAFDEC), Chatuchak, Bangkok, Thailand. Available at: [www.seafdec.org/country-fisheries-trade-philippines/](http://www.seafdec.org/country-fisheries-trade-philippines/) (Accessed on June 26, 2022)
- Tiroba, G., N.J.F. Rawlinson, P.V. Nichols, and J.L. Leqata. 1990. Length-frequency analysis of the major baitfish species in Solomon Islands, p. 113-143. In: S.J.M. Blaber and J.W. Copland (eds). *Tuna Baitfish in the Indo-Pacific Region: proceedings of a workshop, Honiara, Solomon Islands, 11-13 December 1989*. ACIAR Proceedings No. 30. Australian Centre for International Research, Australia.
- Oscar Trujillo-Millán, O. De la Cruz-Agüero, J. Elorduy-Garay J.F. 2006. First reported records of *Prionurus laticlavus* (Perciformes: Acanthuridae) from the Gulf of California. *Bulletin of Marine Science*, 78(2): 393–395.
- Turner, J. 1990. Report on social organization and resource ownership in the baitfishing areas of East and West New Britain. Department of Anthropology and Sociology, University of Papua New Guinea, Port Moresby.
- Tzeng, W.-N. and Y.-T. Wang. 1992. Structure, composition and seasonal dynamics of the larval and juvenile fish community in the mangrove estuary of Tanshui River, Taiwan. *Marine Biology*, 113: 481-490.
- Uchida, R.N. 1977. The Fishery for Nehu, *Stolephorus purpureus*, a Live Bait Used for Skipjack Tuna, *Katsuwonus pelamis*, Fishing in Hawai'i, p. 57-62. In: R.S. Shomura (ed). *Collection of Tuna and Baitfish Papers*. NOAA Technical Report NMFS Circular 408. National Marine Fisheries Service, USA.
- van Hasselt, J.C. 1823. Uittreksel uit een' brief van Dr. J. C. van Hasselt, aan den Heer C. J. Temminck. *Algemein Konst- en Letter-Bode*, 1(21): 329–331.
- van Nguyen, Q. 2019. Impact of Fisheries Management Objective on Technical Efficiency: Case Studies in Fisheries. PhD thesis, Queensland University of Technology, Brisbane, Australia. 236 p.
- van Zailinge, N.P., F. Owfi, S. Ghasemi, K. Khorshidian, and N. Niamaimandi. 1993. Resources of small pelagics in Iranian waters, a review. FAO/UNDP Fisheries Development Project Ira/83/013. Food and Agricultural Organization, Rome. 370 p.
- Varkey, M.J., V.S.N. Murty, and A. Suryanarayana. 1996. Physical Oceanography of the Bay of Bengal. *Oceanography and Marine Biology, an Annual Review*, 34: 1-70.
- Verité. 2016. Research on Indicators of Forced Labor in the Supply Chain of Fish in Indonesia: Platform (Jermal) Fishing, Small-Boat Anchovy Fishing, and Blast Fishing. Verité, Amherst, USA. 136 p.
- Vetter, E. F. 1988. Estimation of natural mortality in fish stocks: a review. *Fishery Bulletin*, 86: 25-43.
- Vijayan, C., V. Ajaykumar, A. Bhattacharya, and S. Rabins. 2017. Detection of biofilm producing *Vibrio parahaemolyticus* from anchovy fish (*Stolephorus indicus*) sold in Puducherry. *Journal of Meat Science*, 12(1): 44-47.
- Villard, P., V. Bretagnolle, and P. Borsa 2015. Segregation in Diet between Black Noddy (*Anous minutus*) and Brown Noddy (*A. stolidus*) from the Southern Lagoon of New Caledonia, *Pacific Science*, 69(2): 197-204.
- Viron, J. 2019. Country Fisheries Trade: Philippines. The Southeast Asian Fisheries Development Center (SEAFDEC), Chatuchak, Bangkok, Thailand. Available at: [www.seafdec.org/country-fisheries-trade-philippines/](http://www.seafdec.org/country-fisheries-trade-philippines/) (Accessed on Jun 26, 2022)
- Wang, Y.-T. and W.-N. Tzeng. 1997. Temporal succession and spatial segregation of clupeoid larvae in the coastal waters of the Tanshui River Estuary, northern Taiwan. *Marine Biology*, 129: 23-32.
- Werry, J.M., S.Y. Lee, C.J. Lemckert, and N.M. Otway. 2012. Natural or artificial? Habitat-use by the Bull Shark, *Carcharhinus leucas*. *PLoS One*, 7: e49796.
- Wetherall, J.A. 1977. Catch statistics and abundance of the nehu, *Stolephorus purpureus* in Kaneohe Bay, p. 69-74. In: R.S. Shomura (ed). *Collection of Tuna and Baitfish Papers*. NOAA Technical Report NMFS Circular 408. National Marine Fisheries Service, USA.

- Whitehead, P., G. Nelson, and T. Wongratana (eds). 1988. An annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, anchovies and wolf herrings. *FAO Fisheries Synopsis*, 7(2 Engraulidae): 305-579.
- Whitley, G.P. 1940. Illustrations of some Australian fishes. *Australian Zoologist*, 9(4): 397-428.
- Widodo, A., W. Wudianto and F. Satria. 2016. Current status of the fishery in the eastern part of Indonesia. *Indonesian Fisheries Research Journal*, 22(1): 43-52.
- Wikipedia. 2022. Fishing industry in China. Available at: [en.wikipedia.org/wiki/Fishing\\_industry\\_in\\_China](https://en.wikipedia.org/wiki/Fishing_industry_in_China) (Accessed on June 28, 2022)
- Wilson, P.T. 1971. Truk live-bait survey. National Marine Fisheries Service Circular 353, United States Department of Commerce, Washington D.C. 10 p.
- Wongratana, T. 1980. Systematics of clupeoid fishes of the Indo-Pacific region. PhD thesis, University of London, England. 923 p.
- Wongratana, T. 1983. Diagnoses of 24 new species and proposal of a new name for a species of Indo-Pacific clupeoid fishes. *Japanese Journal of Ichthyology*, 29(4): 385-407.
- Wongratana, T. 1985. An artificial key for the identification of the Indo-Pacific anchovies of the genus *Stolephorus* (Pisces: Engraulidae). *Chulalongkorn University Journal of Scientific Research*, 10(1): 25-45.
- Wongratana, T. 1987. Four new species of clupeoid fishes (Clupeidae and Engraulidae) from Australian waters. *Proceedings of the Biological Society of Washington*, 100(1): 104-111.
- Woo, K.H. 1967. A Preliminary Study of the Physical, Chemical and Biological Characteristics of Johore Straits. PhD thesis, University of Singapore.
- World Bank/FAO/WorldFish. 2012. Hidden harvest: The global contribution of capture fisheries. World Bank Report, No. 66469-GLB. World Bank, Washington. 69 p.
- Wright, A., M.R. Chapau, P. Dalzell, and A.H. Richards. 1983. The marine resources of the New Ireland Province. A report on the present utilisation and potential for development. Research. Report. 83-13, Fisheries Research and Surveys Branch, DPI, Port Moresby. 52 p.
- Wright, P.J. 1989. The growth and reproductive biology of *Stolephorus heterolobus* (Engraulidae). Master's Thesis. University of Newcastle upon Tyne, England.
- Wright, P.J. 1990. The reproductive strategy of *Stolephorus heterolobus* in the South Java Sea. In: S.J.M. Blaber and J.W. Copland (eds). *Tuna Baitfish in the Indo-Pacific Region: proceedings of a workshop, Honiara, Solomon Islands, 11-13 December 1989*. ACIAR Proceedings No. 30. Australian Centre for International Research, Australia.
- Wyrski, K. 1981. An estimate of equatorial upwelling in the Pacific. *Journal of Physical Oceanography*, 11: 1205-1214.
- Wyrski, K., E.B. Bennett, and D.S. Rochford. 1971. Oceanographic Atlas of the International Indian Ocean Expedition. US Government Print Office, Washington, D.C.
- Yea, S. 2014. The Exploitation of Migrant Fishermen in southeast Asia's Long Haul Fishing industry, p. 85-96. In: W. Hofmeister and P. Rueppel (eds). *Trafficking in Human Beings learning from Asian and European Experiences*. East Asian Institute, Singapore.
- Yenpoeng, T. 2017. Fisheries Country Profile: Thailand. The Southeast Asian Fisheries Development Center (SEAFDEC), Chatuchak, Bangkok, Thailand. Available at: [www.seafdec.org/fisheries-country-profile-thailand/](http://www.seafdec.org/fisheries-country-profile-thailand/) (Accessed on August 20, 2021)
- Yoosooksawat, S. 1990. Anchovy fishery status in the eastern coast of the Gulf of Thailand. Technical Paper. Eastern Marine Fisheries Development Center, Rayong, Thailand.
- Young, S.-S., T.-S. Chiu and S.-C. Shen. 1994. A Revision of the Family Engraulidae (Pisces) from Taiwan. *Zoological Studies*, 33(3): 217-227.
- Yuliantiningsih, A. and J. Barkhuizen. 2021. Modern Slavery in Fishing Industry: the Need to Strengthen Law Enforcement and International Cooperation. *Yustisia*, 10(1): 1-15.
- Zhang, H. 2015. China's Fishing Industry: Current Status, Government Policies, and Future Prospects. Maritime Power Conference, July 28-29, 2015. Center for Naval Analysis, Conference Facility, Arlington, Virginia. 34 p.

## APPENDIX 1:

Scientists at the NOAA Pacific Islands Fisheries Science Center based in Hawai‘i have completed an opportunistic ichthyoplankton survey in 2023 spanning the EEZ of the Hawaiian Archipelago from Hōlanikū (Kure Atoll) through Hawai‘i Island. At the time of writing subsamples from this effort have been examined, with preliminary findings of relevance to this chapter in that large numbers of larval pelagic anchovy (*Encrasicholina punctifer*) were observed at survey stations spanning the western main Hawaiian Islands (O‘ahu and Kaua‘i) through much of the Papahānaumokuākea Marine National Monument. Schools of baitfish were observed from the ship but could not be sampled to verify species identification.

Further sample processing and results from eDNA samples should prove enlightening in identifying relative larval densities of *E. punctifer* and their environmental associations throughout this survey. In similar context, anecdotal observations from pelagic fishers in the main Hawaiian Islands in 2023 have also included mention of large schools of baitfish, presumably *E. punctifer* in nearshore pelagic areas. *Encrasicholina punctifer* does not regularly occur in Hawaii's waters, but schools are not rare in some years (Strasburg 1960). Larval *E. punctifer* have been relatively uncommon or absent in previous ichthyoplankton surveys around Hawai‘i (e.g., Miller *et al.* 1979; Leis 1978; Clarke 1991; Boehlert and Mundy 1996; Whitney *et al.* 2021) suggesting that the 2023 observations indicate a bloom of anchovy abundance in that year.

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## References:

- Boehlert, G.W. and B. C. Mundy. 1994. Ichthyoplankton vertical distributions near Oahu, Hawai‘i, 1985-1986: data report. NOAA Technical Memorandum NMFS. NOAA-TM-NMFS-SWFSC-235. National Marine Fisheries Service, USA. 148 p.
- Clarke, T.A. 1991. Larvae of nearshore fishes in oceanic waters near Oahu, Hawaii. NOAA Technical Report NMFS 101. National Marine Fisheries Service, USA. 19 p.
- Leis, J.M. 1978. Distributional ecology of ichthyoplankton and invertebrate macrozooplankton in the vicinity of a Hawaiian coastal power plant. PhD dissertation, University of Hawai‘i. Hawai‘i, USA. 317 p.
- Strasburg, D.W. 1960. A new Hawaiian engraulid fish. *Pacific Science*, 13: 395-399.
- Miller, J.M., J.M. Leis, and W. Watson. 1979. An Atlas of Common Nearshore Marine Fish Larvae of the Hawaiian Islands. Sea Grant Miscellaneous Report UNIHI-SEAGRANT-MR-80-02. University of Hawaii Sea Grant College Program, Honolulu. 179 p.
- Whitney, J.L., J.M. Gove, M.A. McManus, K.A. Smith, J. Lecky, P. Neubauer, J.E. Phipps, E.A. Contreras, D.R. Kobayashi, and G.P. Asner. 2021. Surface slicks are pelagic nurseries for diverse ocean fauna. *Scientific Reports*, 11: 3197. [doi.org/10.1038/s41598-021-81407-0](https://doi.org/10.1038/s41598-021-81407-0)